Updated Miocene mammal biochronology of Slovakia

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Abstract: Revisory studies together with the new research results have made it possible to update our knowledge about the biochronology of terrestrial records from the Miocene epoch in the Slovak territory of the Western Carpathians. Data from more than 30 localities, mainly based on mammalian assemblages, provide an overview of the evolution of terrestrial vertebrate communities in response to climate and environmental changes in the Central Paratethys region (especially in its NW area) for about 12 million years, from the early Miocene (MN3) to the end of this epoch (MN13). Based on the determined faunistic assemblages, local reference localities (LRL) were determined and correlated with MN units. These are as follows: localities in the territory of Devínska Nová Ves (MN6), Borský Svätý Jur (MN9), Pezinok (MN10), Triblavina (MN11), and Šalgovce (MN12). Well-documented paleontological and geological records at sites from the territory of Devínska Nová Ves have also made possible to introduce the name "Devínska Nová Ves" for the local faunal complex, corresponding to the MN6 unit.

Keywords: Mammalia, Vertebrata, Miocene, biochronology, Western Carpathians, Slovakia.

Introduction

Fossils of mammals play the most important role in the biochronology of Cenozoic terrestrial deposits around the world, although fossilized remains of representatives of other vertebrate groups are also significant. In Slovakia, the last contribution focused on the overall biochronology of Neogene based on the mammalian fossil record from 12 sites was published by Sabol et al. in 2004. Since then, new knowledge on the European Cenozoic land mammal biochronology has been obtained (e.g., Abdul Aziz et al. 2007, 2010; Kälin & Kempf 2009; Van der Meulen et al. 2011, 2012; Reichenbacher et al. 2013; Casanovas-Villar et al. 2014) and new sites have been discovered and excavated in the Slovak territory of the Western Carpathians, dated mainly to the late Miocene (e.g., Joniak 2005, 2016; Joniak & Šujan 2020; Joniak et al. 2020).

Mammal finds as a part of vertebrate fossil assemblages are known in Slovakia until from the Miocene. The pre-Miocene fossil record of vertebrates is limited only to a few isolated finds of Mesozoic sharks and bone fishes (Holec et al. 2005b; Chalupová 2009), sauropsid amniotes from the Triassic (Michalík et al. 1976; Michalík & Kundrát 1998; Čerňanský et al. 2018b, 2020) and Jurassic sediments (Čerňanský et al. 2019), the fossil of a pycnodontid actinopterygian from Cretaceous deposits (Gregorová & Brzobohatý *pers. comm.*), Paleogene fish (Holec et al. 2005a), and the find of an upupiform bird from Lower Oligocene sediments (Fulín & Holec 2008; Kundrát et al. 2015).

The first Miocene vertebrate fossils of Slovakia were recorded in the course of sand exploitation at Devínska Nová Ves - Sandberg, including mammal (von Meyer 1845) and reptile remains (Hoernes 1848). Other findings of Miocene vertebrates were subsequently reported from Slovak territory at the second half of the 19th and at beginning of the 20th century (e.g., Petényi 1864; Schlesinger 1922; Pia & Sickenberg 1934). These first records comprised mostly isolated fossil remains of large-sized animals, whereas the first Miocene small mammalian assemblages began to be reported in the literature during the second half of the previous century after the development of screen washing of fossil-bearing sediments. In Slovakia, it is related to the pioneer systematic fieldwork of Oldřich Fejfar in 1960s at Devínska Nová Ves sites (Fejfar 1974). At the turn of the milenium, not only systematic excavations were renewed at Devínska Nová Ves sites (2000-2002; Holec & Sabol 2004), but also many new late Miocene localities were discovered in the Slovak part of the Vienna and Danube Basins, the systematic research of which continues until now (Joniak 2005, 2016; Joniak & Šujan 2020). All these recent excavations were predominantly organized and conducted by the Department of Geology and Paleontology of the Comenius University in Bratislava, often in collaboration with local museums and authorities. Many terrestrial mammalian assemblages (or entire vertebrate

ones, resp.) turned out to be rich in species and provide insight into various paleoecosystems. They also make it possible to identify local reference sites of key importance for the interregional biochronological correlations within the MN system.

The MN system based on the terrestrial record of mammalian remains, suggested by Mein (1975), and later improved by Falhbusch (1976), De Bruijn et al. (1992), Mein (1990, 1999), and Van Dam et al. (2001, 2006), has become the most widely used tool for the biochronological subdivision of the continental Neogene of Europe, western Asia, and northern Africa. Each of 16 MN units valid today is characterized by a reference locality, representing a certain stage of the evolution, migration events and extinction of index taxa (De Bruijn et al. 1992). The MN system has, however, several issues. One of the most important is the fact that it is based mostly on western European mammalian assemblages, which often differ at the species level from those recorded in other regions, including also central and eastern Europe. Another of the arguing points about the MN system is whether to consider the MN subdivisions as units or zones. Van Dam et al. (2001) argue that these should be considered as MN units, because, unlike zones, they exist only within the reference locality itself. Therefore, non-reference localities do not belong to an MN unit but must be correlated to one of them. It is essential to understand that these criteria are not equivalent to define biozones (intervals of geological strata that are defined based on their characteristic fossil taxa), since the same faunas are not present in different regions. This is one of the key points in the discussion of the usefulness of MN zones. The low faunal resemblance and potential diachrony of species across Europe imply that long-distance correlations based on mammal faunas alone cannot be expected to be precise (Van der Meulen et al. 2011, 2012). The MN system, while provides wide paleogeographical range, can only be used for rough interbioprovincial correlations. Single mammalian taxa have limited geographical ranges and their first appearances and last occurrences differ from region to region. On the other hand, a series of local first occurrences gives information on migrations, and therefore are of interregional importance. However, the reference fauna, and the reference locality from which is described, only captures an intermittent series of a certain range in time and space, which does not comprise all taxa of an MN unit. As De Bruijn et al. (1992) argue, MN units are by no means "filled" by their reference faunas. Thus, the discussion on boundaries between these units is excluded, since first and last occurrences are very rarely documented in the reference faunas.

