



General Palaeontology, Systematics and Evolution (Vertebrate Palaeontology)

Badenian and Sarmatian s.str. from the Carpathian area: Taxonomical notes concerning the Hungarian and Romanian small vertebrates and report on the ruminants from the Felsőtárkány Basin



Badénien et Sarmatien s.str. de la région des Carpates : notes taxonomiques concernant les petits vertébrés hongrois et roumains, ainsi qu'un rapport sur les ruminants du bassin de Felsőtárkány

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ABSTRACT

Over the last decade, important progress has been made in the study of the mammal successions from Hungary and Romania. A critical review of the taxonomy of the published small mammals is provided herein, as well as some new data and an overview of the accompanying vertebrate fauna (excluding fishes) in their stratigraphic context. In addition, the first data regarding the ruminants from Mátraszőlös and Felsőtárkány are presented. This contribution aims to characterize the middle to earliest late Miocene fossil record from these

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Vertebrates
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Amphibians

countries, and provide important data for the chrono(bio)stratigraphic and palaeoenvironmental studies at the European scale.

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R É S U M É

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D'importantes successions de faunes mammaliennes sont maintenant connues en Hongrie et en Roumanie. Une revue critique de la taxonomie des petits mammifères publiée jusqu'ici est présentée, ainsi que de nouvelles additions et une présentation des faunes de vertébrés associées (hormis les poissons) dans leur contexte stratigraphique. Enfin, les premières données concernant les ruminants de Mátraszőlös et Felsőtárkány sont présentées. Cette contribution a pour but de caractériser l'enregistrement fossile Miocène moyen/supérieur basal de ces pays, et de fournir des données importantes pour les études chrono(bio)stratigraphiques et environnementales à l'échelle européenne.

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1. Introduction

Over the last decades, intensive sampling campaigns have yielded an important mammal succession from Hungary and Romania. Based on this fossil material, Hír et al. (2016) provide an overview of the vertebrate assemblages from the latest early–earliest late Miocene in Hungary and Romania and demonstrated the importance of the area for understanding faunal evolution on the European continent.

Compared to other European basins (e.g., Casanovas-Vilar et al., 2016; García-Paredes et al., 2016; Prieto and Rummel, 2016), the study of the Hungarian and Romanian Miocene successions is relatively young, and the taxonomy of the small mammals less settled. We provide herein the basal data to the overview by Hír et al. (2016), consisting of a taxonomical review of the published small mammals, as well as new data regarding their stratigraphic context. Our current knowledge on the accompanying tetrapod fauna is also presented. The first data regarding the ruminants from Mátraszőlös and Felsőtárkány complete the picture.

2. Material and methods

All fossils are stored in the Natural History Collection of the Municipal Museum of Pásztó (Hungary), in the Palaeovertebrate Collections of the Geological Institute of Hungary, (Budapest) and in the Geological and Palaeontological Institute of the Babeş-Bolyai University (Cluj, Romania), and in the Muzeul Țării Crișurilor (Oradea, Romania).

The acronyms used in the text are M/m for molars, P/p for premolars (uppercase for upper dentition, lowercase for lower teeth). All measurements are in mm. The nomenclature and measurement methods, as well as the abundance of the species in each site, are provided in the literature considered in this work. More specifically for the small mammals: bats: Miller (1907); Talpidae: Prieto et al. (2015); Erinaceidae: Prieto et al. (2010a); see also discussion in Prieto et al., 2015); Soricidae: Prieto et al. (2015); Dimyliidae: see comments in Prieto et al. (2012a). Sciuridae:

Cuenca-Bescós (1988); Gliridae: De Bruijn (1966), and partially Heissig (2006); Eomyidae: Engesser (1999); Cricetidae: Mein and Freudenthal (1971; Freudenthal and Daams (1988) for the M3); Cricetodontini: Rummel (1998); Castoridae: Korth, 2001 (see also comments in Prieto et al., 2014a); Lagomorpha: Angelone and Sesé (2009). The studied localities are listed in Section 3. The unpublished localities (Vârciorog, Kozárd) have been included and new preliminary results are presented in the following. Similarly, part of the discussions on the insectivore, bat and pika faunas are based on ongoing research.

3. The small-mammal-bearing localities and their ages

The geographic position of the localities is provided in Fig. 1. The proposed chronostratigraphic positions of each locality, except for those of Váralja and Sámsonháza 0–2, are summarized in Fig. 2 (* refers below to the numbering used in this figure). In the following sections, these correlations are discussed.

3.1. Late Sarmatian s. str.–?earliest Pannonian (middle to?late Miocene, ~12.2 Ma–?11.6 Ma)

Felsőtárkány (Hungary, Heves County; *1–7). Two sections (Felsőtárkány-Güddör-kert and Felsőtárkány-Felnémet) provided seven fossiliferous layers. The stratigraphic arrangement of the localities follows Hír and Kókay (2010). The historical primate-bearing locality Felsőtárkány-Güddör-kert (e.g., Andreánszky and Kovács, 1955; Éhik, 1926; Kretzoi, 1982; Schréter, 1913; Sümeghy, 1923) most probably corresponds to Felsőtárkány 3/2 (Hír, 2004; *3), and is considered as such herein. Felsőtárkány 3/8 and 3/10 (*2 and 1) are positioned higher in the section. Hír and Kókay (2010) correlate the localities to the Sarmatian based on molluscs, but cannot exclude that the deposits belong to Pannon A/B. Felsőtárkány 1 and 2 (*4 and 5) are the oldest fossil faunas from the Felsőtárkány-Güddör-kert section (Hír and Kókay, 2009)

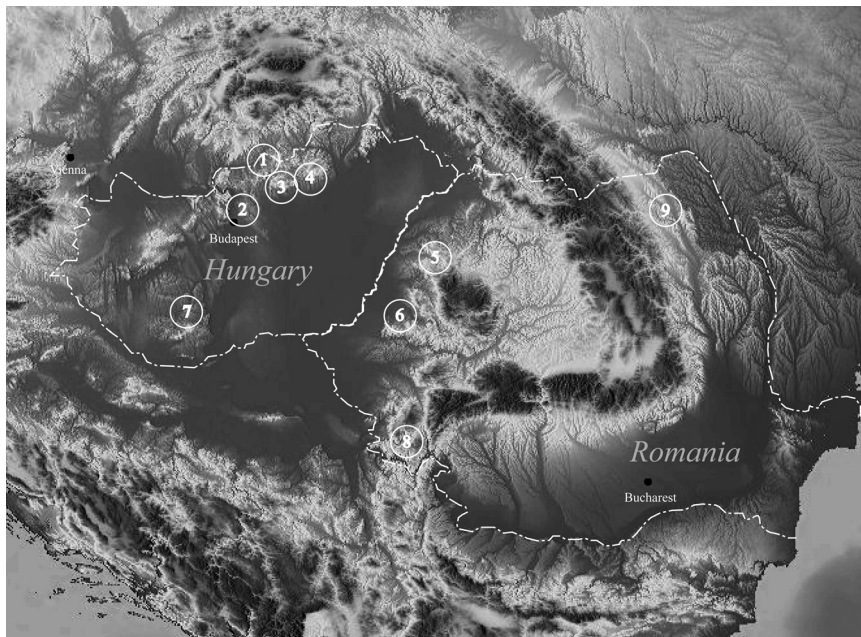


Fig. 1. Geographic position of the small mammal localities. 1: Egerszólát, Felsőtárkány 1, Litke 1 + 2. 2: Szentendre. 3: Sámsonháza, Hasznos, Mátraszőlős, Kozárd. 4: Egerszólát, Felsőtárkány. 5: Subpiatră, Vârciorog, Tășad. 6: Comănești 1, Tauț. 7: Váralja. 8: Bozovici. 9: Bogata.

Fig. 1. Situation géographique des localités à petits mammifères. 1: Egerszólát, Felsőtárkány 1, Litke 1 + 2. 2 : Szentendre. 3 : Sámsonháza, Hasznos, Mátraszőlős, Kozárd. 4 : Egerszólát, Felsőtárkány. 5 : Subpiatră, Vârciorog, Tășad. 6 : Comănești 1, Tauț. 7 : Váralja. 8 : Bozovici. 9 : Bogata.

and are also correlated to the late Sarmatian based on the mollusc content. The Felsőtárkány-Felnémet section is found along the road connecting both settlements and lithostratigraphically underlays the previous section (Felsőtárkány-Felnémet 2/3 and 2/7; *7 and 6; Hír, 2006, Hír and Kókay, 2009).

Egerszólát (Hungary, Heves County; *8). Correlation based on molluscs (pers. communication of J. Kókay in Hír (2011)).

Comănești 1 (Romania, Arad County; *10). The age of the locality ranges between the end of the Volhynian and the base of the Bessarabian based on both the invertebrate and mammal content (Feru et al., 1980).

Tauț (Romania, Arad County; *11). Feru et al. (1980), based on the evolutionary stage of the micromammalian fauna, suggest most probably an early Bessarabian (most probably middle Miocene) correlation for this locality, but Hír et al. (2011) point out the late Miocene affinities of these taxa.

Bogata (Romania, Suceava County; *12). The single find of *Dinosorex* derives from terrestrial gastropods-enriched clays underlying a coaly layer near the top of the Râpa Băieșilor section. It is correlated to the Upper Volhynian based on the malacofauna (see details in Codrea and Țibuleac, 1999).

3.2. Early Sarmatian (middle Miocene, ~12.8 Ma~12.2 Ma)

Vârciorog (or Vércsorog, Romania, Bihor County; *13). The microfossil assemblages from the Vârciorog section include terrestrial vertebrates that are characteristic for

the *Elphidium reginum* Zone and *Mohrensternia* Zone of the early Sarmatian (Filipescu et al., 2014). Two superposed layers rich in small mammals have been excavated, but these are here considered as one single assemblage. First tests show that the palaeomagnetic signal obtained for layers overlaying the vertebrate-enriched deposits are inverse in their polarity, which would fit the probable correlation to the chron C5Ar.1r as proposed by Filipescu et al. (2014).

Tășad (Romania, Bihor County; *14). After Hír et al. (2001), the mollusc fauna correlates to the Volhynian, and to the *Mohrensternia* Zone.

Kozárd (Hungary, Nógrad County; *15). Kozárd is a newly discovered and unpublished small mammal locality; the foraminifer *Elphidium reginum* restricts the stratigraphic range of the locality to early Sarmatian (Tóth and Csoma, 2015).

3.3. Late Badenian (middle Miocene, ~13.8 Ma~12.8 Ma)

Mátraszőlős (Hungary, Nógrad County; *16–18). The three layers contain a late Badenian mollusc fauna, but Mátraszőlős 3 (the uppermost fauna) contains an archaic species of *Bittinum*, a genus known from Sarmatian deposits (Hír and Kókay, 2004, 2011). Mátraszőlős 1 lies a bit deeper than layer 2 and Mátraszőlős 3 is the uppermost level. There are no biostratigraphic differences between the faunas. These are correlated to the latest part of the Badenian herein.

