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Middle and Late Miocene Terrestrial Vertebrate Localities and Paleoenvironments in the Pannonian Basin

by

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Abstract

The Pannonian Basin, surrounded by the Carpathians, Alps and Dinarides, has long been known as a sedimentary catchment area rich in information on the environmental and biological evolution of Central Europe in the Miocene. We present here the results of an integrative study using GIS to synthesize the findings from our last three years of survey and excavation of new terrestrial vertebrate fossil localities of Miocene age, together with the most recent paleogeographic reconstructions of the region and published faunal and environmental data, with the purpose of presenting a revised, comprehensive history of the paleogeography and paleobiogeography of the Pannonian Basin. We also present a preliminary description of changes in faunal diversity over time in response to paleoenvironmental fluctuations.

Our results indicate that between the late Sarmatian (12 Ma) and early to mid Pannonian (9.5 Ma), terrestrial localities are confined to the margins of the basin system and areas of high topographic relief due to a gradual transgression and associated increase in areal extent of Lake Pannon. Following the dramatic contraction of the lake in the Late Miocene between 9.5 and 9.0 Ma, the fossil localities migrate towards the basin interior; possibly indicating faunal tracking of brackish to freshwater lake shoreline habitats. The large mammal faunas known from the Pannonian Basin are well represented in the more northerly regions of the basin system. Incomplete sampling of faunas underestimates generic diversity during MN 7/8, MN 10 and MN 12. Faunal diversity appears to decline after MN 9; however this is significantly influenced by a corresponding decrease in the number of localities during these temporal intervals. We discuss the clearly documented faunal turnover in the Pannonian Basin that occurs at the time of the 'Vallesian Crisis,' in addition to the paleoenvironmental evidence for the location and timing of potential corridors for faunal interchange.

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Kurzfassung

Das Pannonische Becken, umgeben von den Karpaten, Alpen und Dinariden, ist schon lange bekannt für seinen Sedimentreichtum und für seine Informationen bezüglich der Umweltentwicklung und der biologischen Evolution in Zentraleuropa im Miozän. Wir präsentieren hier die Resultate einer integrativen Studie, die unter Verwendung von GIS die miozänen terrestrischen Funde aus Aufsammlungen und Grabungen der letzte drei Jahre zusammenfasst, mit der Absicht eine revidierte, verständliche Geschichte der Paläogeo- und Paläobiogeographie des Pannonischen Beckens zu präsentieren. Weiters stellen wir eine vorläufige Beschreibung der Veränderung der Faunendiversität im Zusammenhang mit den paläoökologischen Fluktuationen vor.

Unsere Ergebnisse lassen vermuten, dass zwischen dem Obersarmat (12 Mill.) und dem frühen bis mittleren Pannon (9,5 Mill.), terrestrische Lokalitäten auf den Rand des Beckensystems und auf Gebiete mit einem höheren topographischen Relief, wegen einer graduellen Transgression und damit verbunden Ausbreitung des pannonischen Sees, beschränkt waren. Nach dem dramatischen Verkleinern des Sees im oberen Miozän, (9,5 bis 9 Mill.) verlagerten sich die Fossillokalitäten Richtung Beckeninneren. Damit kann man möglicherweise den Wechsel von brackischen zu limnischen Uferhabitaten verfolgen. Die aus dem Pannonischen Becken stammenden Großsäugerfaunen sind eher aus der nördlichen Region des Beckens bekannt. Unvollständige Aufsammlungen der Faunen führen zu einer Unterschätzung der Diversität in MN 7/8, MN10 und MN12. Die Diversität scheint in MN9 abzunehmen, allerdings geht dies mit einem Rückgang in der Zahl der Lokalitäten in diesem Zeitintervall einher. Wir diskutieren den deutlich dokumentierten „faunal

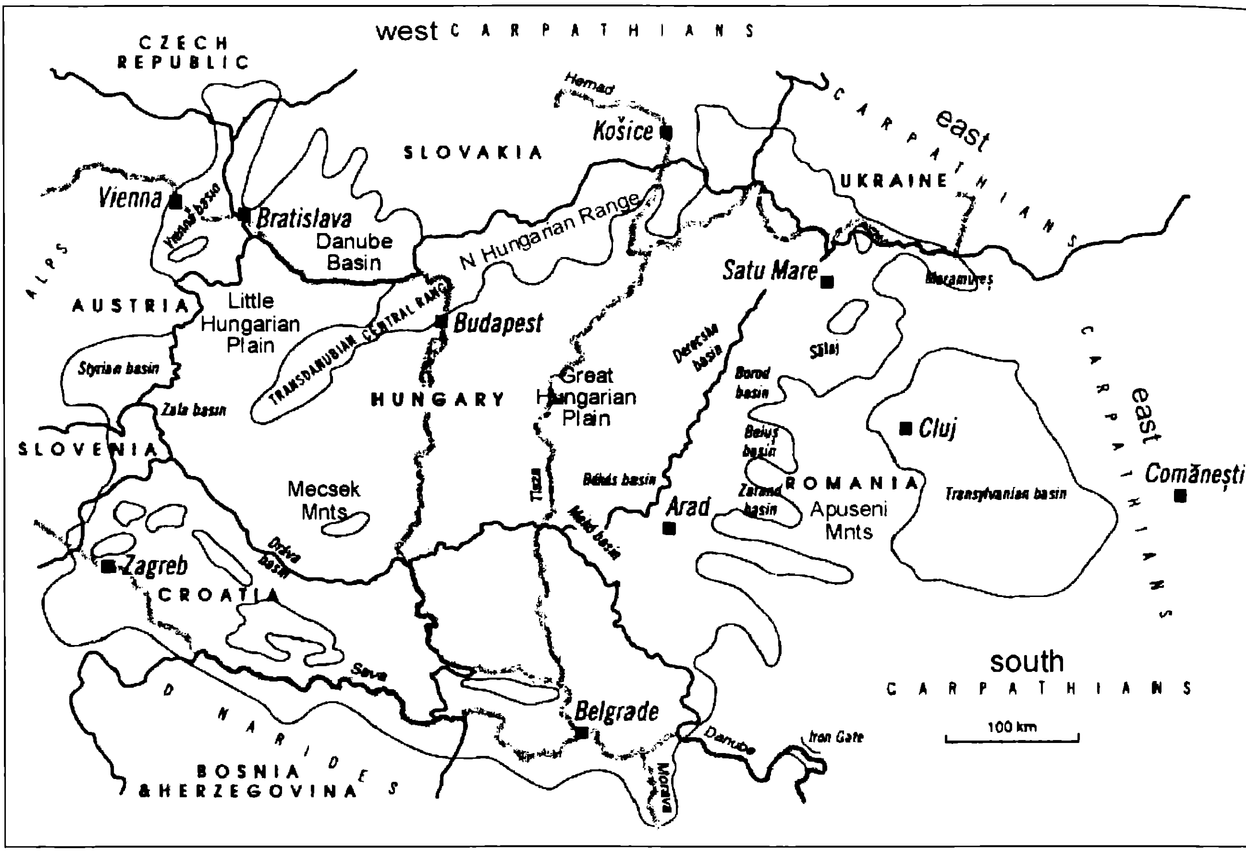

Figure 1: The Pannonian Basin. Caption: modified from MAGYAR et al. (1999).

turnover" in der vallesischen Krise, zusammen mit den paläoökologischen Belegen für die Lokalitäten und potentiellen Korridoren für einen Faunenaustausch.