The MN system remains an imperfect, but necessary tool if it is used as a biochronological succession of reference faunas to which the different mammal assemblages can be relatively placed (De Bruijn et al. 1992). Van Dam (2003) proposed the dual system: the use of the low-resolution MN system on continental scale and local biostratigraphy as a regional approach. The MN system is really useful when comparing faunal assemblages of close geographical areas across the European continent. The second major system is the ELMMZ one (European Land Mammal Mega-Zones), discussed and proposed by Steininger (1999). The system is valid in a biostratigraphic context, including well-established and well-defined Neogene units Agenian, Orleanian, Astaracian, Vallesian, Turolian, Ruscinian and Villanyian that are considered as mega-zones.

However, a detailed stratigraphical framework based not only on local biozonation, but also on radiometric analyses and magnetostratigraphy seems to be a much more appropriate tool (Agustí et al. 2001; Abdul Aziz et al. 2010; Van der Meulen et al. 2011; Reichenbacher et al. 2013). In that sense, the fossil record of mammals has been demonstrated to be a very useful tool for dating terrestrial sediments, biogeographical studies and paleoenvironmental reconstructions because of the limited stratigraphic ranges of species and occasional broad geographic distribution.

The relatively rich and well-stratified fossil record of Miocene mammal assemblages from the Slovak territory of the Western Carpathians provides a good basis not only for the local biochronology but also for the future research focused on the phylogenetic studies, diversification, migration routes, and climatic and environmental changes in the Central European realms at least over the last 14 million years of this epoch.

Material and methods

Since MN units are inherently asynchronous and influenced by many phenomena, their absolute ages and definition often varies in various regions (cf. Aragonian type area vs. Bavarian OSM for example). Just to avoid the confusion, we follow predominantly the synthesis by Hilgen et al. (2012).

The updated biochronology of Miocene sites in the Slovak territory of the Western Carpathians is based mainly on the temporal and spatial distribution of mammalian finds, as well as fossils of other vertebrate groups. The obtained taxonomic data from published and unpublished fossil records are correlated with data from reference localities as well as from localities in neighboring regions. No descriptions of new taxa are included, but the taxonomic revision has been realized in many cases.

The substantial part of fossil material used for the biochronological updation is housed in the collections of the Comenius University in Bratislava (Department of Geology and Paleontology, Faculty of Natural Sciences), Slovak National Museum – Natural History Museum in Bratislava (Paleontological Department), National Museum in Prague (Paleontological Department), Hungarian Natural History Museum (Department of Paleontology and Geology) and Mining and Geological Survey of Hungary (Department of Geological and Geophysical Collections) in Budapest, Museum of Natural History in Vienna (Geological-Paleontological Department), and Natural History Museum in Basel (Earth Sciences Department). A smaller part of the fossils stems from local Slovakian Museum in Banská Bystrica, Horná Nitra Museum in Prievidza, Tríbeč Museum in Topoľčany, Nitra Region Museum – Museum in Zlaté Moravce, and East Slovakian Museum in Košice).

The Miocene fossils stem from more than 30 sites (Fig. 1) of varying sample size and fossil richness, collected mostly during systematic field work. Isolated fossil records often stem from a mining or geological prospection. The Miocene mammalian assemblages found in Slovakia often turn out to

be very important concerning species richness, individual numbers, and biostratigraphic and paleoecologic input.

To update the Miocene West Carpathian biochronology based on mammalian and other vertebrate fossils, data from new systematic research were used in connection with a revisory study of former fossil records based on literature data and an overview of museum collections. For localities processed recently, a standard method of small mammals collecting (Daams & Freudenthal 1988) was used together with classic sampling methods of paleontological excavations for the obtaining of large mammal remains (Prantl 1957).



Fig. 1. Slovakian Miocene vertebrate sites referred in the text, dated to the pre-Astaracian (black), Astaracian (red), Vallesian (green), and Turolian (blue). Black dots are local reference localities (LRL, see "Final Summary"). Map sources: **A** — https://commons.wikimedia.org; **B** — Kováč et al. 2017, modified. *Explanatory notes*: 1 – Mučín, 2 – Dolné Plachtince, 3 – Pôtor, 4 – Baňa Dolina, 5 – DNV–Štokeravská vápenka, 6 – DNV–Bonanza, 7 – DNV–Sandberg, 8 – DNV–Waitov lom, 9 – DNV–Glavica, 10 – Dúbravka–Pole, 11 – Rohožník, 12 – Handlová, 13 and 33 – Nováky, 14 – Bánovce nad Bebravou, 15 – Horné Ozorovce, 16 – Svinná, 17 – Košice–Bankov, 18 – Borský Svätý Jur, 19 – Fulianka, 20 – Perín, 21 – Pezinok, 22 – Dubná skala, 23 – Triblavina, 24 – Krásno, 25 – Hrdovická brázda, 26 – Závada, 27 – Šalgovce, 28 – Topoľčany–Kalvária, 29 – Prusy, 30 – Sereď–Šintava, 31 – Madunice, 32 – Veľké Bielice, 34 – Slepčany.

For taxonomic and stratigraphic purposes, the comparison collections of various European museums and scientific institutions were reviewed and published data in scientific papers and documents were also consulted (see Reference list).

Results

Pre-Astaracian fossil record

The earliest finds of Miocene vertebrates are known from **Mučín**. The local exposed marine sediments, dated to the Eggenburgian regional stage (20.43–18.30 Ma *sensu* Kováč et al. 2018), contained a rich elasmobranchian fauna accompanied by isolated remains of cetacean mammals (Holec et al. 1995; Malíková 2019). This site can correspond to the Austrian locality of Maigen that is correlated with the MN3 unit (Daxner-Höck & Höck 2015). Based on plant fossil remains from coeval coal-bearing sediments of Bukovinka Fm. in the Novohrad Basin, the climate in the West Carpathian realm during this epoch was generally arid and hot (Vass et al. 1999), with short warm and humid intervals (Jablonszky 1914; Rásky 1959; Němejc 1967; Němejc & Knobloch 1973; Hably 1985; Sitár & Kvaček 1997).