Locality of uncertain dating

Egerbocs (Hungary, Heves County; *9). The layer is rich in reworked early Badenian marine fossils, but not

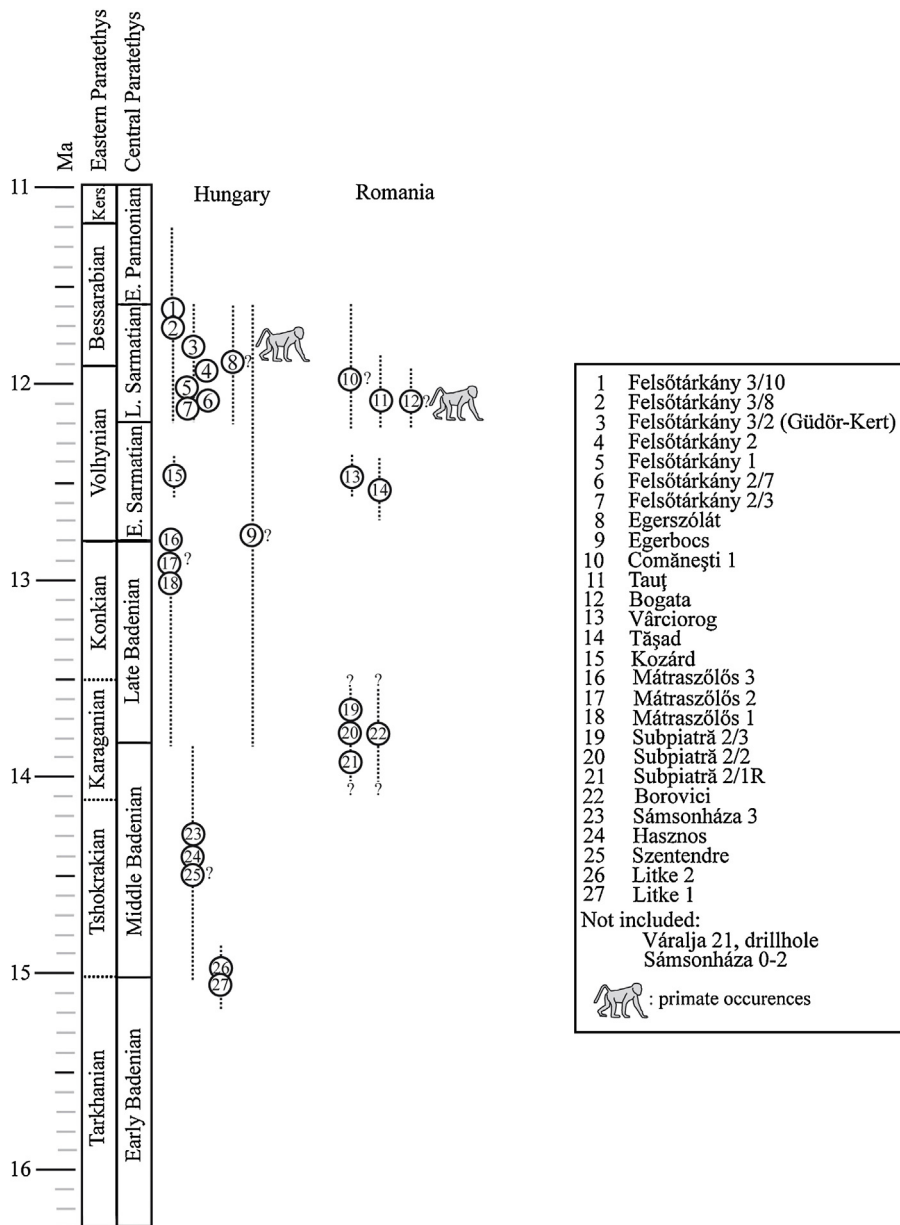


Fig. 2. Chronostratigraphic position of the Hungarian and Romanian small mammal localities. The division and limits of the Badenian follow the proposal of Hohenegger et al. (2014). The dotted lines indicate age uncertainty of the considered sites.

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 lignes pointillées indiquent les incertitudes quant à l'âge des sites.

in small mammals. The presence of the flying squirrel *Forsythia gaudryi* in the fauna allows one to restrict the stratigraphic range to the late Badenian and Sarmatian (Hír, 2001).

3.4. Late to Mid Badenian

Subpiatră (Romania, Bihor County; *19–21). The age of the localities follows Hír and Venczel (2005) based on small mammals. Subpiatră 1/R correlates to MN 6, while Subpiatră 2/2, a layer 25 m meters to the west, is

probably younger (MN 7/8; see text below). We follow Kálin and Kempf (2009), who propose the beginning of the MN 7-type faunas at around 13.9 Ma, consequently roughly equivalent to the middle–late Badenian transition herein. The unpublished level Subpiatră 2/3 are yellowish green clays with carbonate concretions containing the uppermost fossils of the section.

Bozovici borehole #1266 (154.70–155.15 m and 158.33–159.00 m) (Romania, Caraș-Severin County; *22). The small mammals derive from the Valea Slătincului Member, which correlates to the late middle/earliest late

Badenian, or the upper part of the Moravian/base of the Wielician (for details, see [Codrea \(2001\)](#)).

3.5. Mid Badenian (middle Miocene, ~13.8 Ma)

Sámsonháza (Hungary, Nógrád County; *23). The small mammal bearing deposits occur at the top of the Sámsonháza Formation; invertebrate assemblages refer to the middle Badenian ([Hír et al., 1998](#); [Hír and Mészáros, 2002](#)); Sámsonháza 3 is the most productive layer, but three other assemblages of minor importance are available (Sámsonháza 0–2; 2 contains indeterminate vertebrates only).

Hasznos (Hungary, Nógrád County; *24). The historical locality of Hasznos was first sampled by [Kordos \(1981\)](#). Based on small mammals, the locality correlates to MN 6; [Hír and Mészáros \(2002\)](#) propose that the Sámsonháza 3 is only slightly younger than Hasznos and this suggests a middle Badenian correlation also for this locality.

Szentendre (Hungary, Pest County; *25). Based on the presence of *Cricetodon hungaricus* ([Kordos, 1986](#)), the locality is probably close in age to Hasznos and Sámsonháza.

3.6. Early to middle Badenian (middle Miocene, ~15 Ma)

Litke 1+2 (Hungary, Nógrád County; *26, 27). Fossiliferous layers interbedded between the Tar Dacite Tuf (Karpatian) and the Sámsonháza Formation (Badenian). The biostratigraphically most relevant rodent taxon is *Cricetodon meini* ([Hír, 2013](#)). This species is an immigrant from SW-Asia shortly before 15 Ma.

3.7. Ottnangian–?Karpatian (early Miocene)

Váralja (Hungary, Tolna County). After [Kordos \(1989\)](#), the *Anomalomys minor* tooth derives from a borehole in the Szászvár Formation (late Eggenburgian–early Badenian).

4. Small mammal (Rodentia, Lagomorpha, Eulipotyphla, Chiroptera): state of the art

The updated faunal lists (except bats) are provided in [Appendices 1 and 2](#) (after [Hír et al., 2016](#)).

4.1. Order Rodentia Bowdich, 1821

Family CRICETIDAE Fisher, 1817

The faunas in this study are dominated by cricetid rodents. Among these, the tribe Cricetodontini Schaub, 1925 is of primary importance for the biostratigraphy. The Hungarian and Romanian fossil record discussed in this paper covers a time ranging from the first appearance of the tribe in Central Europe to the differentiation of the forms which precede the late Miocene members of true *Hispanomys* in the western part of Europe and *Byzantinia* in Anatolia. A clear and accurate taxonomy of the fossils is thus needed in order to unravel their phylogeny. However, because of high intraspecific variability of the species, the taxonomy is not completely resolved in some cases. Particularly when dealing with small collections, identifications can be problematic (e.g., [López-Guerrero et al. \(2015\)](#) and references therein). Even at the genus

level, some doubts might arise, especially in the early members of lineages, which display a mixture of evolved and primitive morphologic characters. This is the case in the localities considered herein, especially during the late Badenian and the Sarmatian s.str. In order to understand the uncertainties involved, it is important to underline the difficulties encountered during the last years of study.

Genus *Cricetodon* Lartet, 1851

Cricetodon meini Freudenthal, 1963

Fig. 3.1

Molars of this species have been recently described by [Hír \(2013\)](#) from Litke 1 and 2, our oldest localities. *Cricetodon meini* is widespread in Europe, having been reported from Greece (Komotini, Antonios, Thymiana A and B; [Koufos, 2006](#)), Serbia (Paragovo, Popovac, Lazaevac, Bele Vode; [Marković, 2008](#); [Marković and Miliivojević, 2010](#)), Austria (Mühlbach; [Daxner-Höck, 2003a](#)), the North Alpine Foreland Basin (abbreviated NAFB; see for instance [Kälin and Kempf, 2009](#)) and France, where the species has been defined (e.g., [Mein and Freudenthal, 1971](#)). Interestingly, it does not reach the Iberian Peninsula (e.g., [López-Guerrero et al., 2015](#)).

Cricetodon hungaricus ([Kordos, 1986](#))

Fig. 3.2

The taxon was originally defined from Hasznos by [Kordos \(1986\)](#) as a subspecies of *Deperetomys hagni* [Mein and Freudenthal, 1971](#), but [De Bruijn et al. \(1993\)](#) reclassified it as *Cricetodon hungaricus*. They also recognize similarities with species described from Anatolia, namely *C. pasalarensis* ([Tobien, 1978](#)), *C. cariensis* ([Sen and Ünay, 1979](#)) and *C. candirensis* ([Tobien, 1978](#)), even suspecting a synonymy with the latter. Although some evident morphological characters are shared by the Hungarian and the aforementioned Anatolian forms, some clear differences are also notable, as for instance the outline of the labial border of the M1, straighter in *C. hungaricus* than in the other species. Thus, these forms are retained as separate species in this work. In this respect, the report of *C. cf. hungaricus* by [De Bruijn et al. \(2013a\)](#) from Zambal (Anatolia), where the species occurs with another Cricetodontini (*C. cf. pasalarensis*), is interesting. Notably, the figured *C. cf. hungaricus* M1 shows an anterior part being clearly wider than the hypocone/metacone axis, a character found in *Deperetomys hagni* and some Anatolian representatives.

Cricetodon cf. hungaricus from Sámsonháza differs from the material from the type locality only in some morphological details, such as the lack of a funnel-structure and shorter mesoloph in M1 and M2, the m1 missing of the lingual anterolophulid, and lower molars with shorter mesolophids and ectomesolophids. It was considered as an advanced form of *C. hungaricus* by [Hír and Mészáros \(2002\)](#). Apart from these records, the species is only tentatively recognized in the faunal list from Brajkovac (Serbia; [Marković and Miliivojević, 2010](#)).

As final note, one of us (JH), (re)studied the *Cricetodon* material from the type locality, and came to the conclusion that, although *C. hungaricus* and *C. candirensis* are closely related, a direct ancestor–descendant relationship remains questionable.