1. Introduction

Located within the Alpine mountain belt of Central Europe, the Pannonian Basin is almost completely encircled by the Southern and Eastern Alps to the west, the Carpathian arc to the north, east and southeast and the Dinarides to the south. The Pannonian Basin is generally considered to be a Middle Miocene Mediterranean back-arc extensional basin (HORVÁTH, 1988), composed of a series of smaller, deep sub-basins (including the Vienna, Danube and Transylvanian Basins, Fig. 1) separated by relatively shallow basement blocks. The formation of the isolated Lake Pannon occurred at approximately 12 Ma, and by 2.4 Ma, the Pannonian Basin was completely filled with terrestrial sediments covering an area of approximately 250,000 km² across central Europe (KÁZMÉR, 1990).

Diachronous Neogene sedimentation in the Pannonian Basin occurred during the final stages of thrusting and folding in the outer parts of the Carpathians (ROYDEN & HORVÁTH, 1988). Clastic supply was derived from the uplifting Alps and Carpathians, with southerly sediment transport occurring from the north, west and east towards the centre of the Pannonian Basin (KÁZMÉR, 1990). BÉRCZI et al.'s (1988) study of Neogene sedimentation in Hungary concluded that the five basal Miocene stages each represent a transgressive-regressive cycle (i.e., Eggenburgian, Ottnangian, Karpatian, lower Badenian and upper Badenian/Sarmatian). Following the isolation of Lake Pannon from the Paratethys due to the final uplift of the East Carpathians and/or regression during the Upper Badenian to Sarmatian (between approximately 14 and 12 Ma), the lake then experienced a gradual transgressive phase (until 9.5 Ma) followed by a terminal regression during the Late Miocene (MAGYAR et al., 1999). Complete infilling of the Pannonian Basin system due to post-rift delta progradation began in the northwesterly Vienna Basin, and proceeded southeasterly during the Late Miocene and Pliocene, with the deep basins of the Pannonian being formed more basinward during the transgression than the Sarmatian basins (MAGYAR et al., 1999). A wide variety of sedimentary environments were established at the lake margins, consisting of shallow lacustrine, swamp and fluvial sandstone, mudstone and lignite facies.

During this period of intense tectonic activity in the Miocene, the Pannonian Basin also experienced significant biotic change. Mammalian taxonomic diversity was high but fluctuated during the Middle and Late Miocene. Primates are especially diverse compared to other regions. Hominoid, pliopithecoid and cercopithecoid primates known from the Pannonian Basin include *Griphopithecus darwini*, *Pliopithecus platyodon*, *Pliopithecus antiquus*, *Pliopithecus* sp., Crouzelidae indet., *Epipliopithecus vindobonensis*, *Dryopithecus fontani* and *Dryopithecus brancoi*, *Anapithecus hernyaki* and *Anapithecus* sp., *Mesopithecus pentelicus*, and *Dolichopithecus* and *Macaca* in the Pliocene (see BEGUN et al., 2006).

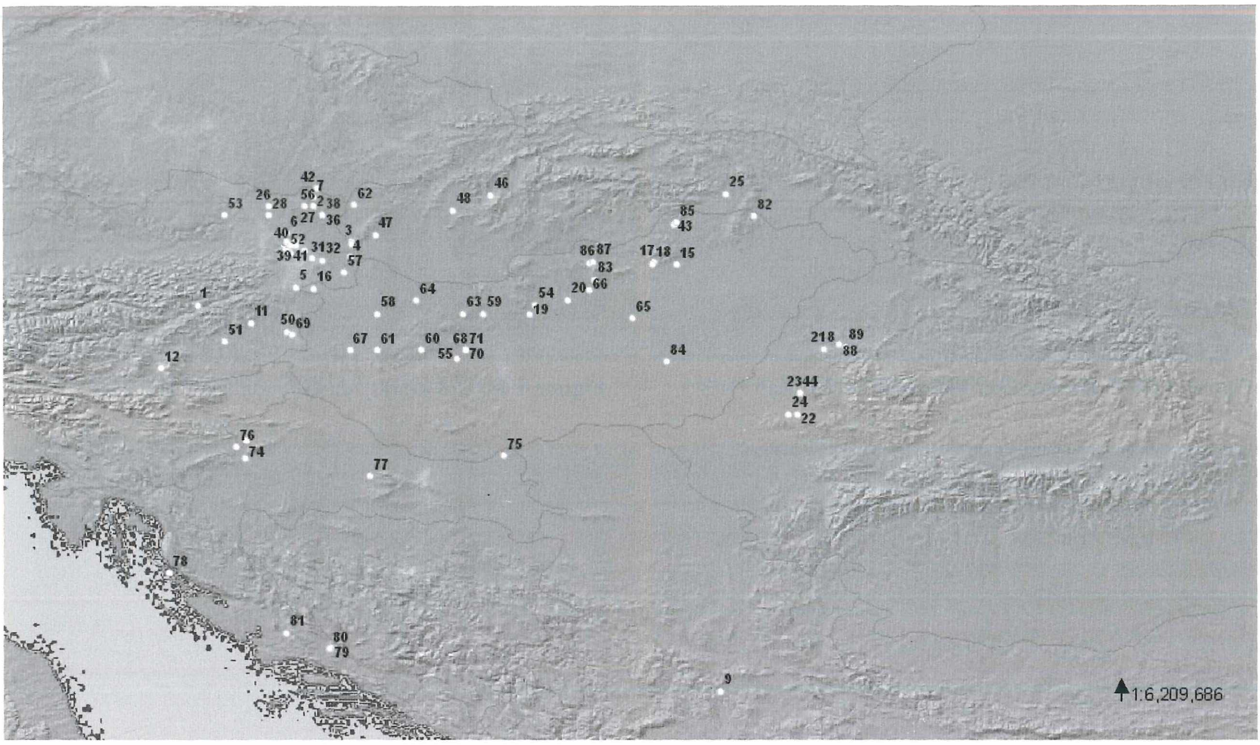

Figure 2: Total distribution of our sample of Middle and Late Miocene terrestrial vertebrate localities in the Pannonian Basin. Numbers represent localities listed in Appendix 1. Our localities are concentrated in Austria and Hungary, but also occur less frequently and in significantly lower numbers in the Czech Republic, Slovakia, Croatia, Romania, Serbia and Bosnia.

We present here the results of an integrative study, providing a detailed and up-to-date paleogeographic and paleobiogeographic history of the Pannonian Basin. We have surveyed and excavated new and previously studied localities in Hungary, Romania and Croatia for the past three years (2003-2005). Our primary focus involves combining new and previously published paleontological and environmental data using GIS technology to describe the complex interrelationship between the spatio-temporal distribution of terrestrial vertebrate localities and the paleoenvironmental flux that is known to have occurred in the Middle and Late Miocene. Here, GIS are invaluable and have great potential in their ability not only to map, but also to store, manipulate and recognize patterns in multiple complex data types across two (x, y), three (z) and four (time) dimensional space (BURROUGH & MCDONNELL, 1998). We also present a preliminary account of changes in faunal diversity over time in response to fluctuations in paleoenvironment.

2. Materials and Methods

To conduct a basin-wide analysis of locality distribution and faunal dynamics in the Middle and Late Miocene, we amassed a sample of 89 fossil vertebrate localities in the Pannonian Basin using the results of our survey effort, together with localities included in the NOW Database (downloaded 17 October, 2005, FORTELIUS, 2005). These localities sample a temporal duration of approximately ten million years, from 15.2 to 4.9 Ma (Appendix 1) and most are dated using the MN system (MEIN, 1975, 1989, 1999). Faunal lists for several of our new and/or re-excavated localities (ie., Felsőtárkány, Hungary; Subpiatră, Romania) are available from the NOW Database.