However, the earliest terrestrial fossil record of early Miocene vertebrates (reptiles and mammals) is known only from the sediments of the Ottnangian stage (18.30-17.30 Ma according to Kováč et al. 2018 sensu Piller et al. 2007). This very rare record is bound to coal seams of Salgótarján Fm. in the Novohrad Basin and so far, it has been documented only from three sites - Dolné Plachtince (Tóth 2010), Pôtor (Vass 1983) and Baňa Dolina coal mine near Veľký Krtíš (Holec 1982; Čerňanský et al. 2012b). In addition to reptile fossils (e.g., Trionyx sp. and Diplocynodon sp.), the mammalian record includes remains of proboscideans (Prodeinotherium cuvieri and Gomphotherium sylvaticum), sirens, artiodactyls (Eotragus sp.), and perissodactyls (probably aceratheriine rhinos). The sampling for small mammals from the Baňa Dolina coal mine yielded only very scarce remains of glirids, talpids and small-sized vespertilionid bats that are currently under study.

The common occurrence of the determined gomphotherid and deinotheriid (Göhlich 1999; Gasparik 2001; Koufos et al. 2003; Gasparik & Markov 2009) make it possible to correlate all these Ottnangian sites with the upper portion of the MN3 (*sensu* Hilgen et al. 2012) or MN4 unit (*sensu* Mein 1999, Steininger 1999, Harzhauser & Piller 2007). This is also supported by abovementioned fossils of the earliest bovid *Eotragus* (Vass 1983), which appeared in Europe at about 18.0 mya (Gentry et al. 1999). Based on that, the age of Dolné Plachtince, Pôtor, and Baňa Dolina coal mine is probably similar to that of Central European sites, such as Oberdorf in Austria (Daxner-Höck & Höck 2015), Dolnice 1 and 2 in Bohemia (Fejfar 1990), Bełchatów C in Poland (Kowalski 1997), or Zagyvapálfalva in Hungary (Gasparik 2001). Animals lived in wet habitat with swamps spread on large alluvial plains (Vass et al. 1999). The climate was humid as documented from plant fossil record, where representatives of Taxodiaceae and Myricaceae dominated (Planderová in Vass et al. 1979).

Early Astaracian fossil record (MN6)

The Astaracian MN6 unit is well documented in Slovakia thanks to the rich fossil record from sites situated at slopes of Devínska Kobyla hill in the vicinity of Devínska Nová Ves (DNV) village (in former literature also known as Neudorf an dem March or Dévényújfalu), nowadays a suburban part of the capital city of Bratislava (Buday et al. 1964; Cicha et al. 1972; Fejfar 1974; Sabol & Holec 2002). From several sites described in this area, DNV-Štokeravská vápenka, DNV-Bonanza, and DNV-Sandberg (Fig. 2) play a key role in understanding the biostratigraphy of the Badenian regional stage (15.97-12.70 Ma; see Kováč et al. 2018: p. 288). Additionally, a faunal succession from early to late Badenian is well documented from fossiliferous deposits of these sites (Sabol & Kováč 2006). Whereas DNV-Štokeravská vápenka (=Neudorf an dem March - die Spaltenfüllung or Zapfe's Fissures) is a site with terrestrial fossil record, vertebrate remains from DNV-Sandberg (=Theben Neudorf) have been found in marine environment. DNV-Bonanza connects both these sites by record on gradual transition from terrestrial to marine conditions.

The succession is also well documented in karst fissure fillings of DNV–Štokeravská vápenka site on the 2nd floor of this abandoned limestone quarry where rusty clay sediments with the terrestrial fossil record are covered by late Badenian transgressive sands. These sandy sediments also form the littoral facies of the Studienka Formation (Sandberg Mb.; Baráth et al. 1994) at nearby DNV–Sandberg site (Hyžný et al. 2012) and were dated by geochronological methods. Sr-ages obtained from ⁸⁷Sr/⁸⁶Sr isotopic ratios in the invertebrate shells from the site profile and converted to SIS numerical scale in range from 13.79 Ma to 12.76 Ma, confirmed their late Badenian age (Fordinál et al. 2014), with a possible overlapping until the late early Badenian as well as the early Sarmatian.

The faunal finds from DNV-Štokeravská vápenka (Holec & Sabol 1996, 2004; Sabol & Holec 2002), although originally mentioned by Zapfe (1949) from several horizons (A-D), most likely form a temporarily uniform assemblage that is somewhat older than the assemblage from DNV-Sandberg. It was dated to various time periods, from 16.5 Ma (Aguilar et al. 1997) through 16.4-15.0 (Sabol 2000) to 15.0-14.0 (Holec & Emry 2001), or it was considered to be younger than 14.9 Ma respectively, corresponding with the paleomagnetic chron C5ADr (14.6-14.8 Ma) (Daxner-Höck et al. 2004). However, despite some contributions that occasionally included the site to the uppermost MN5 (e.g., Kordos 2000), the faunal composition of the DNV-Štokeravská vápenka fossil assemblage unambiguously supports its assignment to MN6 unit (Fejfar 1974; Aguilar et al. 1997). The attribution of DNV-Štokeravská vápenka fossil assemblage to



Fig. 2. Early Astaracian sites at slopes of the Devínska kobyla Hill near Bratislava. *Explanatory notes*: A — Location map of three most important Devínska Nová Ves sites; B — DNV–Štokeravská vápenka; C — DNV–Bonanza; D — DNV–Sandberg; E — Paleogeography of the Central Paratethys during the late Langhian – base of the Serravallian (Early Badenian) with the assumed position of DNV–Štokeravská vápenka site (ŠV); F — Paleogeography of the Central Paratethys during the Serravallian (Late Badenian) with the assumed position of DNV–Sandberg (S); E and F according to Kováč et al. 2017 (AF – Alpine Foredeep, CWC – Central Western Carpathians, NS – Nowy Sącz piggy-back Basin, OWC – Outer Western Carpathians, TRC – Transdanubian High). Photos: M. Sabol.