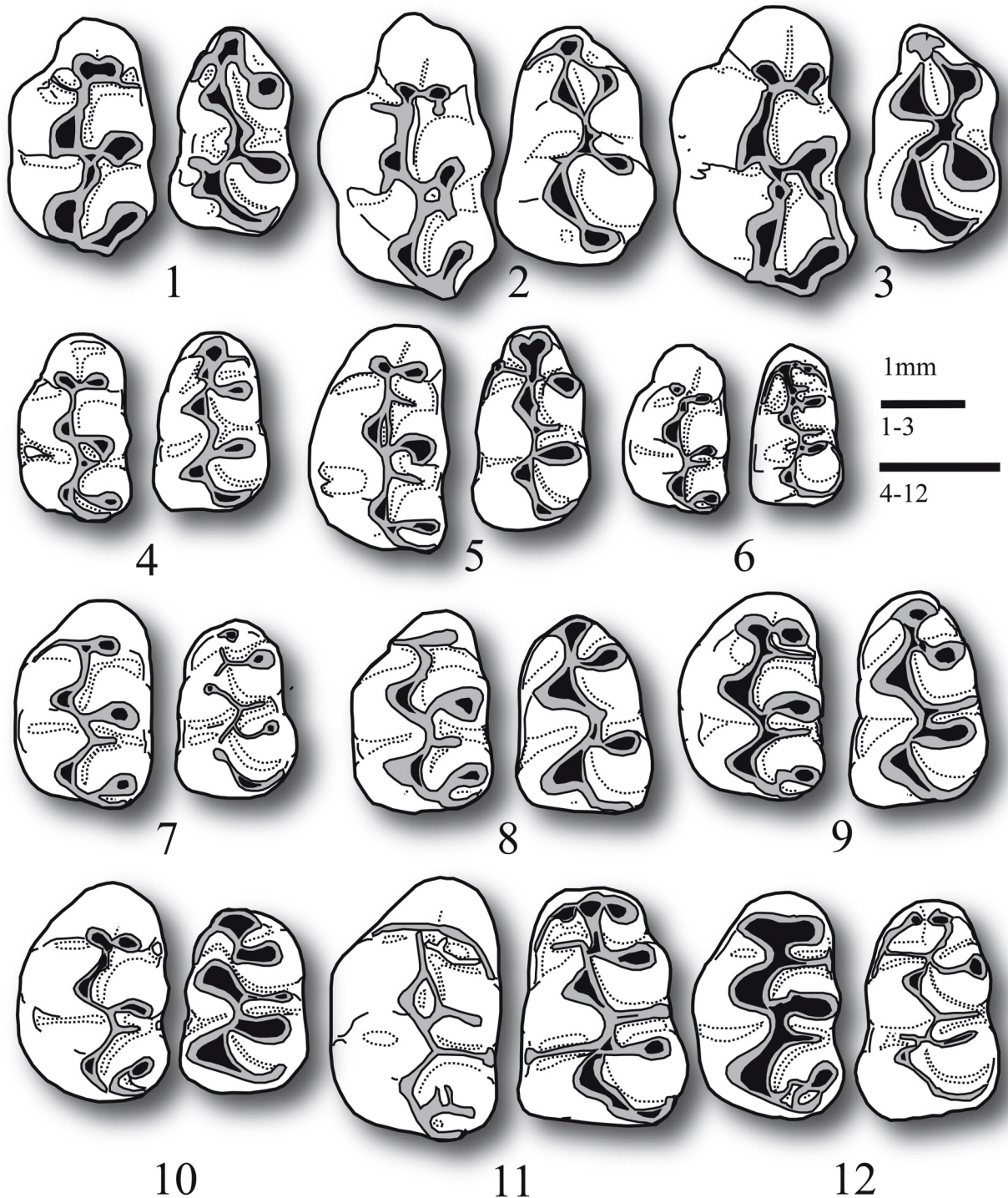


Fig. 3. Cricetid rodents from Hungary and Romania. All specimens presented in left orientation (right elements have been reversed). For each taxon, the first lower m1 (right tooth) and its upper counterpart (left molar) are figured. 1: *Cricetodon meini* from Litke 1. 2: *C. hungaricus* from Hasznos. 3: “*C.*” *klariankae* from Felsőtárkány-Felnémet 2/3. 4: *Megacricetodon minor* from Litke 1. 5: *M. similis* from Subpiatră 2/1R. 6: *M. minutus* from Felsőtárkány 3/2. 7: *Democricetodon mutilus* from Litke 1 and 2. 8: *D. hasznosensis* from Hasznos. 9: *D. zarandicus* from Tauș. 10: *D.* sp. nov. from Felsőtárkány-Felnémet 2/7. 11: *D.* cf. *freisingensis* from Mátraszőlös 2. 12: *Collimys dobosi* from Felsőtárkány 3/2. The molars have been redrawn based on the figures of Hír (2004, 2006, 2007, 2013), Hír and Kókay (2004), Hír and Venczel (2005), Kordos (1986) and Rădulescu and Samson (1988).

Fig. 3. Rongeurs cricétidés de Hongrie et de Roumanie. Tous les spécimens sont présentés, en orientation gauche (les dents droites ont été inversées). Pour chaque taxon, la première molaire inférieure (dent droite) ainsi que son équivalent supérieur (dent gauche) sont figurés. 1 : *Cricetodon meini* de Litke 1. 2 : *C. hungaricus* d’Hasznos. 3 : “*C.*” *klariankae* de Felsőtárkány-Felnémet 2/3. 4 : *Megacricetodon minor* de Litke 1. 5 : *M. similis* de Subpiatră 2/1R. 6 :

“*Cricetodon*” *klariankae* Hír, 2007

Fig. 3.3.

Defined by Hír (2007) on the basis of the collection from Felsőtárkány–Felnémet, the species is characterized primarily in being higher crowned than *C. meini* and *C. hungaricus*. The funnel structure is not developed on the M1 and M2, although the ectolophs are present and especially the posterior one is complete. Both metalophulids are present on the m1. Although recently excavated and thus still under study, the *Cricetodontini* remains from Vârciorog and Kozárd are closely related to “*C.*” *klariankae*, and differ from the type collection only in some characteristics: the molars from Vârciorog are in overall smaller, the crown lower and the metalophulid I much more variable in its development (absent, interrupted or complete) on the m1s. The species from Kozárd is also a bit smaller than in Felsőtárkány–Felnémet, but as high crowned as “*C.*” *klariankae*, and the minor morphologic details could be considered as part of the variation of “*C.*” *klariankae*. We consider the three above-mentioned populations as belonging to a lineage; the lineage involving “*C.*” *klariankae* is characterized by:

- increasing hypsodonty;
- disappearance of the anterior protolophule in M1;
- involution of the protostyl spur and the lingual anteroloph in M1;
- increasing dimensions of the molars;
- involution of labial anterolophid and protosinusid in m1;
- strengthening of metalophulid I in m1.

These new results extend the stratigraphic range of the lineage into the early Sarmatian. As a consequence, the evolution of the lineage “*C.*” *fandli* Prieto et al., 2010–“*C.*” *klariankae* as proposed by Prieto et al. (2010b) has to be re-considered. Indeed, Harzhauser et al. (2008), as well as Gross et al. (2011), correlate Gratkorn, from which “*C.*” *fandli* was described, to the earliest part of the late Sarmatian s.str., at ~12–~12.20 Ma. This implies that Gratkorn is younger than Vârciorog on one hand and close in age to Felsőtárkány–Felnémet on the other. The smaller size of the Austrian species, as well as the lack of well-established metalophulid I on the m1, is not compatible with its inclusion in the Hungarian lineage presented above. Alternatively, the dating of Gratkorn could be questioned and might be older than regarded at present.

Cricetodontini not assigned at the species level.

Mátraszőlős: *Cricetodon* sp. is only known from nine molars derived from three layers; the m1 is missing. The M1 and M2 have the funnel structure, and the teeth are in overall in the upper size range of *C. hungaricus*. Whether or not the species is phylogenetically linked to the species from Hasznos cannot be decided on the basis of the few available teeth from Mátraszőlős.

Tășad: The fossil material is also limited (six molars have been described). These teeth differ primarily from the

previous locality by their higher crown and the absence of mesoloph. Hír et al. (2011) recognize some similarities with *Hispanomys* Mein and Freudenthal, 1971 and *Byzantinia* De Bruijn, 1976, but also some differences, such as the degree of elongation of m3/M3 and of development of the m3 hypoconid. This precluded assigning the Tășad species to any of these genera. Given the chronostratigraphic position of the locality, the species from Vârciorog is interesting to compare. Indeed, the molars from Tășad and Vârciorog are similar in size, are both relatively high crowned compared to the older *Cricetodontini* and lack well-developed mesolophs on M1 and M2. A clear difference is the less developed anterior ectoloph in Vârciorog. This might be explained by a slight difference in age between the two localities. For these reasons, we tentatively include this form into the “*C.*” *klariankae* lineage in Appendix 1.

Comănești 1: Feru et al. (1980) assigned the two m1 from this locality to two different taxa, namely *Hispanomys* cf. *lavocati* (Freudenthal, 1966) and *H.* cf. *bijugatus* (Mein and Freudenthal, 1971). This opinion was emended by Hír et al. (2011), who classified the material as cf. *Byzantinia* sp. or div. sp. In contrast to the original study, they consider that the differences observed between the two m1 are linked to intraspecific variability, but they cannot confidently certify the taxonomical homogeneity of the molar sample as a whole. Considering the stratigraphic position of Comănești 1, “*C.*” *klariankae* would have been expected to be present in the locality. Hír et al. (2011) reject this assignment because of the presence of the spur of the protocone in the upper molars, the similar width of the anterior and posterior parts of the M2 (meaning it is not stretched) and the presence of both metalophulids in the m1 of the Hungarian species. As discussed above, while the metalophulid I is well developed in the m1 from Felsőtárkány–Felnémet, this structure is much more variable in its development in Vârciorog, but the metalophulid II is mostly present, being absent in only one molar out of twenty-four. Thus, the lack of the crest in one molar from Comănești 1 is a character at present very rare in Hungary. Otherwise, in size and morphology, the m1 of the two species are close. The other teeth from the Romanian collection (M2, M3, m3) show evident differences which preclude linking these to “*C.*” *klariankae*.

As a final note, the generic assignment of the Sarmatian *Cricetodontini* species has been debated over the last years. Indeed, the advanced development of the ectolophs and the increase in crown height link these forms to early members or side branches of lineages leading to the late Miocene genera *Hispanomys* and *Byzantinia*. Prieto et al. (2010b), in their discussion of the *Cricetodontini* from Gratkorn, underline the difficulties in confidently assigning the Austrian species. The formal diagnoses of the genera *Cricetodon*, *Hispanomys* and *Byzantinia* should be emended in order to discriminate early species which show a mix of characteristics found in each genus. The suggestion provided by Prieto et al. (2010b), namely assign these forms to “*Cricetodon*” and consider *Cricetodon* only

in its strict sense, seems at the moment the most practical, albeit simplistic, solution. First and evidently, it underlines the difficulties. Secondly, the validity of *Turkomys* Tobien, 1978, which was synonymized by Boon (1991) with *Cricetodon*, has to be carefully reviewed in the light of the discoveries made during the last three decades. Finally, the subjective assignment to either *Hispanomys* or *Byzantinia* would suggest biogeographic relationships with western Europe on one side and Anatolia on the other. This should be avoided, at least for central and eastern Europe, as long as the direct relationship is not demonstrated.

Genus *Megacricetodon* Fahlbusch, 1964

Figs. 3.4–6

Similarly to the Austrian middle/late Miocene fossil record, the *Megacricetodon* finds from Hungary and Romania only consist of small-sized species and the genus is always represented by a single species per locality. Three species are recognized, since the *Megacricetodon germanicus* Aguilar, 1980 specimens from Subpiatră 2/2 (Hír and Venczel, 2005) are now regarded as not belonging to this species, but linked to *M. similis* Fahlbusch, 1964 instead. *Megacricetodon germanicus* from Felsőtárkány 2/7 and Tășad in fact refers to *Democricetodon* (Hír et al., 2011).

According to Hír (2004), the demise of the *Cricetodontini* in the Felsőtárkány basin coincides with the replacement of *M. minor* (Lartet, 1851) by *M. minutus* Daxner, 1967 (Hír, 2006). This proposal needs to be re-evaluated as new *M. minutus* finds from Vârciorog document the taxon as recently as the early Sarmatian s. str. in Romania. Indeed, Hír (2004) and Hír and Kókay (2010) mainly used size criteria to discriminate the two species, with *M. minutus* being slightly smaller. As a result, the distinction between these two species is not always easy. Hír et al. (2011) consider *Megacricetodon crisiensis* Rădulescu and Samson, 1988 from Comănești 1 as a junior synonym of *M. minutus*. These forms are under revision by Hír and colleagues and a detailed comparison will be provided in the near future. Additionally, Prieto in Prieto et al. (2012a: 237) proposes that *M. minor* from Sâmsónháza 3 (among others) approaches in size and morphology *M. aff. similis* from various fissure fillings from Petersbuch (MN 6–8, Prieto, 2007, Prieto and Rummel, 2009a). This assumption might be supported by the presence of *M. similis* in Subpiatră (as *Megacricetodon* sp. in Hír and Venczel, 2005), but needs additional detailed study to be confirmed.

Genus *Democricetodon* Fahlbusch, 1964

Figs. 3.7–11

Democricetodon cf. n. sp. (sensu Kálin and Engesser, 2001) and *Democricetodon zarandicus* Rădulescu and Samson, 1988

Prieto et al. (2014b) remarked that the as yet unnamed *Democricetodon* species from Nebelbergweg and Gratkorn is a common element in Sarmatian and early Pannonian deposits in Central and East Europe. This species was not defined by Kálin and Engesser (2001), because the same species probably occurs in Götzendorf and Rudabánya, and these populations were at the time under study. As the species has not yet been named, we use the term

Democricetodon n. sp. (sensu Kálin and Engesser, 2001). The species resembles *D. brevis*, but is larger and lacks the ectomesolophid. It is also characterised by mesolophids that are usually long or even reach the tooth border.

Hír et al. (2011) reinvestigated the type material from Tauș and came to the conclusion that the species *Democricetodon zarandicus* is valid. They emended its diagnosis, but could not confidently recognize it anywhere else. They also suggested that the Romanian species differs from some European late middle Miocene forms only in small morphological details. Considering the stratigraphic position of Tauș, the *Democricetodon* finds from Felsőtárkány have to be considered, but the lack of sufficient material does not allow a proper assessment of the intraspecific variability of the Sarmatian s.str. species. The richer molar collection from Vârciorog might provide new information in the future. The species is in size and morphology also close to *Democricetodon* n. sp. (sensu Kálin and Engesser, 2001; J. Hír pers. data), extending most probably the range of the species to the early Sarmatian s.str. Although the two aforementioned species are here considered separately, they are very similar, and thus might be viewed as members of a single *Democricetodon*-type.