New and previously known localities were plotted according to their geographic coordinates (Appendix 1), using ArcGIS 9.1 (ESRI 2005) to create distributions per MN zone map layers of our total locality sample. These layers were added to a world topographic basemap (ESRI 2004). Following FORTELIUS et al. (2003), we used modern geographic references (i.e., country boundaries) as neutral landmarks. Temporal data and associated faunal lists were included in a relational database, which we queried for the spatial distribution of localities and taxa within each MN zone. We added the resulting distribution maps to our topographic basemap as individual map layers. From these maps, we describe the locality distributions by MN zone within the context of the geological evolution of the Pannonian Basin. Localities lacking temporal control were excluded.

We used the paleogeographic reconstructions of Lake Pannon published by MAGYAR et al. (1999) for seven consecutive time slices (13.5 Ma, 12.0 Ma, 10.8 Ma, 9.5 Ma, 9.0 Ma, 8.0 Ma and 6.5 Ma) to assess locality distribution in response to fluctuations in the lake system. The lake reconstructions were digitized as polygon shapefiles in *ArcGIS* and converted to map overlays, which were added to the corresponding locality distribution by MN zone map layer. MAGYAR et al. (1999) constructed this map series using the biostratigraphic distribution of sublittoral molluscs and outcrop descriptions from sample localities, together with drill core logs, seismic sections, geological maps and previous paleogeographic maps. In

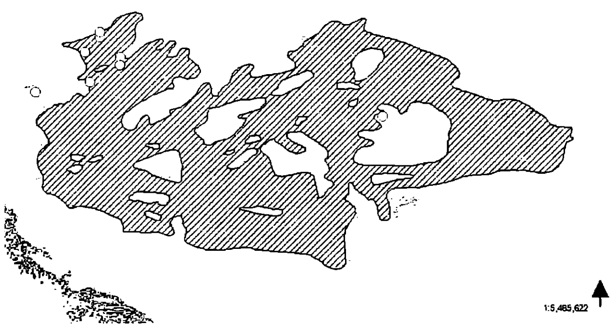

Figure 3: MN6 locality distribution (15.2-12.5 Ma).

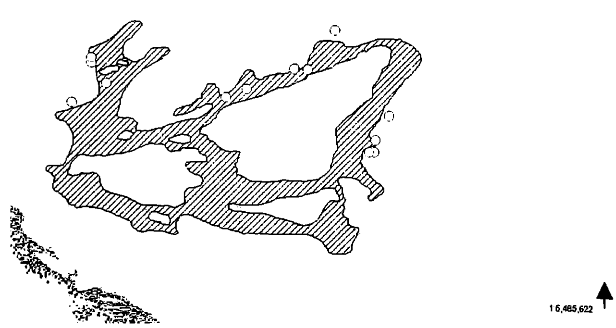

Figure 4: MN7/8 locality distribution (12.5-11.2 Ma).

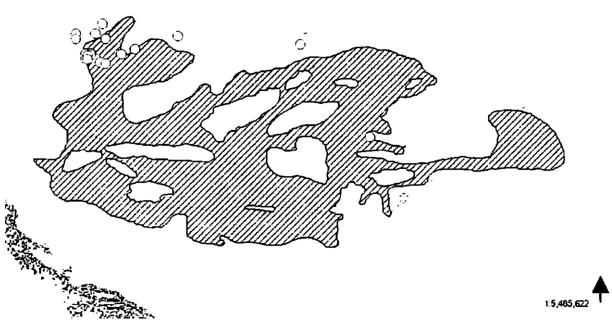

Figure 5: MN9 locality distribution (11.2-9.7 Ma).

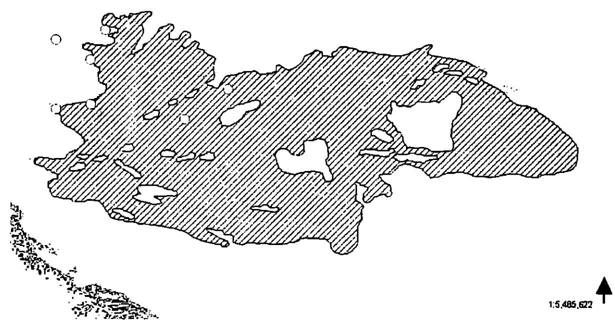

Figure 6: MN10 locality distribution (9.7-8.7 Ma) at 9.5 Ma.

areas where no data points exist, the shorelines have been fitted to the basin margins (MAGYAR et al., 1999). These maps were created on the basis of marine, rather than terrestrial data, and as such do not take into account the presence of known terrestrial localities (MAGYAR, pers. comm.). We also calculated surface area of each lake extent to provide a *relative* indication of transgressions and regressions of Lake Pannon. Since the MAGYAR et al. (1999) reconstructions begin at 13.5 Ma, we focus on Miocene localities within and after MN 6. This time interval coincides with the appearance of primates in the Pannonian Basin. We implemented the less conservative faunal completeness index (*CI*) of KRAUSE & MAAS (1990) and MAAS et al. (1995) over successive temporal intervals to obtain a preliminary assessment of the relative completeness of the Pannonian Basin faunas. *CI* is calculated using the following formula:

$$CI = [N/(N_t + N_{rt})] \times 100$$

Where N = total number of genera known for an interval (here, MN unit) and N_{rt} is the number of range-through taxa (MAAS et al., 1995). This index assumes that if genera are known from before and after a given interval, any absence during the interval (range-through) is due to differential preservation or collecting bias (MAAS et al., 1995). Intervals where the *CI* is below the arbitrary cutoff of 70 are considered to be poorly sampled, whereas indices approaching 100 are considered to be relatively well sampled (MAAS et al., 1995). We then calculated species diversity over time within the Pannonian Basin, bearing in mind sampling completeness.

3. Results

Figures 2-10 illustrate the distribution of Middle and Late Miocene terrestrial vertebrate localities in the Pannonian Basin from 15.2 Ma (base of MN 6) to 4.9 Ma (top of MN 13). Figure 11 illustrates the paleoenvironmental context of these fossil localities in terms of their tectonic, volcanic, sedimentological and environmental setting.

MN 6 (15.2 -12.5 Ma)

Localities dated to within this time interval cluster in the northwestern area of the Pannonian Basin (i.e., the Vienna Basin), together with isolated localities known from the Eastern Alps, the northern Apuseni Mountains in Romania and the northeastern Dinarides on the southern basin margin in Serbia (Fig. 3). The majority of localities in this interval are situated on or adjacent to the 13.5 Ma position of the lake margin derived from MAGYAR et al.'s (1999) paleogeographic reconstructions of the intra-Carpathian extension of the Paratethys. Of note is the presence of 'floating' localities (terrestrial localities falling within the lake margins) in the Vienna Basin and Little Hungarian Plain, which correlate with a deep marine paleoenvironmental setting that would be unsuitable for preservation of terrestrial fossil material (Fig. 11). The isolated localities are all attributed to a 'highland' paleoenvironment.

MN 7/8 (12.5 – 11.2 Ma)

The temporal interval defined by MN 7/8 corresponds with MAGYAR et al.'s (1999) paleogeographic reconstruction of Lake Pannonian margin at approximately 12.0 Ma. The

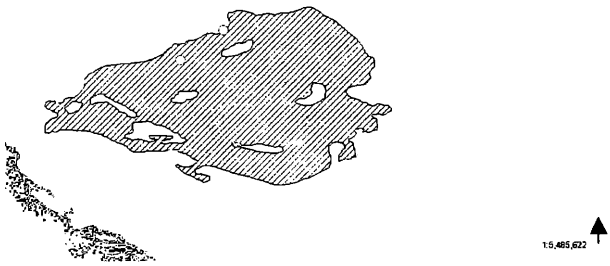

Figure 7: MN10 locality distribution (9.7-8.7 Ma).

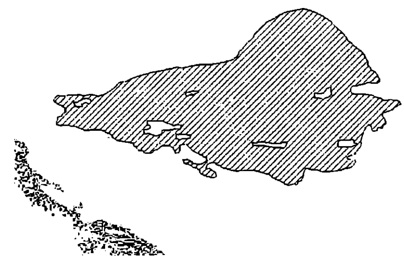

Figure 8: MN11 locality distribution (8.7-8.0 Ma).