MN6 unit is mainly supported by the occurrence of more advanced platacanthomyine cricetid Neocometes brunonis (Schaub & Zapfe 1953; Fejfar 1974, 1999) and anomalomyid Anomalomys gaudryi (Fejfar 1972; Bolliger 1999) as well as glirid, eomyid, and sciurid taxa similar to those from Sansan (Aguilar et al. 1997) together with several taxa of insectivores and carnivores (Peigné & Sen 2012), on the basis of which O. Fejfar introduced the term "Die Faunen-Gruppe Neudorf-Sansan (NS)" (in Cicha et al. 1972). On the other hand, the presence of different species of Democricetodon (D. vindobonensis) or Pliopithecus (P. vindobonensis) can indicate an "endemic condition" of the faunal assemblage in comparison to the contemporaneous assemblages in western Europe and their occurrence can be related to the early phase of the Astaracian migration waves or to the peninsular to insular environment of the area during the mid-middle Miocene. The DNV-Štokeravská vápenka faunal assemblage (Suppl. Table S1) consists so far of ten taxa of amphibians (Herre 1955; Wettstein-Westersheimb 1955; Špinar 1972, 1975; Hodrová 1980), ten taxa of reptiles (Wettstein-Westersheimb 1955; Estes 1969; Klembara 1986; Szyndlar 1991; Ivanov 1998; Čerňanský et al. 2018a), five taxa of birds (Mlíkovský 1996, 2004), two or three proboscidean species (Zapfe 1954; Schmidt 1969a, b; Tóth 2010), one primate (Zapfe 1952, 1958, 1962; Zapfe & Hürzeler 1957), at least 19 taxa of rodents (Schaub & Zapfe 1953; Fejfar 1974, 1999) and 16 taxa of insectivores (Zapfe 1951; Engesser 1975; Fejfar & Sabol 2005, 2009; Hugueney et al. 2012), six taxa of bats (Zapfe 1950b), nine taxa of carnivores (Zapfe 1950a; Sabol 2000), seven taxa of artiodactyls (Zapfe 1983, 1993) and at least three taxa of perissodactyls (Zapfe 1976, 1979; Zervanová 2014; Valentová 2018), which lived in the subtropical karst environment (Sabol & Kováč 2006). The site is also a type locality for several species (Euleptes klembarai, Pliopithecus vindobonensis, Keramidomys carpathicus, Eumyarion weinfurteri, E. latior, Democricetodon vindobonensis, Neocometes brunonis, Dinosorex zapfei, Viretia gracilidens, Plesiodimylus similis, Paleptesicus priscus, or Miniopterus fossilis) and famous for the rich fossil record of the chalicothere Anisodon grande.

A similarly rich terrestrial (incl. semiaquatic) vertebrate assemblage, accompanied by fossil finds of chondrichthyans (Holec 2001; Malíková 2019), bone fishes (Holec & Sabol 1996; Holec 2001), sirenians and cetaceans (Thenius 1952; Holec 1982), is known from late Badenian transgressive sands of nearby DNV-Sandberg site (Thenius 1952; Holec & Sabol 1996; Sabol & Holec 2002). This similarity in macrofaunal elements can be seen mainly in the co-occurrence of the same taxa of mammutids and probably also deinotheres (Thenius 1952; Holec 1982; Tóth 2010), several species of carnivores and artiodactyls, the suid Hyotherium soemmeringi and aceratheriine rhinos on both DNV sites. By contrast, a difference is observed in the absence of amphibians, birds and micromammals (apart from rare finds of lagomorphs and rodent incisors; Thenius 1952) as well as in the presence of different representatives of reptiles (incl. crocodyles; Hoernes 1848;

Holec & Schlögl 2000; Schlögl & Holec 2004; Holec 2006; Danilov et al. 2012), primates (Thenius 1952; Holec & Emry 2001, 2003), felids, hemicyonids, mustelids, suoids, artiodactyls, and perissodactyls at DNV-Sandberg site (Suppl. Table S1). In the absence of small mammals, the correlation of the site with the MN6 unit was made on the basis of taxa such as Hemicyon goeriachensis, Ursavus brevirhinus, Lartetictis dubia, Potamotherium miocaenicum, Taucanamo sansaniense, Palaeomeryx magnus, and Lagomeryx parvulus, but mainly Griphopithecus suessi and Tapirus telleri, which are considered Astaracian immigrants from Africa (hominoid; Köhler et al. 1999) or Asia (tapir; Heissig 1999). Later, this age was confirmed by geochronological methods (Fordinál et al. 2014). However, one of the open questions is the origin of terrestrial elements of the DNV-Sandberg faunal assemblage in littoral sands of the site. Because the fossils do not show traces of long-term transport, these are probably remains of dead animals washed into the sea from the surface, perhaps during the sudden flood events, or (at least partially?) washed out from karst fissures of the limestone coast, attacked by wave erosion. In any case, the DNV-Sandberg faunal assemblage is stratigraphically slightly younger compared to the faunal assemblage from DNV-Štokeravská vápenka. The former also differs in its environment (a subtropical seashore with forested inland) without the chalicotheres, so typical for the stratigraphically older site (Sabol & Kováč 2006).

The third, "transitional" DNV site, Bonanza, is a large karst fissure in the same abandoned limestone quarry as DNV-Štokeravská vápenka, but situated in the opposite quarry wall (Holec et al. 1987a). Single layers of its sedimentary filling, documenting changes of coastal line position associated with a several (possibly orbital) cycles, contain fossils of terrestrial (incl. freshwater), semi-aquatic, and marine vertebrates (Sabol & Kováč 2006). It is the type locality of four species (Bufo priscus, Gerhardstorchia meszaroshi, Devinophoca claytoni, and D. emryi) and its fossil record consists so far of eight chondrichthyan taxa (Holec 2001), at least 18 taxa of bone fishes (Holec 2001; Hensel ex Sabol & Kováč 2006), eight amphibian taxa (Hodrová 1988; Špinar et al. 1993), Ophisaurus sp. (Klembara 1986; Čerňanský & Klembara 2017), four taxa of snakes (Ivanov 1998), Zygolophodon turicensis (Holec 2002; Tóth 2010), 16 taxa of rodents (Sabol 2005b; Mažgút 2010), 10 taxa of insectivores (Fejfar & Sabol 2005; Sabol 2005a; Mažgút 2010), undetermined bat remains, six carnivore taxa (Lupták 1999; Koretsky & Holec 2002; Mažgút 2010; Koretsky & Rahmat 2015; Rahmat & Koretsky 2016) and two taxa of artiodactyls (Holec et al. 1987a). This faunal assemblage resembles those from the abovementioned DNV sites (Suppl. Table S1), and its age (MN6) was determined based on rodent species such as Keramidomys carpathicus, Myoglis meini, Muscardinus sansaniensis, Democricetodon vindobonensis and Neocometes brunonis.