Hír (2006) assigned some molars from Felsőtárkány–Felnémet 2/3 and 2/7 to *Democricetodon brevis*, whereas Prieto et al. (2014b) proposed that they could belong to a species close to *Democricetodon* n. sp. (sensu Kálin and Engesser, 2001). Similarly, Felsőtárkány 1 and 2 contain *Democricetodon* sp. (Hír and Kókay, 2009). This species resembles *Democricetodon* n. sp., but is not identical because of its larger dimensions and the presence of lingual anterolophid in m1.

Surprisingly, the genus is not found in the three youngest localities from Felsőtárkány, where *Collimys* is abundant. This does not mean necessarily that the species disappeared from the record, because its abundance is also variable in the NAFB: while *Democricetodon* n. sp. is a common element in Nebelbergweg (Kálin and Engesser, 2001), only a few teeth are recognized in Hammerschmiede, where *Collimys hiri* is abundant (JP personal observation). The survival of *Democricetodon* n. sp. in the area might also be supported by the presence of a closely-related species in Tășad (Prieto et al., 2014b; as *D. brevis* in Hír et al., 2001).

Democricetodon cf. *freisingensis* Fahlbusch, 1964

The species has been described from Mátraszőlös 2 (Hír and Kókay, 2004; as *D. freisingensis* in Hír and Kókay, 2011: 74). It is characterised by long anterolophids and mesolophids, as well as long ectolophids and mesolophids. Maridet and Sen (2012) discuss the differences between *D. freisingensis* from Giggenhausen and *D. gaillardi* (Schaub, 1925) from Sansan. They only recognize some minor morphological differences between the two, the most impressive being the division of the anteroconid on the m1. In addition and following Maridet (2003), they note that some differences occur in the outline of the first upper and lower molars. Based on these observations, the assignment of the Hungarian specimen fits also to *D. gaillardi* in the division of the anteroconid of the m1, the relative large anterocone of the M1, as well as the straight alignment of the cusps on the labial side of the M1. Notably, the molars from Mátraszőlös are rather large. Taking into consideration that

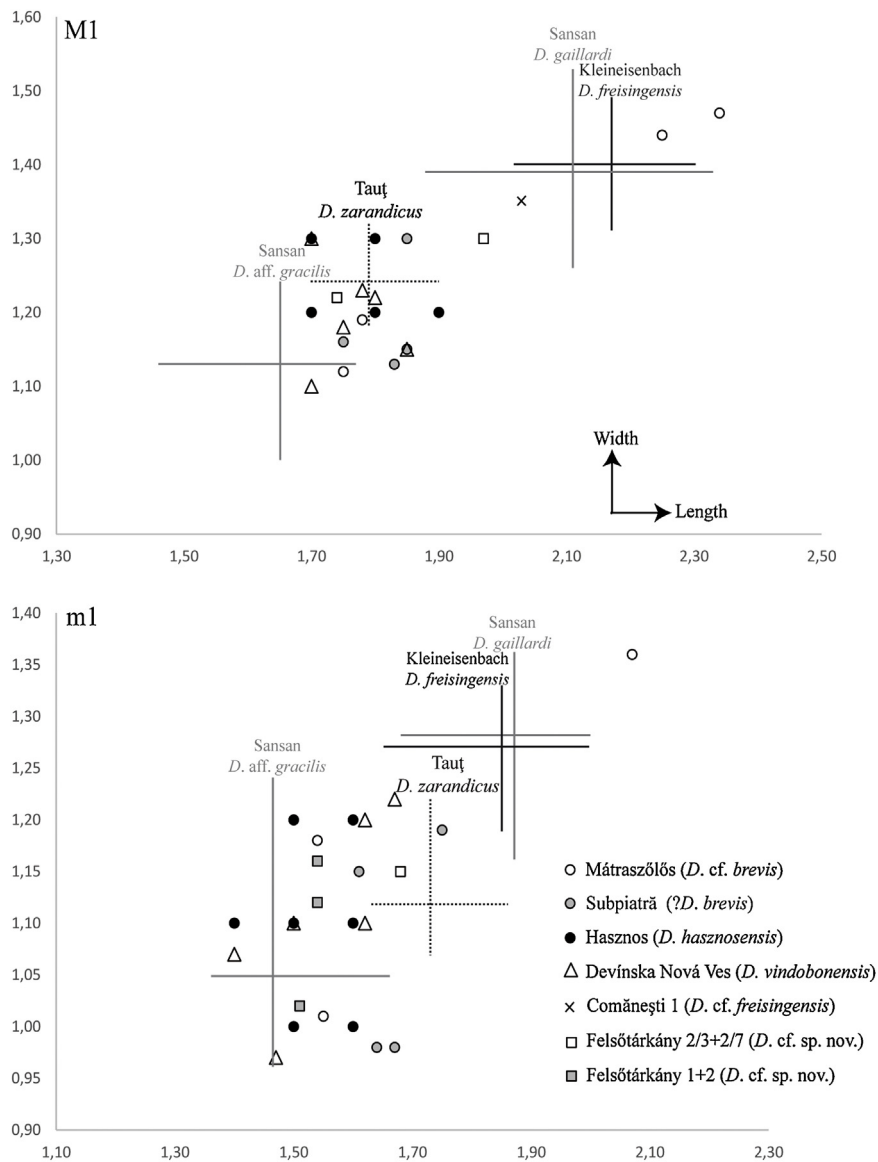


Fig. 4. Size comparison of the upper and lower first molars from some Hungarian and Romanian *Democricetodon* with the species from Sansan (*D. aff. gracilis* (= *D. crassus*) and *D. gaillardii*), Devínska Nová Ves (*D. vindobonensis*) and Kleineisenbach (*D. freisingensis*). Data from Fejfar (1974), Rădulescu and Samson (1988), Hír (2006), Prieto (2007), Hír and Kóky (2009, 2011) and Maridet and Sen (2012).

Fig. 4. Comparaison des tailles des premières molaires inférieures et supérieures de quelques *Democricetodon* hongrois et roumains avec les espèces de Sansan (*D. aff. gracilis* (= *D. crassus*) et *D. gaillardii*), Devínska Nová Ves (*D. vindobonensis*) et Kleineisenbach (*D. freisingensis*). Données d'après Fejfar (1974), Rădulescu et Samson (1988), Hír (2006), Prieto (2007), Hír and Kóky (2009, 2011) et Maridet and Sen (2012).

the debate concerning the synonymy *D. freisingensis*/*D. gaillardii* is not closed, we do not follow proposal from Maridet (2003) herein. *Democricetodon freisingensis* is also reported from Subpiatră 2/2 (Hír and Venczel, 2005). Fig. 4 compares the sizes of the upper and lower first molars from Hungarian and Romanian forms with the species from Sansan, Devínska Nová Ves and Kleineisenbach (*D. freisingensis* as in Giggenhausen, the type locality; Prieto, 2007). It clearly shows that the Romanian species is smaller than *D. freisingensis* and *D. gaillardii* (see discussion below). Finally, Hír et al. (2011) consider *D. iazygum* Rădulescu and Samson, 1988 from Comănești 1 as *nomen dubium* because of the

lack of sufficient material. They attribute this material to the large *Democricetodon* studied here.

Democricetodon cf. brevis (Schaub, 1925)

Hír and Kóky (2004) recognize a medium-sized form in Mátraszőlös 2. Originally assigned to *D. mutilus*, the identification was later emended to *D. cf. brevis* by Hír and Kóky (2011). Only a few specimens are available and no m1 was found in Mátraszőlös 2. Hír and Kóky (2004) based their original assignment on the larger measurements than *D. gracilis* Fahlbusch, 1964, while still being smaller than *D. hasznosensis*. In fact, the specimens fall inside the size range of the species from Hasznos (see Fig. 4), but differ

in three morphologic characters: the absence of the anterior protolophule in M1, shorter mesolophs in M1 and M2 and a well-developed entoconid in m3. These characters are highly variable, and actually the length of the mesoloph does not differ much in the two localities. Thus, an assignment of the molars from Mátraszőlös 2 to *D. hasznosensis* cannot be definitively excluded. In contrast, and although of similar size, *D. vindobonensis* Schaub and Zapfe, 1953 is out of consideration, because of the long anteromesolophs on the M1. However, the single M1 from Mátraszőlös 3 shows a low but long anteromesoloph, and the m1 have a variable mesolophid (Hír and Kókay, 2011). Herein, the assignment to *D. cf. brevis* is maintained for Mátraszőlös 2+3, albeit tentatively. As noticed above, the specimens from Subpiatră 2/2 were originally assigned to a species related to *D. freisingensis*, but are, in fact, too small to belong to that species. Indeed, they near the size of *D. hasznosensis*, *D. vindobonensis* and *D. brevis*, and the m1 are only a bit larger than these species. Considering the limited material from Mátraszőlös 2, as well as the complexity of the taxonomy of *Democricetodon*, it is at present better to classify the molars from Subpiatră 2/2 as belonging to *D. cf. brevis* as well. Finally, and as stated above, the taxonomic status of the *Democricetodon* from Tășad, originally linked to *D. brevis*, might represent another species, but the material is very limited.

Democricetodon hasznosensis Kordos, 1986

The species is only surely recognized in the middle Badenian from Hungary and only well represented in its type locality Hasznos. Only three molars from Szentendre are assigned to *D. hasznosensis* (Kordos, 1986) and their size correlates to the upper range of Hasznos. The medium-sized species is characterised by the mesolophid on m1 mostly being absent. The two molars from Sámsonháza (M2, m2), a locality very close in age and geography, belong to the upper size range or are even larger than the type collection, but the material is too limited to draw any conclusions regarding their affinity.

Democricetodon mutilus (Fahlbusch, 1964)

This species occurs in Litke (Hír, 2013). All the molars, except the m2, fit within the lower size range of *D. mutilus* from the Austrian localities Mühlbach (Daxner-Höck, 2003a). The second lower molar from Litke is a bit smaller and fits within the upper size range of *D. gracilis* from Oberdorf (Daxner-Höck, 1998). Thus the presence of a second *Democricetodon* species in Litke cannot be excluded.

Democricetodon sp.

The new finds from Vârciorog show that, beside *Democricetodon* cf. n. sp. (sensu Kálin and Engesser, 2001), a second larger species is present. Unfortunately, the lack of sufficient material does not allow at present any confident taxonomical assignment.

Genus *Collimys* Daxner-Höck, 1972

Fig. 3.12

The genus *Collimys* is a common element of the late Sarmatian faunas from the Felsőtárkány Basin. One species is recognized, namely *C. dobosi* from Felsőtárkány 3/2 (type locality; Hír, 2005). This relatively large species is also known from Germany (Hillenloh; Prieto and

Rummel, 2009b). These authors propose the lineage *C. hiri* Prieto and Rummel, 2009–*C. longidens* Kálin and Engesser, 2001–*C. dobosi* based on size increase and minor morphological differences between the species. However, Prieto et al. (2014b) consider that this lineage is not suitable for biostratigraphic purposes at present, basically because of conflicts with the first occurrence of *Microtocricetus molassicus*. Moreover, while size differences are clear between the German species, this cannot be easily extrapolated at a larger scale. Whether or not the genus is oversplitted cannot be decided at present, but the morphological similarities of the above-listed species at least indicate a relationship of the central and eastern European faunas around the transition between the middle and the late Miocene. For now, *Collimys* has not been found in Hungarian/Romanian localities older than late Sarmatian (also absent in Vârciorog, JH pers. data).

Genus *Microtocricetus* Fahlbusch and Mayr, 1975

Microtocricetus molassicus Fahlbusch and Mayr, 1975 is the first highly specialized microtoid cricetid that appears in Europe (e.g., Fejfar et al., 2011) at around 11.6 My, but recent study shows that similar forms are present in Asia as early as the early Miocene (Maridet et al., 2012). In the Hungarian record, the species was long only known from Rudabánya (e.g., Bernor et al., 2004; Kretzoi and Fejfar, 2004). The find of some rare molars in Felsőtárkány 3/8 and 3/10 extends the range of the genus in the area (Hír and Kókay, 2010), and corresponds to the traditional estimate of its first occurrence in Europe. By contrast, new discoveries from the German Molasse indicate a more complex history for the genus (Prieto and Rummel, 2016).