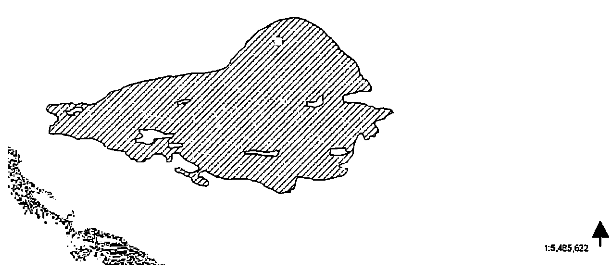

Figure 9: MN12 locality distribution (8.0-6.6 Ma).

Figure 10: MN13 locality distribution (6.6-4.9 Ma).

distribution of localities during this interval occur in the northwest and west of the Pannonian Basin (i.e., the Vienna and Styrian Basins and the Little Hungarian Plain), but also in the North Hungarian Range and Apuseni Mountains of Romania (Fig. 4). The relative number of localities has increased from MN 6 to MN 7/8, and as before they are situated immediately adjacent to the reconstructed position of the lake margin (with the exception of three 'floating' localities). During MN 7/8, Lake Pannon experiences a marked regression (Fig. 11) that resulted in the formation of narrow water corridors separated by large, low-lying islands.

MN 9 (11.2 – 9.7 Ma)
The temporal duration of MN 9 corresponds to MAGYAR et al.'s (1999) 10.8 Ma paleogeographic reconstruction of Lake Pannon. Localities during this interval cluster in the Vienna Basin, with additional occurrences in the Danube Basin (in the Slovakian Carpathians), the North Hungarian Range and the central Apuseni Mountains of Romania (Fig. 5). The localities again are situated immediately adjacent to or near the lake margin, however 'floating' localities are especially prevalent in the southern Vienna Basin area during this time interval. An increase in lake areal extent following isolation from the Paratethys (Fig. 11) results in the reconstruction of highland or shallow, brackish lacustrine paleoenvironments in the majority of the sub-basin systems of the Pannonian Basin.

MN 10 (9.7 – 8.7 Ma)
Figures 6 and 7 illustrate the distribution of localities assigned to MN 10, together with the reduction in the number of localities in comparison to earlier intervals. Localities are known from the Vienna and Styrian Basins, and in proximity to the Transdanubian Central Range in Hungary. During this time interval, MAGYAR et al.'s (1999) lake reconstructions document a dramatic regression between 9.5 Ma (fig. 6) and 9.0 Ma (Fig. 7). It is likely that due to the proximity of the northwestern localities to the reconstructed lake margin in Figure 6, they represent early MN 10 shoreline habitats, with the central localities indicating a late MN 10 shoreline adjacent to the Transdanubian Central Range. The MN 10 maps also document the initiation of a southeasterly shift in distribution of localities from the margin to the interior of the Pannonian Basin associated with final Neogene lake regression (Fig. 11).

MN 11 and MN 12 (8.7 – 6.6 Ma)
The temporal intervals defined by both MN 11 (Fig. 8) and MN 12 (Fig. 9) both coincide with MAGYAR et al.'s (1999) paleogeographic reconstruction of Lake Pannon at 8.0 Ma. During both of these intervals, the number of localities continues to decline. MN 11 localities are known from lowland environments (Fig. 11) in the Vienna Basin of Austria and Slovakia, and in proximity to the Transdanubian Central Range of Hungary. MN 12 localities remain in proximity to the Transdanubian Central Range, with one other 'floating' locality situated more centrally in the basin south of the elevated highland of the North Hungarian Range.

MN 13 (6.6 – 4.9 Ma)
The temporal duration of MN 13 corresponds with MAGYAR et al.'s (1999) 6.5 Ma paleogeographic reconstruction of Lake Pannon. Localities occurring during MN 13 are

again located centrally, in the lowland of the Transdanubian Central Range and in proximity to the freshwater lacustrine paleoenvironment of the Little Hungarian Plain to the west (Figs. 10, 11).

4. Discussion and Conclusions

Locality Distribution in the Pannonian Basin

The uneven distribution of terrestrial vertebrate localities in the Pannonian Basin is related to a number of factors. The intensity of research has varied over the region, and suitable outcrops are also unevenly distributed. However, the large number of localities in the north and northwest of the Pannonian Basin system can be explained by frequent fluctuations in shoreline movement throughout the history of Lake Pannon (attributed to minor climatic fluctuations or localized tectonics, Fig. 11). Due to these fluctuations, a wide variety of sedimentary environments were established at the northern lake margins including shallow lacustrine, swamp and fluvial sandstone, mudstone and lignite facies. These facies are more suitable for preserving faunal and floral material, compared to those of the southern margin, which remained in a relatively fixed position on the northern flanks of the Dinarides. Unlike the north, clastic and freshwater input was relatively low in the southern lake due to the prevailing carbonate-dominated terrain surrounding the lake margins.

From MN 6 to MN 10 (Figs. 3-7), terrestrial vertebrate localities in our sample are restricted to reconstructed lakeshore environments located on the margins of the Pannonian Basin, or to areas of higher topographic relief in response to the large areal extent of Lake Pannon. During the early period of this interval (i.e., MN 6, Fig. 3), renewed thrusting in the outer Carpathians resulted in the opening of the extensional Pannonian back-arc system, with the deepest Badenian marine depocentres developing in the central basin areas, i.e., Great Hungarian Plain (east of the Apuseni Mountains), and the Sava and Drava Basins to north of the Dinarides (Popov et al., 2004). Differential and rapid (Hámor, 2001) subsidence in the Badenian resulted in a continued, but fragmented increase in accommodation space for marine deposition, with shallow water basin margin limestones interfingering with hemipelagic mudstones. The late Badenian regression (at approximately 13.5 Ma, Fig. 11) was controlled by further basement movement and volcanism, resulting in the formation of brackish water, lagoonal and lignitic facies on the basin margins and islands (in the Mecsek and Bakony mountains – Bérczi et al., 1988; Hámor, 2001; Popov et al., 2004). It is interesting to note that despite the potential facies type suitability in these latter areas, no known fossil localities have been found in these regions to date.

The Sarmatian (corresponding to MN 7/8) is traditionally defined as a brackish sequence between the fully marine sediments of the Badenian and the brackish to freshwater Pannonian deposits (Trunkó, 1996). This transition is due the uplifting Carpathians causing the isolation of the lake from the Eastern Paratethys and Indopacific realms (Kázmér, 1990). The palaeoenvironmental and salinity reconstructions in figure 11 highlight this transition, with freshwater inflow from southerly flowing rivers now considered to be greater than the rate of evaporation (Kázmér, 1990). Salinity data has been estimated by many authors using marine fauna, with values falling from the Badenian fully marine environments of 30-50‰ to 15-20‰ at the Sarmatian/Pannonian boundary (e.g., Kázmér, 1990 – but see Piller & Harzhauser, 2005 for an alternate view).

The thickness and facies of Sarmatian sediments can be described in relation to the basin types that existed within the Pannonian Basin at this time (see the MN 7/8 map, Fig. 4). The small, narrow back-arc basins located close to the emergent Carpathian thrust front rapidly subsided and were filled by deep-water facies during the Sarmatian. The central Pannonian Basin (e.g., the present day elevated areas of the Transdanubian Central Range, North Hungarian Range and Apuseni Mountains) were covered by a shallow, brackish lake. The littoral carbonate and clastic facies deposited in the lake in these regions indicate the presence of numerous islands (Popov et al., 2004).