Stratigraphic remarks: Whereas the correlation of DNV– Sandberg site with MN6 unit is supported by the Sr-ages obtained mainly from molluscan shells from the central part of site profile (Fordinál et al. 2014), the deposition time of

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fossiliferous sediments in karst fissures of DNV-Štokeravská vápenka can be determined only based on its terrestrial fossil record and geological settings. As mentioned above, the composition of terrestrial fauna of the latter site unambiguously corresponds with the MN6 faunal assemblages. However, it stems from sediments deposited before the late Badenian transgression in the area, which rules out the younger age than 13.30 Ma, the assumed top of the Badenian Salinity Crisis (BSC) - the Central Paratethys event with the duration of approximately 500 kyr (Kováč et al. 2018). The MN6 faunal assemblage of DNV-Štokeravská vápenka can therefore correspond either to the BSC event (~13.8-13.3 Ma) or to the early Badenian. However, as its faunal assemblage is very similar to that from the Sansan reference locality with an age of 14.10 Ma (De Bruijn et al. 1992; Hilgen et al. 2012), it is more likely that originated before the BSC event. In addition, Kälin and Kempf (2009) consider the DNV-Štokeravská vápenka as the oldest locality corresponding to MN6 unit and correlate it with the Swiss localities Uzwil-Nutzenbuech and Chatzloch, which is magnetostratigraphically dated at ca. 14.7 Ma (Schlunegger et al. 1996; Kempf et al. 1997). All these sites are also connected with the first occurrence of the species Anomalomys gaudryi (Kälin & Kempf 2009). Based on that, it is possible to place DNV-Štokeravská vápenka around 14.7 Ma, indicating an older age for MN6 unit in Central Europe. Thus, three DNV sites with the unquestionably proven transition from terrestrial to marine conditions during the Badenian form an unique case in the whole Central Paratethys area and we are introducing for them a designation Devínska Nová Ves local faunal complex, corresponding to the MN6 unit. In addition, the palynofloral record from DNV sites and localities from adjacent areas (Doláková et al. 2011) also yield data on climatic changes almost immediately after the so-called mid-Miocene Climatic Optimum (MCO), an episode of global warming that occurred near the early/ middle Miocene transition, approximately between 17 and 15 Ma (Zachos et al. 2001). After this relatively brief warm phase, the global climate kept gradually cooling with an effect also on continental ecosystems and vertebrate/mammal communities (Böhme 2003, 2006; Van Dam 2006; Van Dam & Utescher 2016).

From other Slovak sites with an isolated fossil record, **DNV–Waitov lom** with fossil remains of bone fishes (Holec 2001), reptiles (Holec 2006) and phocids (Zagoršek 1985), **DNV–Glavica** with a *Mesocetus* find (Holec & Sabol 1996; Sabol & Holec 2002) and **Horné Strháre** with fossilised teeth of chondrichthyans (Holec 2004; Malíková 2019), cetaceans (*Squalodon* sp.) and terrestrial mammals (Holec 2004) can also be assigned to this local faunal complex.

Late Astaracian fossil record (MN7+8)

Like the sites from the pre-Astaracian period, the eight so far documented Slovak localities correlatable to MN7+8 unit and corresponding predominantly with the Sarmatian regional stage (12.70–11.60 Ma; *sensu* Piller et al. 2007) yielded only

isolated fossil remains (Suppl. Table S2). The dating of single sites (from the latest Badenian to the (early) Sarmatian) was realized only based on fossil record and/or geological settings (Holec 1982, 1985, 1986; Fejfar et al. 1987; Holec et al. 2007), without any data from geochronological and magnetostratigraphical research. Fossils of large mammals have been found in coastal marine deposits (Rohožník, Dúbravka-Pole), brown coal mine pits (Handlová, Nováky), tuffaceous deposits (Svinná) and andesite tuffs (Bánovce nad Bebravou, also including its suburban part of Horné Ozorovce) or in karst fissures in a magnezite mine (Košice-Bankov) and provide a limited picture of the late middle Miocene faunal community from the West-Carpathian lowlands. So far, it consists of Prodeinotherium bavaricum (Tóth 2010; Tóth & Hyžný 2013), Gomphotherium angustidens (Petrbok 1930; Tóth 2010; Tóth & Gasparik 2012), Zygolophodon turicensis (Holec 1982, 1985; Tóth 2010), an undetermined primate (Prantl 1959; Holec & Emry 2001), Lophocyon carpathicus (Fejfar et al. 1987), Dicrocerus sp. (Holec et al. 2007), Hoploaceratherium cf. tetradactylum (Takáč 1982; Holec 1986; Zervanová 2014) and other undetermined aceratheriine rhinoceros, as well as Brachypotherium cf. brachypus and Lartetotherium sp. (Zervanová et al. 2013). The fossil record of terrestrial taxa is supplemented by finds of Pelocetus sp. (Sarlós 2018) and an undetermined pomatodelphinine odontocete (Lambert et al. 2008) from the latest Badenian marine sediments of Rohožník site, situated directly below the Sarmatian ones (Fordinál et al. 2013).

The correlation itself with other MN7+8 European sites is very limited because of scarce fossil finds, consisting only of large mammal species, often with the wide range of their biostratigraphical distribution (a redeposition, especially for fossils from tuffs, is also not excluded). A certain similarity can be found, for example, in fossil assemblage from Polish locality of Przeworno 1 and 2 with the common occurrence of aceratheriine and teleoceratine rhinos (Kubiak 1981) or trilophodont gomphotheres (Kubiak 1975). However, the estimated age of individual sites under study is based primarily on lithostratigraphy.