Genus *Anomalomys* Gaillard, 1900

While *Anomalomys rudabanyensis* Kordos, 1989 occurs in the Vallesian of Rudabánya, the genus is mostly represented by *A. gaudryi* (Gaillard, 1899) in the localities considered herein. The species is a common element in the fauna from Felsőtárkány as shown by its dominance in Felsőtárkány 1, being the second most abundant species behind *Collimys dobosi* in Felsőtárkány 3/2 and 3/8 (Hír and Kókay, 2009). Surprisingly, this dominance is not a rule and the genus might also be completely absent, as it is in Felsőtárkány 2. In the Badenian and early Sarmatian faunas, the genus is scarce. A single find of *Anomalomys minor* Fejfar, 1972, an early Miocene species, has been recovered from the drill hole Váralja 21 (Kordos, 1989).

Genus *Eumyarion* Thaler, 1966

The systematic problems related to *Eumyarion* have been often debated (e.g., De Bruijn, 2009; De Bruijn and Saraç, 1991; De Bruijn et al., 2013b; Duncan, 2012; Joniak, 2005). As a result, there are some confusion regarding the late early–middle Miocene species. Here, the taxonomic approach follows the proposals of J. Hír, as described in his previous works (e.g., Hír and Kókay, 2010).

Three species are presently recognized in our study area. The oldest representative of the genus in the study

area is documented in Hasznos, where *Eumyarion* aff. *bifidus* is found (Kordos, 1986). Almost at the same time, *E. medius* appears in Sámsonháza. The species is the most abundant, being present in localities as young as Felsőtárkány 3/8 and 3/10 (Hír and Kókay, 2010). A third form was found in the upper Miocene fauna from Rudabánya (*E. cf. latior*; Kretzoi and Fejfar, 2004). *Eumyarion* is present in Mátraszőlős 3 and Tauț, but the material is too limited to be confidently assigned to any known species.

Family SCIURIDAE Fischer, 1817

Genus *Spermophilinus* De Bruijn and Mein, 1968

Spermophilinus is the most common sciurid in our studied faunas. *Spermophilinus bredai* von Meyer, 1848 is recorded from the late Badenian onwards in the Carpathian area. A second species, *S. besana* Cuenca-Bescós, 1988, is only recognized in Litke. The two species do not differ morphologically and the taxonomic assignment of some populations remains questionable (e.g., De Bruijn, 1995). For instance, Daxner-Höck (2003a) considers the molars from Mühlbach, a locality close in age to Litke, as belonging to *S. besana*, although the specimens are of intermediate size. Basically, these fit within the lower size range of our *S. bredai* assemblages (Mühlbach M1,2: 1.60 to 1.65 × 2.05; Felsőtárkány 3/2: 1.58 to 1.72 × 2.03 to 2.18). This underlines the taxonomic difficulties, and the limitations of the genus for biostratigraphic studies. Furthermore, Bosma et al. (2013) challenge the suggestion of De Bruijn (1995) that *Spermophilinus* underwent a size increase through time, because southeastern Europe and Anatolia might have served as a refuge for some species during the Miocene.

Genus *Palaeosciurus* Pomel, 1853

Only a few specimens of *Palaeosciurus* are recorded in Hungary and Romania. Some erroneous determinations have been emended by Hír and Pászti (2012; Felsőtárkány 3/2 and Egerbocs). The oldest species, *P. sutteri* Ziegler and Fahlbusch, 1986, is documented by a single m2 from Litke 2, which, however, is worn and damaged. The larger species *P. ultimus* Mein and Ginsburg, 2002 is present in Hasznos with one M1/2 and one p4. *Palaeosciurus* sp. is also found in Subpiatră 2/2 (Hír, 2013), but has not yet been described. The morphology of the two M1/2 from this locality completely agrees with the finds from Hasznos, but the dimensions are substantially larger (2.73 × 3.30, 2.75 × 3.38; Hasznos: 2.50 × 2.92).

Genus *Blackia* Mein, 1970

The small-sized *Blackia miocaenica* Mein, 1970 is the most common gliding squirrel studied herein. It first occurs in the late Badenian of Mátraszőlős 3, and the genus is still present in Rudabánya (Kretzoi and Fejfar, 2004) and survives well into the Pliocene (Csarnóta, Hungary; Van de Weerd, 1979).

Genus *Neopetes* Daxner-Höck, 2004

The four teeth from Felsőtárkány 3/2 were originally ascribed to *Hylopetes* sp., but this has been emended in

Neopetes by Hír and Kókay (2010; following Daxner-Höck, 2004). In addition, they report an upper milk tooth from Felsőtárkány 3/10. *Neopetes hoeckarum* has been described by Hír et al. (2011) from Tauț and unpublished material is also known from Subpiatră 2/3. Recently, Bosma et al. (2013) synonymized *Pliopetes* Kretzoi, 1959 and *Neopetes* with *Hylopetes* Thomas, 1908. Here, we follow the concept of Daxner-Höck (2004).

Genus *Forsythia* Mein, 1970

The medium-sized genus *Forsythia* is generally rare in Europe and the Hungarian/Romanian record is no exception. *Forsythia gaudryi* Gaillard, 1899 is only recorded in Egerbocs by an M1/2 (Hír, 2001).

Genus *Miopetaurista* Kretzoi, 1962

This large-sized flying squirrel is a rare element of the faunas. The m2 from Litke is assigned to *M. dehmi* De Bruijn et al., 1980 based on its relatively small dimensions (Hír, 2013). Two M1/2 from Subpiatră have no posterior spurs of the metaloph. The presence of this structure is a distinctive characteristic of *M. crusafonti* Mein, 1970 (Casanovas-Vilar et al., 2015; Mein, 1970) and the molars are thus, based on their size, assigned to *M. gaillardii* Mein, 1970 instead.

The large-sized molars from Felsőtárkány and Tauț are probably identical to *Miopetaurista* sp. described from Rudabánya (Kretzoi and Fejfar, 2004).

Genus *Albanensia* Daxner-Höck and Mein, 1975

The second large-sized flying squirrel has a complicated tooth morphology and is relatively abundant in Rudabánya and Felsőtárkány 3/2. Both assemblages are referred to *A. grimmi* (Black, 1966) (Hír, 2004; Kretzoi and Fejfar, 2004). The species is characterized by its size (larger species of the genus). Unfortunately, no upper molar is available from its type locality (Markt). Comparing the size of the lower (pre)molars of squirrels based on literature can be risky, because it is not always clear which measurement method is used, which differs from one author to the other (JP, pers. opinion). The upper (pre)molars are in this sense more adequate. In addition, Daxner-Höck (2004, 2010) underlined the taxonomical difficulties related to the scarce type material of both *A. grimmi* and *A. albanensis quiricensis* (Villalta, 1950) (the type material also lacks the upper dentition). Her proposal is followed herein. The genus is, beside the above-mentioned rich populations, very rare in our succession, and finds cannot be ascribed to any given species (Kozárd, Felsőtárkány-Felnémet 2/3 and Subpiatră), the generic ascription being even questionable in some cases (Mátraszőlős 3, Tauț; deciduous teeth).

Sciuridae gen. et sp. indet.

? *Palaeosciurus* sp. from Egerbocs is assigned to Sciuridae gen. et sp. indet. (Hír and Pászti, 2012). The single large-sized m2 (Hír, 2001: fig. 11) fits in size with *Miopetaurista*, but it lacks the characteristic ornamentation of the enamel and has a low crown.

Family EOMYIDAE Winge, 1877

Genus *Keramidomys* Hartenberger, 1966

The differences between *Keramidomys thaleri* Hugueneu and Mein, 1968 and *K. carpathicus* (Schaub and Zapfe, 1953) are discussed by Daxner-Höck (1998), Mein (2009) and Prieto (2010a), and the two species can be only recognized when abundant material is available. Hír (2013) assigns the few teeth from Litke to a species close to *K. thaleri*.

Keramidomys mohleri Engesser, 1972 is the most commonly recorded species. It has been defined in the late Badenian from the NAFB (Engesser, 1972), but older finds have been recently described from Sansan where the species is extremely rare (Hugueneu, 2012). The species is listed in Felsőtárkány 3/10 by Hír and Kókay (2010: Table 1; ?earliest Pannonian), but this is incorrect. Thus, the species ranges from the late Badenian (Mátraszőlős 2) to the late Sarmatian (Felsőtárkány 3/2).

Finally, Hír (2011) assigns a single M1/2 from Egerszólát to *K. pertesunatoi* Hartenberger, 1967, a species which is characterized by its simple morphology. However, this specimen should be left in open nomenclature because of the lack of sufficient relevant morphologic data.

Genus *Eomyops* Engesser, 1979

This bunodont eomyid is restricted to Europe, although the distinction, based on teeth only, of some morphologically close Asian and North-American genera is subtle (e.g., De Bruijn et al., 2012; Engesser, 1979, 1990; Qiu, 1994). Among the four named species, only *Eomyops oppligeri* Engesser, 1990 is recorded in the localities considered herein (*E. catalaunicus* (Hartenberger, 1967) from Rudabánya and *E. bodvanus* (Jánossy, 1972) from Osztramos are clearly younger; Daxner-Höck, 2003b; Jánossy, 1972). The assignment of an assemblage to either *E. oppligeri* or *E. catalaunicus* can be difficult. For instance, Kálin and Engesser (2001) consider that both species occur in Nebelbergweg, in contrast to the proposal of Prieto (2012), who recognizes only *E. catalaunicus* in this locality. Thus, the assignment of the European late middle Miocene forms remains confusing. Because the Hungarian assemblages are not large, the previously published attributions stay also questionable.

Family GLIRIDAE Muirhead, 1819

Genus *Microdyromys* De Bruijn, 1966

The genus is rare in our faunal succession; only three specimens of *M. complicatus* are described from Felsőtárkány 2/7 (D4, M1, m3) and one from Felsőtárkány 1 (M1). A questionable presence of the genus in Hasznos is also proposed (Hír personal data in Prieto et al., 2015). A second species, *M. koenigswaldi* De Bruijn, 1966, occurs in Sámsonháza 3 (originally assigned to *M. complicatus* De Bruijn, 1966 by Hír and Mészáros, 2002; Prieto et al., 2015).

Genus *Glirulus* Thomas, 1906

Glirulus lissiensis (Hugueneu and Mein, 1965) has a long stratigraphic range and is best documented in Rudabánya, although relatively rare in that locality (Daxner-Höck, 2003b). The other Hungarian finds, always scarce, derive from Egerszólát and Felsőtárkány 3/8 (Hír, 2011; Hír and Kókay, 2010). The presence of *Glirulus* sp. in Felsőtárkány

3/2 as stated by Hír (2004) has been recently emended by Hír and Kókay (2010) and these fossils are now assigned to *Paraglrulus werenfelsi* Engesser, 1972. Two *G. lissiensis* teeth also occur in Tauț (Hír et al., 2011).

Genus *Paraglrulus* Engesser, 1972

Besides the above-mentioned occurrence in Felsőtárkány-Felnémet 2/3, *Paraglrulus werenfelsi* has also been described from Subpiatră. It is a widespread form with relative long stratigraphical range (early to late Miocene).

Genus *Miodyromys* (Kretzoi, 1943)

Litke 1 and 2 provide the older evidence of *Miodyromys* in the basin. The species is small sized and differs from any other species described from biostratigraphically close faunas from Europe (see details in Hír (2013)). Hír (2013) recognizes the highest similarity in both morphology and measurements to *Miodyromys* cf. *biradiculus* Mayr, 1979 from the Zaisan Depression (eastern Kazakhstan; Kowalski and Shevyreva, 1997).