At approximately 12.0 Ma (Fig. 4), a regression and decrease in water areal extent marked the formation of Lake Pannon (Magyar et al., 1999). The extent of this regression is uncertain, and the driving forces have been tentatively linked to either compression within the Carpathians and basin updoming (tectonics) or a major global sea level fall (eustasy). During this initial regressive interval of the lake, the northern shoreline comprised a delta plain environment (suitable for fossil preservation) with a strong fluvial influence and a freshwater mollusc faunal assemblage in the shallows (Magyar et al., 1999). Our localities are adjacent to the reconstructed lakeshore, and situated in present-day regions of elevated topography. It further remains to explain the anomalous absence of MN 7/8 localities adjacent to the island margins (Fig. 4). The low-lying islands may have been subjected to repeated submersion by variations in the shallow lake water level, thus making them unsuitable for prolonged habitation by terrestrial vertebrates, or that sediments of suitable age have not yet been uplifted in these present day flat areas of Central Europe.

The observed migration of our localities towards the basin interior between MN 10 and MN 13 (Figs. 6-10) is indicative of lakeshore 'tracking' by the Pannonian Basin vertebrate fauna, and is essentially explained by analysing the paleogeographical and environmental changes occurring in the basin from 9.5 Ma onwards. Following a gradual transgression, where the central basin area was flooded to its greatest extent at approximately 9.5 Ma during MN 10 (Fig. 6), Lake Pannon started to fill by southerly delta progradation from the northwest (initiated in the Sarmatian) and northeast (initiated later by approximately 9.5 Ma) – see Magyar et al. (1999). By approximately 9.0 Ma (Fig. 7), Lake Pannon had dramatically shrunk to half its former areal extent, and suitable vertebrate habitats had migrated towards the centre of the basin.

Between 9.5 and 8.5 Ma (Magyar et al., 1999; Popov et al., 2004), the northeastern basins, including the Vienna Basin, were completely infilled by deltaic sediments and much of

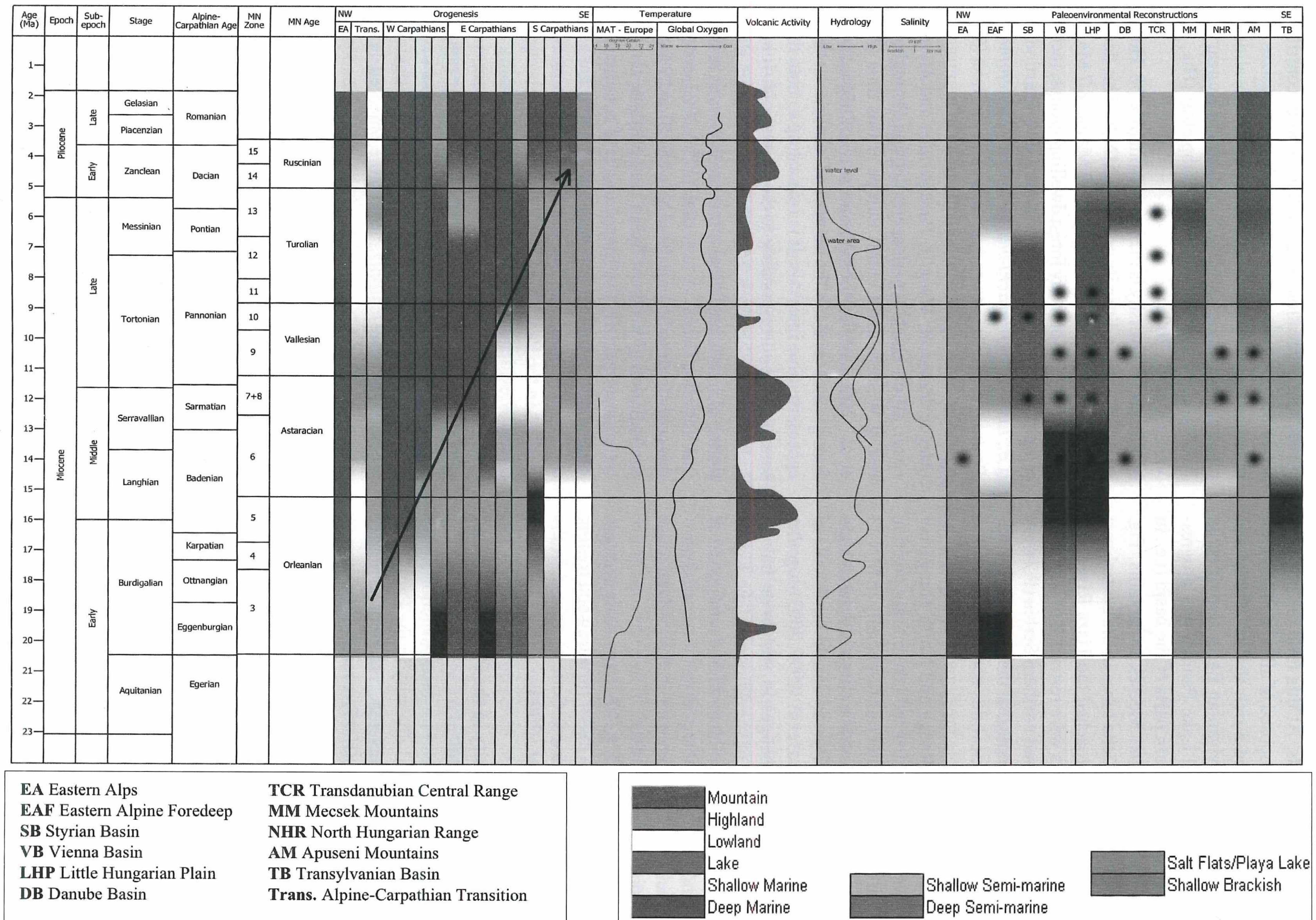

Figure 11: Pannonian Basin Paleoenvironments. Arrow represents uplift of the Carpathian arc from northwest to southeast during the Neogene, and black circles represent general distribution of vertebrate fossil localities within the Pannonian Basin.

Timescale: AGUSTÍ et al. (2001), BÖHME (2003), GRADSTEIN et al. (2004), HÍR (2004), NAGYMAROSY & MÜLLER (1988), STEININGER (1999), STEININGER et al. (1988, 1996) **Orogenesis**: POPOV et al. (2004), ROYDEN (1988), **Temperature**: BÖHME (2003), ZACHOS et al. (2001) **Volcanic Activity**: HAMOR (1995), NAGYMAROSY & MÜLLER (1988) **Water Level**: NAGYMAROSY & MÜLLER (1988) **Water Area**: MAGYAR et al. (1999), POPOV et al. (2004) **Salinity**: KÁZMÉR (1990) **Paleoenvironmental Reconstructions**: POPOV et al. (2004)

the Pannonian Basin was now characterized by 'lowland' alluvial plain and shallow, freshwater lacustrine/paludal environments (Fig. 11). The presence of these freshwater lakes during MN 11, especially on the Little Hungarian Plain, may explain the anomalous clustering of vertebrate localities (e.g., Mönchhof and Nyárád) in this area to the northwest of the lake margin. Apart from a brief transgression at approximately 8.0 Ma (at the end of MN 11), the terminal regression of the lake occurred in the late Pannonian from 9.0 Ma onwards. At this time the northern shoreline was essentially composed of alluvial plains with a strong fluvial influence and a rich shallow, freshwater molluscan fauna. The Transylvanian Basin also dried up during this time period, and Lake Pannon was progressively restricted to the southern parts of the basin (i.e., in the region of the Apuseni and Mecsek Mountains, Fig. 11) from MN 12 to MN 13. Delta lobes in the central part of the Pannonian Basin approached the Tisza River, and deep lacustrine environments were restricted to southeast Hungary, northeast Croatia and northern Serbia (Popov et al., 2004). It is interesting to note that the general distribution of MN 12 and MN 13 localities corresponds well to the present day linearly elevated regions of Hungary (i.e., the Transdanubian Central Range and North Hungarian Range), but not to the reconstructed lake margin position as observed in earlier time intervals (especially in MN 13 - Fig. 10). This may be explained by climatic deterioration (i.e., an increase in seasonality and deciduous woodland cover in elevated areas – Agustí et al., 1999, 2003), together with associated potential changes in vertebrate habitat preference towards the end of the Miocene. The higher topographic regions may also have offered a refuge from the intense and highly variable sedimentary and hydrological regimes that were dominant in the lowland areas as the Pannonian Basin 'filled up'.