The environment was formed by coast of the Sarmatian sea with slightly reduced salinity (Hudáčková & Kováč 1993; Báldi 2006; Kováčová & Hudáčková 2009) caused by fresh-water input by rivers (Popov et al. 2010), although shallow marine hypo- and hypersaline environments may have developed locally in the Central Paratethys western parts (Harzhauser & Piller 2004, 2007; Kováč et al. 2005; Koubová & Hudáčková 2010; Zlinská et al. 2010; Gozhyk et al. 2015). The animals that lived along the seashore inhabited wet habitats formed by peat bogs and swamp forests with the abundant Taxodium (Kováč et al. 2017), while coniferous forests with spruce and spruce-fir assemblages together with various Tsuga species were widespread at higher altitudes inland (Syabryaj et al. 2007). The inland was often affected by andesite, dacite, and rhyolite volcanic activity (Pécskay et al. 2006). Due to global cooling (Bicchi et al. 2003), the mean annual temperature (MAT) dropped from 18-22 °C in previous periods to

15–17 °C during the Sarmatian and the following late Miocene Epoch (Kováčová et al. 2009).

Early Vallesian fossil record (MN9)

The earliest late Miocene faunal assemblage in the Slovakian territory of the Western Carpathians is documented from an abandoned brickyard situated SE from **Borský Svätý Jur** village in the Záhorie area, western Slovakia (Pipík & Holec 1998; Joniak 2005). From a geological point of view, the site (Fig. 3A) is located in the northern part of the Vienna Basin and sedimentary layers are formed by pelitic to sandy deposits of the Pannonian Zone E (*sensu* Papp 1951), which represent a transition from lake clays with *Congeria* fauna and pre-delta silts to fine-grained delta sands (Bzenec Fm.).

The vertebrate fossil record (Suppl. Table S3) consists of ray-finned fish otoliths from the families Sciaenidae and Sparidae (Pipík & Holec 1998; Joniak 2005), osteological remains of amphibians (Joniak 2005), reptiles (Pipík & Holec 1998; Joniak 2005; Čerňanský 2011; Danilov et al. 2012) and birds (Joniak 2005), but mainly of mammalian finds. Despite the smaller sample in comparison with invertebrate fossils (mollusc and ostracods), the mammal assemblage is relatively well diversified, including both large and small species. The large mammals are represented at the site by Deinotherium levius (Schmidt 1969a, 1972; Tóth 2010), Ictitherium viverrinum and Eomellivora sp. (Lupták 1995a, b; Valenciano et al. 2015), hipparionine horse (Pipík & Holec 1998) and undetermined remains of cervids and suids (Pipík & Holec 1998; Joniak 2005). The small mammal assemblage includes, in addition to rare finds of lagomorphs (Eurolagus sp.) and bats (Myotis sp., Vespertilionidae gen. et spec. indet., Chiroptera indet.), fossils of insectivores (erinaceids, soricids, and talpids) and rodents (sciurids, eomyids, glirids, castorids, and cricetids), which are important for the precise biochronology of the site (Joniak 2005).

Based on the analysis of ostracod and mollusc assemblages (Pipík & Holec 1998), the fossiliferous sediments from Borský Svätý Jur were correlated with the Panonian Zone E (sensu Jiříček 1985), while the large mammal fossil record (except for deinotheres) was considered younger and correlated with the MN10 or MN11 unit (Pipík & Holec 1998). However, small mammal finds, especially these of cricetids such as Microtocricetus mollasicus and Megacricetodon minutus, clearly support the correlation of site fossiliferous sediments with the MN9 unit (Joniak 2005). This correlation is also supported by the similarity of the assemblage with those from other MN9 sites in the Vienna Basin. The composition and evolution level of determined small mammal species correspond mostly to faunal assemblages from Austrian sites such as Vösendorf and Richardhof-Golfplatz (Daxner-Höck & Höck 2015), allowing to correlate the age of Borský Svätý Jur to the upper part of the MN9 unit. Such a correlation is also supported by preliminary research of insectivore finds, showing the evolution level of some species (e.g., Lantanotherium sanmigueli) somewhat more ancestral in shape and size than in

those from another Austrian site, Götzendorf, correlated with the Pannonian Zone F (*sensu* Papp 1951).

The Pannonian Zone E is also a period with so far the earliest occurrence of hipparionine horses in the territory of Slovakia, although these (*Hippotherium primigenium*) have already been found in the Vienna Basin at the Pannonian Zone C base with an age of 11.2 Ma (Rögl & Daxner-Höck 1996). It very well corresponds with the "*Hipparion* datum", one of the most significant datum events in the Neogene mammalian biochronology.

The site of Borský Svätý Jur belongs to the key localities within the Vienna Basin also from the viewpoint of climatic changes. The quantitative and qualitative changes in mammalian communities from adjacent areas of Pannonian Lake indicate a gradual decrease in humidity and expansion of larger open grasslands during the Vallesian. In the Borský Svätý Jur rodent fauna, the ground dwellers dominated (cricetids) but semi-arboreal to arboreal (sciurids, glirids and eomyids) and semi-aquatic (castorids) taxa are also present. This faunal composition corresponds to the open environment with forested areas and proximity to a lake and smaller rivers (Joniak 2005). However, the small mammal assemblages from MN9 sites in Vienna Basin are generally characterized by higher diversity of semi-aquatic (Castoridae, Desmaninae, Dimylidae), arboreal (Gliridae, Sciuridae), and gliding taxa (Eomyidae, Petauristini) in comparison with the diversity of terrestrial species (Cricetidae, Zapodidae). This still indicates the presence of an extensive swampy environment with a humid, wooded habitats with relatively dense vegetation. Moreover, this part of Central Paratethys area was probably without clear seasonality during the early Pannonian (Kováč et al. 2005, 2006), with the mean annual precipitation (MAP) 1129-1328 ±270 mm (Böhme et al. 2006).

From the other Slovakian sites correlated with the MN9 unit, only two could be considered with some doubts based on the isolated fossil record – **Fulianka** with the find of *Deinotherium levius* (Tóth 2010) and **Perín** with the discovered fossil remains of *Tetralophodon longirostris* (Tóth 2010) and *Aceratherium* sp. (Schmidt 1969c; Zervanová 2014), both situated in eastern Slovakia.