In the middle Badenian, the genus is abundant in Sámsonháza, but it is, by contrast, absent in Hasznos, where the dormice are anyway extremely rare. While the M1/2 show a clear bimodal size distribution, the discrimination of the other dental elements into two groups is more problematic. This is indicating, after Hír and Mészáros (2002), the presence of two species, and does not reflect differences in size between the first and second molars because such bimodal distributions were not observed in other large *Miodyromys* collections. Hír and Mészáros (2002) come to the conclusion that the larger upper molars belong to *Miodyromys* aff. *aegercii* (Baudelot, 1972) and the smaller ones to *M. aegercii*. The coexistence of two *Miodyromys* species was also proposed in the middle Miocene faunas of the NAFB (Heissig, 2006). With regards to *M. aff. aegercii*, its size approaches that of the larger species from Nebelbergweg (Switzerland). Kálin and Engesser (2001) consider the Swiss form as belonging to *M. aegercii*, which would make it one of the largest and youngest known representatives of the genus in central Europe. They also observe a unique morphological character, namely the presence of two extra crests in the posterior syncline, which is not observed in Sámsonháza. The small-sized molars from Vârciorog agree with those of *Miodyromys* sp. from Gratkorn (Austria; Daxner-Höck, 2010).

In contrast, two species occur in the late Sarmatian. *Miodyromys hamadryas* (Forsyth Major, 1899) is only recognized on the basis of size of a single M1/2 in Felsőtárkány-Felnémet 2/3. *Miodyromys* aff. *grycivensis* Nesin and Kowalski, 1997 (type locality Gritsiv, Ukraine) from Comănești 1 is also rare (two molars). The small size of the specimens, coupled with the absence of a posterior extra crest, relates them to the Ukrainian species.

Genus *Muscardinus* Kaup, 1829

Although frequent in the European Miocene, *Muscardinus* is rarely abundant in the Hungarian and Romanian middle Miocene faunas. Relatively rich material

was obtained from Subpiatră 2 and Felsőtárkány 3/2. The *Muscardinus* material from Subpiatră was preliminary attributed to two species, namely *M. sansaniensis* (Lartet, 1851) and *M. aff. sansaniensis* (Hír and Venczel, 2005). New field campaigns in 2007 and 2008 yielded a larger fossil collection which allows now to recognize only *M. aff. thaleri* De Bruijn, 1966 in the locality. The most important characteristics of the species are: 1) although the shape of the M1 is variable, some teeth have the same anterior and posterior width, 2) in some of the M1, the fourth ridge does not connect to the endoloph, but to the sixth ridge instead, 3) the second ridge never reaches the labial margin in m1 and m2; the latter condition is characteristic for *M. thaleri* (Daams, 1985).

Similarly, *Muscardinus* material from Felsőtárkány 3/2 was originally seen as a mixture of two species (*M. aff. sansaniensis* and *Muscardinus* sp.). The presence of *Muscardinus* sp. was based on a slender M1 with simple morphology (Hír, 2004: plate III/4), but this molar (MMP.2003. 523) is indeed strongly worn. The revision of the fossil material shows that *Muscardinus* from Felsőtárkány 3/2 differs from all known Astaracian–early Vallesian *Muscardinus* species of Europe. The dimensions are close to *M. hispanicus*, but some specific characteristics are recognized (e.g., long third ridge and lingual connection of the 4th ridge in M1). Herein, this population is not classified to the species level.

At present, *M. sansaniensis* or closely-related forms are recognized from localities ranging from the middle Badenian (Sámsonháza) to the early Sarmatian (Vârciorog and Kozárd; JH pers. data). This makes the presence of *M. aff. thaleri* in Subpiatră at the middle to late Badenian transition surprising, as it indicates that two species occurred in the area at this time.

With regard to the late Sarmatian, *Muscardinus* aff. *hispanicus* De Bruijn, 1966 is reported from Tauț, but the other records cannot be recognized at the species level and even display some original morphological characters. Thus, a detailed revision of the genus is needed, but it is out of the scope of this contribution.

Genus *Paraglis* Baudelot, 1970

This genus has been restored by Freudenthal and Martín-Suárez (2007), a proposal we concur with (Hír, 2013) but which is not always followed (e.g., De Bruijn et al., 2013b). A *Paraglis* P4 from Mátraszőlős 2 was misinterpreted by Hír and Kókay (2004) as M1/2 of *Eliomys truci* Mein and Michaux, 1970. The revision of *E. truci* population from southern Spain (García-Alix et al., 2008) clearly showed that the find from Mátraszőlős 2 cannot be assigned to this species because of the rounded occlusal surface and the smaller width. García-Alix et al. (2008) refer it to *P. astarensis* Baudelot, 1970, a species also known from Litke 1 (Hír, 2013), but not to *Paraglirulus werenfelsi* as listed in Prieto et al. (2014b).

Genus *Myoglis* Baudelot, 1965

Except for the presence of *Myoglis* in Subpiatră, all other records are from Sarmatian localities and only one species is present, *M. meini* De Bruijn, 1966. A notable exception

is *M. ucrainicus* Nesin and Kowalski, 1997, which can be recognized in Tauț based on morphological characters of the M1 (Hír et al., 2011).

Genus *Glis* Brisson, 1762

Hír and Kókay (2010) described a single and relatively large-sized m2 of *Glis vallesiensis* Agusti, 1981 from Felsőtárkány 3/10. This molar outranges the size of *G. minor* Kowalski, 1956 from Rudabánya (Daxner-Höck, 2003b), and documents the first occurrence of the genus in Hungary.

Gliridae indet.

Codrea (2001) describes an isolated m1/2 from Bozovici borehole #1266 (158.33–159.00 m). The tooth resembles *Paraglis*. Finally, *Eliomys truci* from Tășad (Hír et al., 2011) is now considered best classified as Gliridae indet.

Family CASTORIDAE Hemprich, 1820

Euroxenomys minutus Samson and Radulesco, 1973

Only this small-sized beaver is recorded in our succession. It occurs in the Hungarian late Sarmatian (Felsőtárkány Basin). The larger beaver *Chalicomys* Kaup, 1832 is at present only known from younger faunas from Hungary in our studied area (Vallesian and Turolian; Hugueney, 1999).

Finally, Kordos (1985) recognizes an indeterminate rodent in Bakonyozslop (not listed in the tables).

4.2. Order Lagomorpha Brandt, 1855

Family OCHOTONIDAE Thomas, 1897

Rooted ochotonids

“*Amphilagus*” Tobien, 1974 and *Eurolagus* López-Martínez, 1977 are primitive lagomorphs characterized by rooted teeth, simple p3, and the presence of a hypoconulid on the lower teeth. Both genera are recorded in the Miocene of Europe, but they are not closely related phylogenetically (Angelone, 2009). *Eurolagus* is a monospecific genus with a quite limited temporal distribution, traditionally considered as a MN7/8 biochronological marker (Angelone, 2008 and references therein). So far, there is no record of *Eurolagus* prior or later than MN7/8 (discussion in Angelone et al., 2014 and references therein). “*Amphilagus*” is a wastebasket genus in which European primitive lagomorphs from MP30 to the first part of middle Miocene are crammed (Angelone, 2009). Pending a general revision of European primitive lagomorph taxonomy, it is preferable to classify all European rooted lagomorphs as “*Amphilagus*”, except for those clearly pertaining to the well-characterized genus *Eurolagus*.

The fossil record of rooted lagomorphs in Romania consists of a sole record (Subpiatră 2/1R Hír and Venczel, 2005; also from Subpiatră 2/3; CA pers. data). In Hungary, rooted lagomorphs are known from the late Badenian of Mátraszőlős 2 and Mátraszőlős 1 onward (Gál et al., 1999) and are at present not reported from the early Sarmatian localities, but are known from late Sarmatian–earliest-Pannonian ones (Felsőtárkány 2, 3/2, 3/8, 3/10 and Egerszólát; Hír, 2004, 2011, Hír and Kókay, 2009). In the literature, all the above-listed remains are classified

as *E. fontanesi* Depéret, 1887. In the area, the genus is even the only ochotonid found in Rudabánya (Bernor et al., 2004). However, *E. fontanesi* from Rudabánya is not figured nor described, so this report from the Vallesian still has to be verified.

Remains of central European rooted lagomorphs are rare and scattered (larger collections are available from middle Miocene German fissure fillings but mostly not published (Prieto, 2007)). By contrast, Romanian/Hungarian findings are quite numerous considering that they are distributed in a relatively limited area (seven records in about 2 My). Moreover, their relative abundance in the fossil sample is unusually consistent compared to the percentage observed in western and central European assemblages (CA pers. obs., 2009). For these reasons, rooted lagomorphs from Romania and Hungary are ideal to start a detailed study of *Eurolagus* (in particular of its possible morpho-dimensional variations through time), and to study central-eastern European forms of “*Amphilagus*”, comparing them with central European ones.

Genus *Alloptox* Dawson, 1961

Alloptox is an early-middle Miocene genus, distributed from Anatolia to Japan, and recently also reported in the middle Miocene of northern Africa and of central and eastern Europe (see references in Angelone and Hír, 2012). The westernmost Eurasian record of the genus is *A. katinkae* from the Hungarian locality Litke 2 (Angelone and Hír, 2012). *Alloptox katinkae* shows some very peculiar characters compared to its congeners; it lived in a wooded and wet environment and probably was a continental endemic, raising interesting palaeobiogeographical scenarios at the regional scale.

Genus *Prolagus* Pomel, 1853

The genus *Prolagus* appeared in the early part of the MN2 of Switzerland (references in Mennecart et al., 2016) and expanded rapidly in western and central Europe. Thanks to favourable palaeogeographical conditions, *Prolagus* continued to expand its distribution area after the early Miocene, colonizing eastern Europe and Anatolia. At present, and concerning our study area, middle Miocene *Prolagus* are only known from the Romanian locality Comănești 1 (*P. oeningensis* König, 1825; neither described nor figured). It is also reported from the late Miocene of Comănești 2 (Feru et al., 1980). In Hungary, *Prolagus* is recorded for the first time in the early Badenian (Litke 2; JH pers. data). Other occurrences are available from the late Sarmatian of Felsőtárkány-Felnémet 2/3 and 2/7 (Hír, 2006). The Hungarian middle Miocene populations are ascribed to *P. oeningensis*, a species that, in the current taxonomy, dominates European and Anatolian middle Miocene. However, Prieto et al. (2012b) and Angelone et al. (2014) noted a longitudinal gradient in the dental morphology of *P. oeningensis* in the late middle Miocene of Europe, and hypothesize a possible “drift” in the evolution of *Prolagus*. Indeed, recent studies on late Miocene *Prolagus* from Hungary and Austria demonstrate an uncommonly high lagomorph palaeobiodiversity in this limited area, as a result of palaeoprovinciality/endemism and probable

delayed evolutionary rate in the genus in those areas (Angelone and Čermák, 2015; Angelone and Veitschegger, 2015). A revision of the middle Miocene *Prolagus* from Romania and Hungary is thus of primary importance for the understanding of the role of isolation and faunal relationships at the end of the middle Miocene.

4.3. Order Eulipotyphla Waddell, Okada and Hasegawa, 1999

Family ERINACEIDAE Fischer, 1814

Genus *Parasorex* von Meyer, 1865

Originally assigned by Hír and Mészáros (2002) to *Galerix* sp., the species from Sámsonháza 3 was classified as *Parasorex* sp. by Prieto et al. (2012a; see also comments on the taxonomic assignments of the Galericipini therein). The species is mainly characterized by a p4 with paralophid, M1 and M2 with long posterior arm of the metaconule and only slightly S-shaped mesostyle. It has been recently also recognized in Hasznos (Prieto et al., 2015) and similar forms are also present in Litke (JP pers. observation).

Genus *Schizogalerix* Engesser, 1980

Schizogalerix first appears in Mátraszőlös (as *S. anatolica* Engesser, 1980 in Gál et al., 1999) and is a common element of the faunas from the Felsőtárkány basin. Indeed, Galericipini had been earlier reported from the former basin and Kretzoi (1954) even defined *G. ehiki* based on this material. Zijlstra and Flynn (2015) suspect that the species should be better ascribed to *Schizogalerix*, which is in accordance with our own observations of the new fossil material. This species has an evolutionary stage close to that of *S. voesendorfensis* (Rabeder, 1973) (as *S. voesendorfensis* in Prieto et al., 2014b, herein as *S. cf. voesendorfensis*), but a detailed study is needed to confirm its affinities. Rzebiak-Kowalska (2005) recognized *Parasorex socialis* von Meyer, 1865 in Comănești 1 based on the listing of Feru et al. (1980). The material has never been described nor figured. The same holds true for *Parasorex cf. socialis* from Comănești 2, an assemblage in need of detailed study.