During the latest Miocene (Fig. 10), large scale tectonic reorganization, together with major thrusting and folding (uplifting the south Carpathians) came to an end in the Pannonian realm (Popov et al., 2004).

Mammalian Faunal Diversity in the Pannonian Basin – A Preliminary Description

Another goal of this research is a reconstruction of the evolution of vertebrate faunal diversity in the Pannonian Basin. Application of the completeness index of Krause & Maas (1990) and Maas et al. (1995) reveals some interesting findings, which require caution in their application to measures of diversity. The *CI* is influenced in our study by generic richness and also often by the number of localities in each sampling interval (MN zone). For instance, several intervals exhibit relatively incomplete sampling, including MN 7/8, MN 10 and MN 12 (Table 1). In each case, relative incompleteness is due to the very low number of genera, coupled with a higher number of range-through taxa. In the cases of MN 10 and MN 12, faunal incompleteness is also due to a low number of localities. Conversely, the relative completeness of faunas seen in MN 6 is largely influenced by the presence of rich localities (i.e., Göriach, Neudorf-Spalte), that are few in number. The very high index in MN 13 (100) should be considered with caution, since very few faunas exist on either side of this interval from which to determine the number of range-through taxa.

The large mammal faunas in the Pannonian Basin demonstrate a peak in diversity in MN 6 (Fig. 12). However, there is a sharp decline in the number of species in MN 7/8. This corresponds with the relative incompleteness of generic sampling during this interval, where diversity is certainly being underestimated. The results from our survey and excavations suggest that another contributing factor may be a sampling strategy that emphasizes small mammal recovery almost exclusively at new localities and renewed excavations at MN7/8 localities in Hungary (i.e., Felsőtárkány) and Romania (i.e., Subpiatră) (Hír, 2004; Venczel et al., 2005).

MN 9 species diversity is increased from MN 7/8. However a second crash in diversity occurs in MN 10. This decrease in large mammal faunas between 9.7 Ma and 8.7 Ma is due to the extinction of many forest dwelling groups, including pliopithecoid and hominoid primates, several artiodactyls (i.e., *Listriodon, Parachleuastochoerus, Lartetotherium, Protragocerus, Amphiprox*), several carnivore taxa (*Sansanosmilus* and *Amphicyon*), and many small mammal taxa (*Megacricetodon, Myoglis, Paraglirulus* and *Miopetaurista*), all of which experience extinction throughout the rest of Western and Central Europe at this time (Agustí et al., 2003, 1997, 1999; Vislobokova, 2005). Another factor is a decrease in the number of localities at this and successive time intervals. It is interesting to note that the time interval corresponding to the dramatic shrinkage of Lake Pannon (between 9.5 and 9 Ma) coincides with the timing of significant faunal turnovers that occur in Europe (the Vallesian Crisis). Agustí et al. (1999, 2003) recognize this crisis from sediments dated between 10 and 9 Ma from the Vallesian of northern Spain, and attribute the faunal turnovers (especially the disappearance of hominoids from Europe) to a geographically widespread floral change from evergreen to deciduous forests. Although turnover is also obvious in the Pannonian Basin faunas, there is currently a lack of evidence as to the precise synchronicity of the crisis between these two separate geographic areas. More importantly, the question of what effect did the rapid lake shrinkage have on climate in the Pannonian Basin (being almost fully encircled by mountains) and on vegetational replacement or re-colonization of the emerged land requires attention.

Species diversity increases in MN 11 due to an influx after MN 10 of larger bodied, more open country taxa (i.e., the suid *Microstonyx*, carnivores *Indarctos, Adcrocuta, Paramachaerodus*, the bovid *Tragoportax* which persists pre- and post Vallesian Crisis, and the rodent taxa *Progonomys* and *Cricetulodon*) and drops to 0 in MN 12, due to an absence of large mammal localities at this time. In MN 13, species diversity is again increased. Despite the instances of incomplete generic sampling which coincide with low species diversity, there is an overall trend towards a decrease in large mammal diversity through time. However, this is again due to a diminishing number of localities after MN 9.

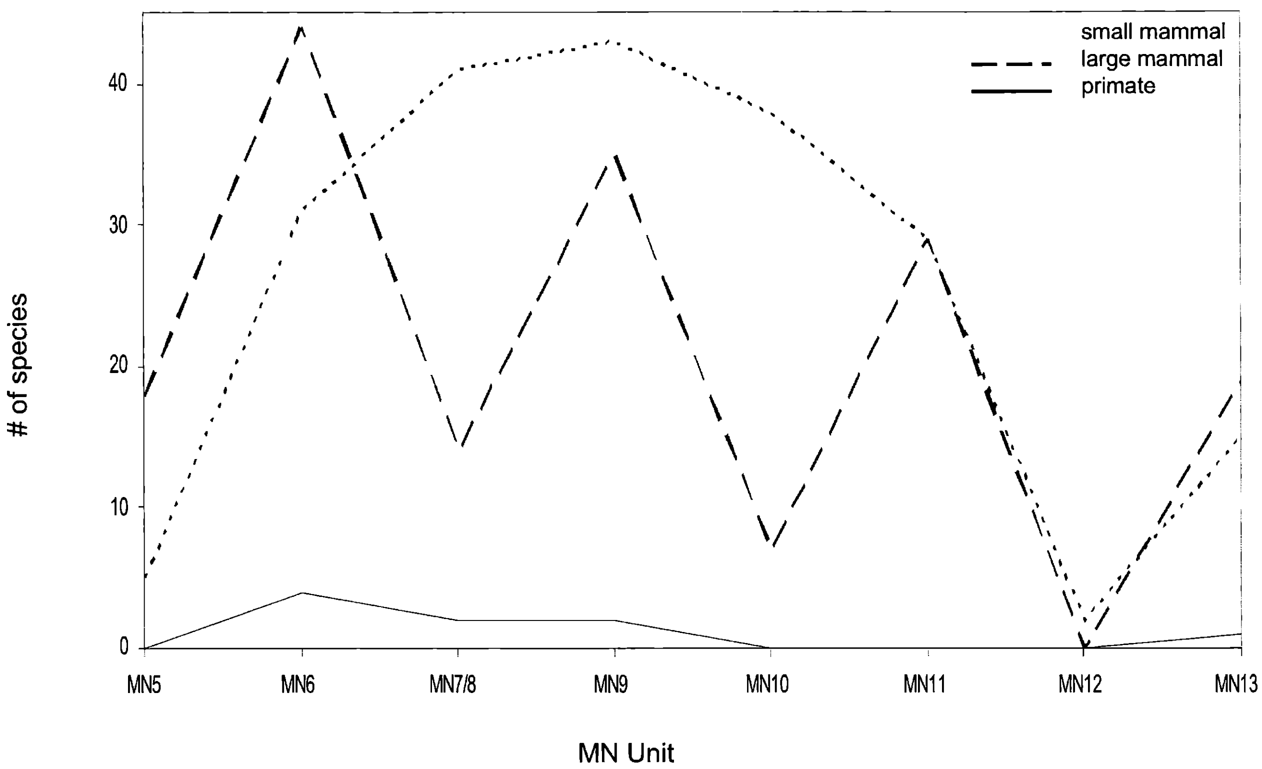

Figure 12: Mammal diversity in the Pannonian Basin.