Late Vallesian fossil record (MN10)

So far, only one locality with relatively abundant late Vallesian fossil record is known from the Slovak territory of the Western Carpathians (Holec 1981, 1982, 2005; Joniak 2016). This site, named **Pezinok** (or Pezinok A and Pezinok B sub-sites resp., Fig. 3B), is situated in an active brickyard clay pit (also called as a new clay pit) located approximately 1 km south from Pezinok town at the eastern margin of the Danube Basin. The small mammal assemblage was collected from a sandy layer with a rich organic detrite (mainly fragmented molluscan shells) in the middle portion of the site profile, which is formed by variegated and spotted clay, lignite clay, lignite, fine-to-medium grained sand, and silt. The lower part of the profile consists mainly of massive blue-gray clay with



Fig. 3. Important Vallesian and Turolian sites in the Slovak territory of the Western Carpathians within the Pannonian Basin System. *Explanatory notes*: A — abandoned brickyard near Borský Svätý Jur village; B — brickyard clay pit near Pezinok; C — Triblavina outcrop; D — Šalgovce outcrop; E — Paleogeography of the Pannonian Basin System during the early Tortonian (early Pannonian) with the assumed position of Borský Svätý Jur site site (BJ), Pezinok site (P), Triblavina site (T), and Šlagovce site (Š); E according to Kováč et al. 2017 (SB – Styrian Basin, ZB – Zala Basin). Photos: P. Joniak.

rich molluscan fauna (Lymnocardium conjugens Zone *sensu* Magyar et al. 2007), although it contains also small layers of limnic clay, alluvial sand and clay and lagoon lignite clay to lignite (Joniak 2016). The age of these middle and lower profile portions (Beladice/Volkovce Fm.) was originally proposed as the Pannonian Zone E (Holec et al. 1987b; Fordinál 1997; Pipík 1998). The correlation of the site with the MN10 unit is supported by co-occurrence of the first true murine *Progonomys hispanicus* together with *Microtocricetus molassicus*, documented also in Austrian sites, such as Richardhof-Wald or Neusiedl am See (Joniak 2016). The co-occurrence of these rodent species is an indicator of the MN10 lower part (Daxner-Höck & Höck 2015) and this age assignment is also supported by fossils of other rodent taxa from the site, such as *Spermophilinus* sp. (corresponds to *S. turolensis* in size), *Anomalomys* gaillardi and *Graphiurops austriacus* (Joniak 2016).

The rodent fossils are accompanied in Pezinok by finds of bone fish, lagomorphs, insectivores, and large mammals, as well (Joniak 2005; Suppl. Table S4). The large mammal remains are, however, rare and limited to just one premolar and fragmented McIII of hipparionine horse (Holec 1981, 1982) and one molar of *Deinotherium giganteum* (Holec 2005; Tóth 2010). Moreover, these were found during the surface prospection without an affiliation to a specific layer.

The Pezinok rodent fauna is characterized by a large diversity of both forest and open land taxa and consists of ground dwellers (Progonomys hispanicus, Neocricetodon sp., Microtocricetus mollasicus, Spermophilinus sp.), fossorial (Anomalomys gaillardi), arboreal (Graphiurops austriacus, Paraglirulus sp.), gliding (Eomyops catalaunicus, Keramidomys sp., Albanensia sp.) and semi-aquatic (Euroxenomys minutum) representatives. This faunal composition indicates the presence of probably frequently flooded open and forested areas and the proximity to a lake and rivers. Based on the analysis of palynomorphs (Sitár 1958), a mixed, cold-adapted vegetation predominated during the deposition of middle profile portion sediments with the mammalian fossil record (MN10), while vegetation of the temperate zone was mostly identified in sediments from the lower profile portion. It suggests a gradual change from a period with the relatively humid and warm climate to a period with the onset of seasonality with dry summers and relatively humid winters (Kováč et al. 2005, 2006). The sedimentological research revealed that the area of the Pezinok locality was probably located in a bay, isolated from the main deltaic distributary system during the late early Pannonian, with the onset of a purely terrestrial environment later, perhaps only after 9.70 Ma (Kováč et al. 2011).

Stratigraphic remarks: The mammalian fossil assemblage from the middle profile portion of the Pezinok clay pit unambiguously corresponds to the lower part of the MN10 unit. The sediments of this profile portion contain also shells of Congeria neumayri (Fordinál 1997), which is a bivalve species typical for the Pannonian Zone F (Harzhauser et al. 2004). By contrast, the underlying layers of the lower profile portion are characterized by the presence of the molluscan assemblage with Lymnocardium conjugens (Fordinál 1997), allowing to date these sediments to the Pannonian Zone E (sensu Papp 1951; according to Harzhauser et al. 2004) with an age ca. 11.00-9.60 Ma (Magyar et al. 2007). Recently, these sediments from the lower part of the outcrop were dated by authigenic ¹⁰Be/⁹Be dating. The calculated age is 10.95±0.6 Ma (Šujan et al. 2016, p. 41). Since the authors assume a low sedimentation rate during the deposition period lasting more than 1.0 Ma, the biochronologic correlation of the Pezinok mammal assemblage with the early MN10 is consistent with the obtained authigenic 10Be/9Be age. The age of found mammalian assemblage can thus be defined as ~9.70-9.60 Ma (sensu Hilgen et al. 2012).

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The isolated find of insectivore *Paenelimnoecus* sp. from the **Dubná skala** limestone quarry in northern Slovakia may also be included to this MN unit (Pipík & Sabol 2005).

Early Turolian fossil record (MN11)

Although so far 12 Turolian sites are known from Slovakia, the fossil record from this European Land Mammal Mega Zone (8.90–5.30 Ma, *sensu* Hilgen et al. 2012) is relatively limited in the amount of fossil finds.