?*Galerix* Pomel, 1848

Besides *Parasorex* sp., the fauna from Litke has delivered a p4 without paralophid, indicating thus the presence of *Galerix* in the sample. On the other hand, a recent study dealing with interesting Pakistani forms underlines the variability of this characteristic (Zijlstra and Flynn, 2015). Pending of a detailed description/comparison of the Hungarian specimens, the presence of the genus is tentatively accepted herein. In addition to *G. ehiki* mentioned above, another galericipini has its type locality in the studied area. *Galerix hipparionum* from Csákvár (late Vallesian, Kretzoi, 1954) is considered, correctly in our opinion, as *Lantanoherium* by Zijlstra and Flynn (2015) awaiting for re-evaluation of the scarce specimens. The best record of the genus derives from Bozovici borehole #1266 (154.70–155.15 m). Codrea (2001) describes a few isolated teeth of *G. aff. symeonidisi* Doukas, 1986. As important taxonomic characteristic, the damaged

p4 bears a strong paraconid and metaconid, as in the *Galerix* p4 from Litke, but a low ridge connects them. In contrast to [Codrea \(2001\)](#), we consider herein the figured damaged P3 ([Codrea, 2001](#): plate 1: figs. 6 and 7) as P4, and, inversely, the P4 as P3 ([Codrea, 2001](#): plate 1: figs. 8 and 9). Both have two lingual cusps. On the upper molars, the mesostyle is undivided and almost straight. Regarding the proposed correlation of the layer(s) (middle to late Badenian), *Parasorex*-like species are expected in view of the Hungarian record. Considering that no data are available at present for Subpiatră, and the taxonomic problems regarding the *Galericini*, it is best to assign the specimens to cf. *Parasorex* sp.

Genus *Lantanotherium* Filhol, 1888

The medium-sized *Lantanotherium sansaniense* Lartet, 1851 vel *L. longirostre* Thenius, 1949 has been described from Sámsonháza 3 and Hasznos ([Prieto et al., 2012a](#); [Prieto et al., 2015](#)). The genus is also known from Tauț, where it is a dominant component of the fauna ([Feru et al., 1979](#); not described) and Rudabánya (*L. sanmigueli* Villalta and Crusafont, 1944, [Ziegler, 2005a](#)). Unpublished material is also available from Litke (J.P., pers. data).

Erinaceinae gen. et sp. indet.

Spiny hedgehogs are rare as a whole in the studied area. Only *Postpalerinaceus* sp. from Rudabánya ([Ziegler, 2005a](#)) and *Amphechinus* sp. from Tauț ([Feru et al., 1979](#)) have been reported. The taxonomy of the subfamily is difficult, even at the genus level ([Ziegler, 2005b](#)). For this reason, the large-sized species from Hasznos and Sámsonháza 3 stays in open nomenclature ([Prieto et al., 2012a, 2015](#)). *Mioechinus* sp. from Sámsonháza ([Hír and Mészáros, 2002](#)) is here referred to *Lantanotherium*. The material collected in Litke has not yet been published (JP pers. data).

Family SORICIDAE Fischer, 1814

Genus *Dinosorex* Engesser, 1972

Whether the Heterosoricinae deserve their own family or not does not meet at present full unanimity (see [Klietmann et al., 2015](#) and references therein). It is clearly out of the scope of this paper to conclude on this subject, and *Dinosorex* is considered herein as a Soricidae.

Apart from *Dinosorex engesseri* Rabeder, 1998 from Rudabánya ([Ziegler, 2005a](#)) and a single and very questionable fragmentary *Dinosorex* tooth from Sümeg ([Kretzoi, 1982](#); [Mészáros, 1996](#)), which are all from upper Miocene deposits, only *D. zapfei* Engesser, 1975 is known from Bogata, represented by a fragmentary mandible with m1–m3. Given the taxonomic problems related to the genus at the end of the middle Miocene (e.g., [Furió et al., 2015](#)), an assignment to *Dinosorex* sp. is preferred for the specimen. *Dinosorex* fossils are at present only available from the Felsőtárkány basin (JP, pers. data). [Gál et al. \(1999\)](#) recognized one M1 of *D. cf. zapfei* in Mátraszőlös 1. Our own observations do not confirm the presence of the genus there.

Soricidae gen. et sp. indet. 1

The relatively large-sized shrew species that is recorded in Sámsonháza 3 and Hasznos is characterized by the oblique cristid that does not connect to the trigonid ([Prieto et al., 2012a](#); [Prieto et al., 2015](#)). This characteristic is also found in specimens from Litke 1 under study. Because neither the taxonomically important condyle nor the p4 has been recovered from these localities, any assignment of the material is hazardous, even at the subfamily level.

Crocidosoricinae gen. et sp. indet.

The species, present in Sámsonháza 3 and Hasznos, is clearly smaller than the above-mentioned shrew. A fragmentary mandible preserving the p4 in situ allows to confidently assign the fossils to the Crocidosoricinae ([Prieto et al., 2012a, 2015](#)).

cf. *Paenelimnoecus* sp.

This shrew from Sámsonháza was originally assigned to *Paenelimnoecus crouzeli* Baudelot, 1972 ([Hír et al., 1998](#); [Hír and Mészáros, 2002](#)). [Prieto et al. \(2012a\)](#) remark that the dental elements are too large to be assigned to this species, being above the size of all known *Paenelimnoecus* Baudelot, 1972. It is also characterized by the almost lack or high reduction of the entoconid. The assignment of the species to *Hemisorex robustus* Baudelot, 1967 has been discussed by [Prieto et al. \(2012a, 2015\)](#), who did not, at present, recognize this species in Hasznos and Sámsonháza 3. A similar form might be also present in Litke 1 (JP pers. obs.).

Soricidae indet. and unpublished shrews

[Codrea \(2001\)](#) reports one m3 from Bozovici borehole #1266 (158.33–159.00 m). He considers this specimen belongs to *Miosorex*. For not specialized forms, the taxonomy of shrews is very dependant of the completeness of the remains. Therefore, this record is emended herein as Soricidae gen. et sp. indet. In regard to the unpublished shrew fossils from the end of the Badenian and the Sarmatian, our first observations promise very interesting results (see tables in [Prieto et al., 2014b](#)). *Paenelimnoecus* is present, as well as probably *Paenesorex* [Ziegler, 2003](#), a genus currently only recognized in Germany ([Ziegler, 2003](#)). While *Crusafontina* Gibert, 1965 is well known from the early part of the late Miocene, especially in our studied area (e.g., [Mészáros, 1998](#)), older occurrences are rarer (e.g., [Prieto and Van Dam, 2012](#)). As a result, the presence of the genus in the late Sarmatian from Hungary (JP pers. data) is of first importance for the understanding of the Anourosoricini evolution in Europe.

Family TALPIDAE Fischer, 1814

Desmanodon aff. *crocheti* Prieto, 2010 is surprisingly the only talpid recognized in the early and mid Badenian of the studied area (Litke 1 (unpublished), Hasznos and Sámsonháza 3, [Prieto et al., 2012a](#); [Prieto et al., 2015](#)). The species is linked to *D. crocheti* from the late Badenian of Germany and seems to be part of a lineage originating in the east ([Prieto, 2010b](#)). We did not recognize *Desmanodon* Engesser, 1980 in Mátraszőlös, although moles are part of the assemblage. The younger deposits are characterized by much more diverse mole communities, with at least occurrences of the genera *Proscapanus* (Lartet, 1851), *Talpa* Linnaeus, 1758 and *Desmanella* Engesser, 1972.

Family DIMYLIDAE Schlosser, 1887

Genus *Plesiodymylus* Gaillard, 1897

At present the only published material is a single M1 (Hír and Mészáros, 2002; Prieto et al., 2012a) from Sámsonháza 3, but the genus is also present in younger deposits (JP pers. observation).

Genus *Metacordylodon* Schlosser, 1911

Metacordylodon aff. *schlosseri* (Andreae, 1904) is well represented in Rudabánya (Ziegler, 2005a), but related forms have also been reported from Mátraszőlös as *Chainodus* n. sp. (Gál et al., 1999).

4.4. Order Chiroptera Blumenbach, 1799

While Pliocene and Quaternary bats are well known from both Hungary (e.g., Jánossy, 1986; Kormos, 1934; Kretzoi, 1956; Topál, 1974, 1979, 1983, 1989) and Romania (Kormos, 1930a, b; Topál, 1963), most of them from karstic localities, Hungarian fossil bats are very rare for localities older than Pliocene and they have even not been recorded in Romania up to now. The richest upper Miocene fauna is known from Rudabánya (Hungary), where *Eptesicus campanensis* Baudelot, 1972, *Eptesicus* sp. nov. and cf. *Miostrellus risgoviensis* Rachl, 1983 were reported (Bernor et al., 2004). Polgárdi (uppermost Miocene, Hungary) is the type locality of *Plecotus (Corynorhinus) atavus* Topál, 1988, but only a list of the other bat species is provided, including *Rhinolophus* cf. *lissiensis* Mein, 1964, *R. delphinensis* Gaillard, 1899, *Miniopterus* cf. *fossilis* Gaillard, 1899 and *Myotis* ssp. (Topál, 1989). Both above-cited Hungarian sites derive from a karstic environment. Fossil bats from non-karstic sites, e.g., from fluvio-lacustrine deposits, are as a rule very sparse and fragmentary. However, the middle Miocene localities have recently shown that they contain bats (Rosina et al., 2015). Some mandible fragments of two vespertilionid bat species are available from Hasznos (Hungary) in marshy-lagoonal deposits. The preliminary investigations also show the presence of vespertilionid bat remains in the fossil assemblage from Litke 1 (Hungary). Moreover, some remains of molossid bats confirm the presence of the family in Mátraszőlös.

5. The associated large mammal fauna

The association of both small and large mammals is poorly documented in the studied area, and most often the data collected from the literature are based on outdated faunal lists or only partially described material.

Besides the rodent *Anomalomys*, large mammals have been discovered in the borehole Váralja 21, including *Palaeomeryx* sp. (Kordos, 1985).

Regarding the Badenian, Codrea (2001) recognizes a naviculo-cuboid of a small artiodactyl in Bozovici borehole #1266 (158.33–159.00m). Several large mammal taxa have been excavated in Hasznos, but have never been described in detail. Kordos (1981) provides the following list (to be updated): *Dorcatherium* sp., *Palaeomeryx* sp. I–II–III, *Palaeomeryx eminens* von Meyer, 1847 and *Heteroprox elegans* (Lartet, 1837). An indeterminate artiodactyl



Fig. 5. The ruminants from Felsőtárkány. 1. *Micromeryx* sp. from Felsőtárkány 3/2. Left mandible fragment with m1–m2 (embedded in sediment). 2. Cervidae indet. from Felsőtárkány 2/3. Right mandible fragment with alveolus of p2, and p3–p4 + m2–m3.

Fig. 5. Les ruminants de Felsőtárkány. 1. *Micromeryx* sp. de Felsőtárkány 3/2. Fragment de mandibule gauche avec m1–m2 (dans le sédiment). 2. Cervidae indet. de Felsőtárkány 2/3. Fragment de mandibule droite avec alvéole de la p2, et p3–p4 + m2–m3.

occurs also in Sámsonháza (Kordos, 1985). The small mammal bearing layers from Szentendre contain a diverse large mammal assemblage with (to be updated; Kordos, 1985): Suidae indet., *Lagomeryx* seu *Palaeomeryx* sp., *Eocerus* sp. (junior synonym of *Eotragus* Pilgrim, 1839), *Chalicotherium grande* (Lartet, 1851) (belongs nowadays to *Anisodon* Lartet, 1851), *Aceratherium tetractylum* Lartet, 1837 and *Anchitherium aurelianense* (Cuvier, 1825). Hír and Venczel (2005) report on Cervidae indet. and Suidae indet. from Subpiatră 2/1R. Besides *Aceratherium* sp. and *Palaeomeryx* sp. listed by Kordos (1985), a single left m3 of Pecora indet. is now known Mátraszőlös (Appendix 3).