Lake Margin Reconstructions – New Insights

Our sample includes a number of localities lacking temporal control, which were excluded from our analysis (Appendix 1). However, several of these localities are located towards the interior of the basin and it is plausible that these represent later Miocene or Early Pliocene localities when Lake Pannon was diminishing in its extent. Alternatively, these localities could represent areas of subareal exposure during varying phases of Lake Pannon. Whatever the case, the occurrence of these localities provides testable hypotheses that could clarify and further define lake margin boundaries or islands within the lake margins.

During several of our intervals, localities occurred within the margins of Lake Pannon. While most probably due to a culmination of factors, we consider several reasons here. First, as mentioned previously, the lake reconstructions are based on marine rather than terrestrial data. In unsampled areas, the lake extent has been fitted to the basin margins (MAGYAR et al., 1999). Unsampled regions correspond to those having higher incidence of localities falling within the lake margins, such as the Vienna Basin, and may not be providing an accurate reconstruction of paleoshorelines in these areas. Secondly, our localities are dated using a biochronologic system, which places fauna within intervals of time based on their first and last appearances. These intervals range between 700 Ka and 2.7 Ma, while the paleogeographic lake extents are reconstructed at specific time periods, i.e., 9.5 Ma, 9.0 Ma. We consider it plausible that the temporal intervals defined by the MN system lack the resolution to capture fluctuations in lake extent and hence the occurrence of localities within the lake margins may be due in part to temporal discrepancies. However, for some time intervals significant changes in water level occurred in specific areas of the basin system, which are not depicted in MAGYAR et al.'s (1999) reconstructions. For example, according to MAGYAR (pers. comm.), Lake Pannon had entirely withdrawn from the Vienna Basin by 9.5 Ma, but is not represented as such in their reconstruction for that time period. MAGYAR (pers. comm.) also notes that his reconstructions do not account for the shallow transitional zones between purely lacustrine deposits of Lake Pannon and completely terrestrial deposits. For this reason, terrestrial localities may be situated in areas within these transitional zones. One solution to the issue of having localities falling within the lake margins is to integrate our data on the presence of known terrestrial localities into lake reconstructions, such as those of MAGYAR et al. (1999), which rely exclusively on marine data, so as to increase the accuracy of lake reconstructions.

Potential Corridors for Faunal Exchange

Due to its profound influence on basin sedimentation and potential faunal migration pathways, it is perhaps relevant to include a discussion of the evolution of the Carpathian arc in this section. The overall trend of mountain building, due to northeasterly escape driven thrust tectonics, was from northwest to southeast during the Neogene (ROYDEN, 1988; CSONTOS, 1992), following the arc of the present day Carpathians (Fig. 11). The Eastern Alps attained full elevation during the Karpatian and early Badenian, with the Southern Carpathians forming predominantly during the Late Pliocene (ROYDEN, 1988; POPOV et al., 2004). During the late Badenian (i.e., MN 6), orogenic processes severed the marine connection with the Mediterranean, and established a new connection with the Dacic Basin

MN Zone	Temporal Duration (Ma)	N_t	N_{rt}	*CI*	# of Localities/Zone
MN6	15.2 – 12.5	32	1	97	9
MN7/8	12.5 – 11.2	13	8	62	16
MN9	11.2 – 9.7	31	5	86	23
MN10	9.7 – 9.0	7	13	35	7
MN11	9.0 – 8.0	23	5	82	7
MN12	8.0 – 6.6	0	9	0	3
MN13	6.6 – 4.9	17	0	100	6

Table 1: Relative completeness of large mammal faunas in the Pannonian Basin. Caption: N_t - # taxa/MN unit, N_{rt} - # range-through taxa, *CI* – completeness index.

to the southeast. The polyhaline late Badenian marine faunas were highly diverse (including molluscs, corals, red algae, echinoids, ostracods and foraminifera) and were indicative of a cooler climate than in the early Badenian (Popov et al., 2004). The paleogeographic and facies patterns persisted into the early Sarmatian. During the Sarmatian, the area surrounding the eastern extent of the Western Carpathians and much of the Eastern Carpathians was attaining full elevation. There also existed lowland or flooded regions located in the Vienna Basin, west of the uplifted southern extent of the Eastern Carpathians and in the South Carpathians during the Sarmatian and early to middle Pannonian (Fig. 11). These regions potentially provided remnant marine connections for the now almost completely isolated Lake Pannon (Kázmér, 1990). In addition, they provide evidence for potential lowland migration pathways at this time (especially via the Vienna Basin). Although lowland existed immediately west of the Eastern Carpathians (Popov et al., 2004), the presence of recently uplifted mountains and the deep waters of the Carpathian foreland basin to the east may have hindered direct exit of fauna from the Transylvanian Basin at these locations.

Popov et al. (2004) also suggest a possible marine connection extending directly south into the Dacic Basin from the Pannonian Basin in their paleogeographic reconstructions (map 7 – middle Sarmatian). This may have been a potential lowland migration route from the Pannonian Basin for fauna migrating southwards around the interior margin of the Eastern Carpathians. However, we are currently uncertain as to the effectiveness of these southerly migration corridors due to the effects of partially uplifted areas of the South Carpathians, and of the almost permanent position of the southern margin of Lake Pannon (Magyar et al., 1999).

Magyar et al.'s (1999) 9.5 Ma reconstruction marks the greatest areal extent of Lake Pannon. However, as previously mentioned these authors note that towards the end of the *Spiniferites paradoxus* Biochron, the Vienna Basin had dried up. This is significant because terrestrial conditions could have potentially provided a corridor for faunal interchange in and out of the Pannonian Basin.

Future Research

In this study, we present the most recent paleogeographic and paleobiogeographic reconstructions of the paleoenvironments and locality distribution in the Pannonian Basin during the Middle and Late Miocene. Our sample of new localities and their respective faunas, together with previously published data have clarified aspects of the spatial and temporal distribution of terrestrial vertebrate localities and presented a preliminary account of changes in faunal diversity in response to paleoenvironmental change in this region. Importantly, our study has also served to form new ideas and hypotheses about the nature of paleoenvironmental data, and has generated three main areas for future research, which we outline below:

1. Continued survey

We plan to continue our survey in our current survey locations, but are hoping to extend our geographic range. This study has served as a foundation from which to identify areas where vertebrate localities are more likely to be found. It has also highlighted the importance of understanding the palaeoenvironmental change that occurred in the Pannonian Basin during the Miocene. Further work will focus on increasing our knowledge of the interplay between tectonics and sea/lake level changes in the basin, and ultimately how this influenced migration corridors into and out of the basin system.

2. Bioprovincial division of the Pannonian Basin

We also plan to explore in more detail any regional variation in the Pannonian Basin faunas. Fortelius et al. (1996) define two geographic blocks, "East" and "West" in which they compare faunal diversity and dynamics. Interestingly, these blocks subdivide the Pannonian Basin, separating Austria, the Czech Republic and Slovakia in the West, from Hungary, Bosnia and the Ukraine in the East, despite the fact that most of these countries occur within the same basin system. Although the faunas from the northern regions of the basin are better known than those to the south, we are interested in whether any interbasin differences exist to support Fortelius et al.'s (1996) geographic division, or conversely whether the Pannonian Basin faunas are more similar to each other than to faunas occurring outside the basin system. In the case of the latter, this could warrant the definition of a Pannonian faunal bioprovince.