For the Sarmatian localities, Feru et al. (1980) listed two cervids in Comănești 1 and rhinocerotids are known from Tășad (Codrea, 2000). Feru et al. (1979) recognize only cervid remains in Tauș, but a representative fauna is available in the area from Minișu de Sus, including *Deinotherium giganteum* (Kaup, 1829), *Alicornops simorrense* (Lartet, 1851), *Gomphotherium angustidens* (Cuvier, 1817), *Anchitherium aurelianense*, *Dorcatherium crassum* (Lartet, 1839), and *Listriodon splendens* von Meyer, 1846 (e.g., Codrea et al., 2007, Codrea and Ciobanu, 2008). In addition, McNulty et al. (1999) report also a catarrhine tooth. Finally, a fragment of a cervid antler is documented near the section of Bogata (Codrea and Țibuleac, 1999; Țibuleac and Codrea, 1997).

The Felsőtárkány Basin is indeed well-known because of the presence a proximal phalanx of a pliopithecoid (Kordos and Begun, 2003). Kretzoi (1982) recognizes in addition an undetermined proboscidean and a cervid. New ruminant remains have been found, comprising fifteen isolated teeth, two fragmentary mandibles with teeth and one caput mandibulae, five autopodial bones and many little tooth fragments mostly from molars from four layers (Felsőtárkány 1, 2/3, 2/7, 3/2; Fig. 5). Dental remains indicate that the moschid *Micromeryx* Lartet, 1851 (Fig. 5-1) and cervids (Fig. 5-2) are present. No bovids have been

recognized based on teeth, and postcranial material is not diagnostic enough to prove their presence. The recorded moschids are the easternmost occurrence in Europe so far.

6. The associated other tetrapods

6.1. Birds

The fossil bird assemblages of the region are relatively well known (e.g., Kessler, 2014; Kessler and Hír, 2012a, b, Appendix 5). Important data are available for both Badenian and Sarmatian localities (Litke, Subpiatră, Mátraszőlős, Egerszólát, Felsőtárkány, Tășad). Remarkably, the faunas are often rich in specimens, diversified and allowed to recognize numerous new species: the waterfowl *Cygnopetrus neogradensis* is described from Mátraszőlős 3 and Litke 2 (Kessler and Hír, 2009), as well as the shelduck-like *Tadorna minor* in Mátraszőlős 3 (Kessler and Hír, 2012a). The rail *Rallixerex litkensis* is widespread (Litke 2, Felsőtárkány-Felnémet 2/7, Mátraszőlős 1; Kessler and Hír, 2012a). Three larks are defined respectively in Litke 2 (*Galerida cserhatensis*), Mátraszőlős 1 (*Lullula neogradensis*), and Felsőtárkány (*Praealauda hevesensis*) (Kessler and Hír, 2012b). The latter is also the type locality of *Anthus antecedens* (Kessler and Hír, 2012b), while the dipper *Cinclus major*, the thrush *Turdicus minor*, the flycatchers *Muscicapa leganyii*, *Erithacus horisitzkyi* and *Luscinia praeluscinia*, the tree creeper *Certhia janossyi*, the warbler-like *Phylloscopus miocaenicus*, the shrike *Lanius schreteri*, the waxwing *Bombycilla hamori*, the starling *Sturnus kretzoi* and the bunting *Emberiza bartkoi* have their type locality respectively in Litke 2, Mátraszőlős 3, Felsőtárkány-Felnémet 2/3, Mátraszőlős 1, Litke 2, Rudabánya 2, Felsőtárkány, Felsőtárkány-Felnémet, Rudabánya 2 and Litke 2 (Kessler and Hír, 2012b).

6.2. Reptiles and amphibians

Caudates and albanerpetontids

The single record of the land salamander *Parahynobius* sp. (Hynobiidae) is known from the Felsőtárkány 3/10 locality (Venczel and Hír, 2013), which may be considered the first occurrence datum (FOD) for this group in the Pannonian region. At present, with the exception of the genus *Salamandrella* Dybowski, 1870, which has its westernmost distribution in the Ural Mountains, the remaining hynobiids have exclusively an Asiatic distribution.

The peculiar small salamandrid *Salamandrina* sp., or spectacled salamander, was reported from the Felsőtárkány 1 locality. The record of this presently Italian endemic species suggests for a distinctly larger past distribution (Venczel and Hír, 2013).

Among 'true' salamanders, *Salamandra sansaniensis* Lartet, 1851, a large-sized form that closely resembles *S. inframaculata* (Martens, 1885) presently inhabiting the Near East (Sanchiz, 1998), is recorded from the early Badenian locality of Litke (Venczel and Hír, 2015), whereas *S. salamandra* was reported from the latest Sarmatian/?earliest Pannonian of Felsőtárkány 3/10. The other salamander genus, reported as *Mertensiella* cf. *caucasica*

Waga, 1876 (Venczel and Hír, 2013), is known also from Felsőtárkány 3/10.

The most common elements among the newts, in both the older and younger localities, were assigned to the genus *Lissotriton* Bell, 1839 (identified either as *Lissotriton rohysi* Herre, 1955, *L. vulgaris* (Linnaeus, 1758) or *Lissotriton* sp.), which is frequently associated with aquatic habitats. *Triturus marmoratus* (Latreille, 1800), also linked to aquatic habitats, was recorded from two geologically younger localities (Tauț and Felsőtárkány 3/10). *Carpathotriton matraensis* Venczel, 2008, a putatively endemic form for the Pannonian region, was described for the first time from the Mátraszőlős 1 and 2 localities (Venczel, 2008) and later reported from Tauț (Venczel and Știucă, 2008). Extremely high neural spines on the pre-caudal vertebrae of *C. matraensis* suggest that it was a permanent water dweller. In contrast, the genus *Chelotriton* Pomel, 1853 (the remains from Tauț were assigned to *Ch. paradoxus* Pomel, 1853, whereas those from Litke and Sámsoháza to *Chelotriton* sp.) may be associated with terrestrial habitats.

The only record of Allocaudata (as Albanerpetontidae indet.) is from Felsőtárkány 3/10 locality. This enigmatic group of superficially salamander-like Lissamphibia is known from the Middle Jurassic–Pliocene of Laurasia and North Africa (Venczel and Gardner, 2005).

Frogs

The most common elements among the frogs, *Palaeobatrachus* (Tschudi, 1839) and *Pelophylax* Fitzinger, 1843, recorded from both the older and younger localities, were linked to aquatic habitats, whereas *Latonia gigantea* (Lartet, 1851) and *Hyla* sp. preferred periaquatic environments along streams, rivers and in the vicinity of lakes and marshlands. A form closely related to the large-sized discoglossid *Latonia* von Meyer, 1843 is *Discoglossus* Otth, 1837, identified on the basis of angulosplenials from Mátraszőlős 1 and 2 (Venczel, 2004). *Bufotes* cf. *viridis* (Laurenti, 1768), preferring various habitats including drier environments, is recorded from a number of localities (Appendix 4). The spadefoot toads (identified as *Pelobates* cf. *sanchizi* Venczel, 2004 or *Pelobates* sp.) probably preferred open habitats with sandy and non-groundwater-influenced soils (Böhme, 2010), similarly to the recent representatives of the genus that are feet-first burrowing frogs with a nocturnal lifestyle. A sole record of the parsley frog (*Pelodytes* cf. *causicus* Boulenger, 1896), presently having a disjunctive distribution in the Caucasus and Iberia, is known from the Felsőtárkány 2/7 locality (Venczel and Hír, 2013).

Lizards

Among the lizards, the most common elements are the lacertids (identified as *Miolacerta* Roček, 1984, *Lacerta* Linnaeus, 1758, or Lacertidae indet.) and the anguils (assigned taxa are: *Anguis* cf. *fragilis* Linnaeus, 1758, *Ophisaurus* sp., *O. spinari* Klembara, 1979 and *Pseudopus* Merrem, 1820). The geckonids (identified as Geckonidae indet.) are moderately frequent, whereas the scincids (as *Chalcides* cf. *ocellatus* (Forsskål 1775), *Chalcides* sp. and Scincidae indet.) are present in the younger localities only. The single record of the fossorial and limbless worm lizard (*Blanus* cf. *gracilis* Roček, 1984) is known from the locality of Tauț (Venczel

and Ştiucă, 2008). The thermophilous agamids (as *Agama* sp.) and *Varanus* Merrem, 1820 are recorded from the older localities only (Appendix 4).

Snakes

The primitive group Scolecophidia is present in at least eight localities, whereas the Boidae are only represented by members of Erycinae in the studied localities (as *Eryx* sp. in Litke and *Albaneryx volynicus* Zerova, 1989 in Felsőtárkány 2 locality). Older localities, such as Litke, yielded more ancient representatives of colubrid snakes (e.g., *Texasophis* sp., *Neonatrix crassa* Rage and Holman, 1984 and *Coluber* cf. *caspioides* Szyndlar and Scheich, 1993), whereas the younger localities were dominated by modern colubrids (e.g., *Natrix rudabanyaensis* Szyndlar, 2005, “*Coluber*” *poucheti* (Rochebrune, 1880), *Hierophis hungaricus* Bolkaý, 1913). The Mátraszölös 1 and 2 localities yielded the first putative member of the genus *Zamenis* Wagler, 1830 (Gál et al., 1999; Gál et al., 2000). The assignment of the latter is based on the fact that the hypapophyses of the cervical vertebrae have an anteroventral orientation, a feature observed only in some egg-eating colubrids (e.g., *Dasypeltis* Wagler, 1830 and *Elaphe* Wagler, 1833). In species of *Coluber* Linnaeus, 1758, such a morphological character has never been observed (Szyndlar, 2005). The first record of *Coronella* Laurenti, 1768 (as *C. mio-caenica* Venczel, 1998) is known from Tauţ (Venczel and Ştiucă, 2008). Small-sized Elapidae, resembling the North-American genus *Micrurus* Wagler, 1824 (reported as *M. gallicus* Rage and Hofman, 1984 or Elapidae indet.), were recorded on the basis of presacral vertebrae only. *Macrovipera* sp., from the “Oriental vipers” group is known from Tauţ and Vârciorog localities, whereas the vipers from the “*Vipera aspis*” (Linnaeus, 1758) group are known from Mátraszölös 3, Subpiatră 2/1 and Felsőtárkány 2/3; The first occurrence of the “*V. berus*” (Linnaeus, 1758) group in central Europe is reported from Felsőtárkány (1, 2 and 3/10 localities) (Venczel, 2011; Venczel and Hír, 2013).

Crocodylians

Some early and middle Badenian localities from northern regions (Sámsonháza 3) of Hungary and few middle to late Badenian (Subpiatră 2/1 and 2/2) and early Sarmatian (Tăşad, Vârciorog) localities from western Romania yielded remains of crocodylians, probably belonging to the genus *Diplocynodon* Pomel, 1847. The above distribution suggests that a north–south thermal gradient was already present during the Badenian (Böhme, 2003) and even strengthened during the early Sarmatian.

Turtles and tortoises

While chelonians are not rare in the fossil localities, representing even the majority of the finds in some, like in Hasznos (*Testudo* sp. in Kordos, 1981), little attention has been paid to their taxonomy. *Testudo* sp. is also recorded in Szentendre (Kordos, 1985). Vremir et al. (1997) describe well-preserved specimens of *Trionyx stiriacus* Peters, 1855 from Minişu de Sus (Romania, Arad County).

7. Conclusions

As shown above and thanks to the intensive fieldwork carried out the last decades, a representative vertebrate collection from the Carpathian area is now available to

science, and the taxonomy is discussed and updated in this work. The time covered by the localities (early Badenian–?earliest Pannonian) is the theatre of drastic changes in the terrestrial communities at large scale (e.g., Casanovas-Vilar et al., 2016; García-Paredes et al., 2016; Hír et al., 2016 and references therein). Thus, the geographic position of the studied area is of primary importance to document the faunal migrations between Europe/Asia minor. In particular, the late Sarmatian fossil sites, abundantly represented in Hungary and Romania, is extremely poorly documented elsewhere. Thus, the vertebrate assemblages provide a rare window into the continental palaeoecosystems and environmental conditions at the critical time of end of the middle Miocene (see details in Hír et al., 2016).

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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.2016.11.006>.

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