Preliminary comparison of the Pannonian Basin faunas to the West and East blocks of Fortelius et al. (1996) indicate that not surprisingly, the Pannonian Basin faunas experience the same decline in sampling completeness in MN 7/8 and in MN 10, however influenced by Hungarian faunas in MN

11 and MN 12, experience the same respective increase and decrease in diversity as faunas from the East during these time intervals. In terms of diversity, the Middle Miocene Pannonian Basin faunas behave more like faunas in the West, while towards the terminal Miocene the Pannonian Basin faunas behave more like faunas in the East, due to an influx of taxa from the Eastern Mediterranean (VISLOBOKOVA 2005). Further sampling and subsequent analysis of these trends can potentially elucidate aspects of faunal interchange, specifically directionality. We hope that our continued efforts will improve sampling and provide further data with which to analyze these patterns more fully.

3. Primate Evolution

Lastly, a diversity of primates existed in the Pannonian Basin from the Middle Miocene into the Early Pliocene. The Pannonian Basin preserves a continuous record of primates from 15.2 Ma until 9.5 Ma and then after 6.6 Ma, which seems to be relatively unaffected by sampling biases. By examining the environmental tolerances of these primates further, it will be possible to understand the sensitivities of Pannonian hominoids and pliopithecoids that led to their extinction during the Vallesian Crisis.

5. Acknowledgements

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Appendix 1: Terrestrial Vertebrate Fossil Localities in the Pannonian Basin. Caption: * unknown

ID	Locality	Country	MN Zone	Lat (DD)	Long (DD)
1	Göriach	Austria	MN 6	47.5	15.3
2	Klein Hadersdorf	Austria	MN 6	48.599998	16.6
3	Neudorf-Spalte (Devínska Nová Ves)	Austria	MN 6	48.200001	17.016666
4	Neudorf-Sandberg (Devínska Nová Ves)	Austria	MN 6	48.033333	17
5	Walbersdorf	Austria	MN 6	47.700001	16.4
6	Nussdorf (WIEN)	Austria	MN 6	48.299999	16.299999
7	Mikulov	Czech Republic	MN 6	48.700001	16.6
8	Subpiatra 2/1R	Romania	MN 6	47.006667	22.311944
9	Prebreza	Serbia	MN 6	43.189999	21.15
10	Atzgersdorf (WIEN)	Austria	MN 7-8	48.099998	16.299999
11	Schildbach	Austria	MN 7-8	47.299999	15.9
12	St. Stephan im Lavanttal	Austria	MN 7-8	46.799999	14.9
13	Heiligenstadt (WIEN)	Austria	MN 7-8	48.200001	16.299999
14	Türkenschanze (WIEN)	Austria	MN 7-8	48.200001	16.299999
15	Sály	Hungary	MN 7-8	47.95	20.6667
16	Sopron	Hungary	MN 7-8	47.683334	16.6
17	Felsőtárkány	Hungary	MN 7-8	47.976111	20.412778
18	Felsőtárkány -Felnémet	Hungary	MN 7-8	47.955278	20.393889
19	Szentendre	Hungary	MN 7-8	47.400002	19.02
20	Hasznos	Hungary	MN 7-8	47.560001	19.440001
21	Subpiatra 2/2	Romania	MN 7-8	47.006667	22.311944
22	Minisu de Sus	Romania	MN 7-8	46.283333	22.016666
23	Comanesti-1	Romania	MN 7-8	46.516666	22.033333
24	Taut	Romania	MN 7-8	46.28333	21.91667
25	Kosice-Bankov	Slovakia	MN 7-8	48.733334	21.216667
26	Mariathal	Austria	MN 9	48.599998	16.1
27	Mistelbach	Austria	MN 9	48.599998	16.5
28	Oberhollabrunn	Austria	MN 9	48.5	16.1
29	Himberg	Austria	MN 9	48.099998	16.5
30	Wien-Belvedere	Austria	MN 9	48.200001	16.4
31	Götzendorf	Austria	MN 9	48.016666	16.583334
32	Sommerein	Austria	MN 9	48	16.700001
33	Wien 3	Austria	MN 9	48.200001	16.4
34	Wien 10	Austria	MN 9	48.200001	16.4
35	Wien 12	Austria	MN 9	48.200001	16.299999
36	Zistersdorf	Austria	MN 9	48.5	16.700001
37	Vösendorf (WIEN)	Austria	MN 9	48.099998	16.299999
38	Gaiselberg	Austria	MN 9	48.5	16.700001
39	Laaerberg	Austria	MN 9	48.166668	16.4
40	Meidling	Austria	MN 9	48.166668	16.333334
41	Biedermannsdorf	Austria	MN 9	48.083332	16.333334
42	Nikolsburg	Czech Republic	MN 9	48.799999	16.633333
43	Rudabánya	Hungary	MN 9	48.383335	20.633333
44	Comanesti-2	Romania	MN 9	46.516666	22.033333
45	Dubraska hlavica	Slovakia	MN 9	48.183334	17.016666
46	Novaky (Mine Mier)	Slovakia	MN 9	48.716667	18.583334
47	Pezinok	Slovakia	MN 9	48.283333	17.283333
48	Topolcany-Kalvaria	Slovakia	MN 9	48.549999	18.15
49	Poysbrunn	Austria	MN 10	48.700001	16.6
50	Kohfidisch	Austria	MN 10	47.200001	16.299999
51	Lassnitz	Austria	MN 10	47.099998	15.6
52	Eichkogel -upper	Austria	MN 10	48.099998	16.299999
53	Stratzing	Austria	MN 10	48.5	15.6
54	Budapest - Szecheuxi	Hungary	MN 10	47.5	19.083334
55	Balatonszabadi	Hungary	MN 10	46.900002	18.200001

ID	Locality	Country	MN Zone	Lat (DD)	Long (DD)
56	Hauskirchen	Austria	MN 11	48.599998	16.6
57	Mönchhof	Austria	MN 11	47.866665	16.933332
58	Nyárád	Hungary	MN 11	47.400002	17.299999
59	Csakvar	Hungary	MN 11	47.400002	18.5
60	Tihany	Hungary	MN 11	47	17.799999
61	Sümeg	Hungary	MN 11	47	17.299999
62	Borsky Svaty Jur	Slovakia	MN 11	48.616665	17.049999
63	Tardosbánya	Hungary	MN 12	47.400002	18.27
64	Györszentmárton	Hungary	MN 12	47.549999	17.75
65	Jászladány	Hungary	MN 12	47.349998	20.166666
66	Hatvan	Hungary	MN 13	47.666668	19.683332
67	Baltavar	Hungary	MN 13	47	17
68	Polgárdi	Hungary	MN 13	47	18.299999
69	Genesapati	Hungary	MN 13	47.169998	16.360001
70	Polgardi 2	Hungary	MN 13	47	18.299999
71	Polgardi 4	Hungary	MN 13	47	18.299999
72	Veliko Trgovišče	Croatia	*	45.99	15.838611
73	Tudmanov Brijeg (?)	Croatia		45.99	15.838611
74	Podsused - Dolje	Croatia		45.8	15.8333
75	Vlašković	Croatia		45.8178	18.7194
76	Marija Gorica	Croatia		45.9167	15.7333
77	Daruvar	Croatia		45.5905556	17.225
78	Pag	Croatia		44.516944	14.976389
79	Ruda	Croatia		43.676111	16.7825
80	Rudagreb	Croatia		43.668056	16.766389
81	Otavice	Croatia		43.843056	16.278889
82	Füzerradvány	Hungary		48.4833	21.5333
83	Rózsaszentmárton	Hungary		47.7833	19.75
84	Szarvas	Hungary		46.8667	20.55
85	Alsótelekes	Hungary		48.4167	20.6667
86	Mátraszöllös	Hungary		47.9667	19.6833
87	Samsonhaza	Hungary		47.9833	19.7333
88	Grosi	Romania		47.057778	22.484444
89	Luncșoara	Romania		47.030833	22.551111