The early Turolian faunal assemblage, corresponding to MN11 unit, is recorded mainly at two sites - Triblavina and Krásno. The Triblavina site (Fig. 3C) with its small mammal assemblage indicating the lowermost MN11 unit (Joniak & Šujan 2020; Joniak et al. 2020) is an artificial temporary outcrop exposed at a roundabout construction pit next to the highway D1 near Bernolákovo in Senec District, western Slovakia. The fossiliferous horizon is situated within the sedimentary complex of Volkovce Fm. in Blatné depression of the Danube Basin. The molluscan assemblage at this outcrop may be roughly correlated with Papp's Pannonian Zones G and H defined in the Vienna Basin and indicates a paleoenvironment of freshwater lakes affected by rivers with evidence for a nearby riparian forests (Joniak et al. 2020). The mammalian assemblage (Suppl. Table S5) consists only of insectivores and rodents (Joniak & Šujan 2020; Joniak et al. 2020), with the dominance of murids (Apodemus lugdunensis). Based on the morphological and metric characteristics, it correlates with microfaunal assemblages from Austrian sites Eichkogel and Kohfidisch (Joniak & Šujan 2020), which correspond to the MN11 unit (Daxner-Höck & Höck 2015). This age assignment was also supported by the authigenic 10Be/9Be dating of the sedimentary sequences with the mean weighted age range 9.65±0.61-8.85±0.32 Ma (Joniak et al. 2020). The ~0.1 Ma inconsistency between absolute dating and biostratigraphic dating (< 8.90 Ma) at the site area might be explained either by the variation of initial 10Be/9Be ratio in the depositional environment or/and by diachronous development of the mammal faunas across the Europe (Joniak et al. 2020).

Another early Turolian site, Krásno, is situated at the northern foothills of the Tribeč Mts. near the eponymous village in the Partizánske District, western Slovakia. Its mammalian fossil record is much richer (over 1500 rodent teeth) and more diverse than the assemblage from the previous site, but is still under study. The preliminary list of fauna (Suppl. Table S5) consists not only of rodents and insectivores, but also representatives of bats, feliform and caniform carnivores, artiodactyls (suid, bovoid, cervoid), and perissodactyls (tapir and rhino). Based on the common occurrence of sciurids (Spermophilinus turolensis, Blackia miocaenica, Pliopetaurista cf. bressana), eomyids (Keramidomys cf. ermannorum), glirids (Myomimus cf. dehmi), zapodids (Eozapus intermedius), but mainly murids (Apodemus lugdunensis and Epimeriones austriacus), the site was correlated with the MN11 unit. The similarity with the Triblavina mammal assemblage is also supported by finds of erinaceids (Lantanotherium sanmigueli),

soricids (*Crusafontina kormosi*, *Blarinella* cf. *dubia*, *Pae-nelimnoecus* cf. *repenningi*) and uropsiline talpids (*Desma-nella* sp.) in both asssemblages. Concerning large mammals, the rare fossil remains of small tapir (cf. *Tapiriscus panno-nicus*) can be used for the biochronology. This tapir species is known from the type site of Csákvár (MN11) (Kretzoi 1951; Heissig 1999) in Hungary as well as from Melchingen (MN9) and Dorn-Dürkheim (MN11) in Germany (Tobien 1980; Franzen 2013) and Aubignas (MN11-12) in France (Azanza et al. 1993).

Isolated finds of rodents (*Apodemus lugdunensis* and *Glirulus lissiensis*), insectivores (Talpidae indet. and Anourosoricini indet.) and hipparionine horses (Čerňanský et al. 2012a) from the **Hrdovická brázda** hill near the village of Čeľadince (Hlavina Mb., Volkovce Fm., *ca*. 8.00 Ma; Šujan et al. 2017), as well as isolated fossils of an undetermined tetralophodont gomphothere (Schlesinger 1922; Tóth 2010) and poor micromammalian fauna with *Spermophilinus* from **Závada** (also Hlavina Mb., Volkovce Fm.) complete the MN11 fossil record in Slovakia.

Middle Turolian fossil record (MN12)

The middle Turolian fossil record is documented at **Šalgovce** site (Fig. 3D), representing an artificial temporal trench located on the southwest margin of the eponymous village. The assemblage of small mammals (rodents, insectivores and bats; Suppl. Table S6) stems from the late Pannonian fossiliferous freshwater limestone and clay (Hlavina Mb., Volkovce Fm.). Excavations at the site are still ongoing, but preliminary identifications show some differences compared to early Turolian localities from Slovakia, such as Triblavina or Krásno. The presence of *Pliopetaurista dehneli*, a large-sized *Muscardinus* species and slightly larger teeth of *Apodemus lugdunensis* suggest a moderately younger age. Thus, the Šalgovce assemblage of small mammals corresponds to the middle Turolian MN12 unit.

The middle Turolian record of mammals in the area under study is supplemented by fossils of an amebelodontine mastodont (*Konobelodon atticus*?) from **Prusy**, **Sered'-Šintava**, and **Topol'čany-Kalvária** (Holec 1981, 1982; Tóth 2010). From the last mentioned site (Topol'čany-Kalvária), fossils of *Anancus* sp. (Tóth 2010), hipparionine horses (Holec 1981, 1982) and tapirs (*Tapirus priscus*) are also known. However, these finds have probably been collected from various strata, most likely of a different age, and remnants of *Anancus* sp. could also be considered younger (MN13?).

Late Turolian fossil record (MN13)

The late Turolian fossil record is very scarce, maybe because of the absence of suitable environments for fossilisation. This period is also characterised by paleoclimatic and paleoenvironmental changes caused by the Messinian Salinity Crisis, which led to the extinction of some genera from the previous interval and the subsequent immigration of new genera from Asia and Africa (Agustí et al. 2001). The fossil record is so far documented only in three sites and consists of isolated findings of large mammals, mainly of proboscideans. Among these, three taxa have been identified – *Deinotherium proavum* from **Madunice** (Musil 1959; Schmidt 1969a, 1972; Tóth 2010), "*Mammut*" aff. *borsoni* from **Vel'ké Bielice** (Holec 1982; Tóth 2010) and *Anancus* aff. *arvernensis* from unspecified site near to **Nováky** (Tóth 2010). The latter taxon was also found in **Slepčany** (Buday et al. 1964; Holec 1981; Tóth 2010), in a site situated east from Nitra town. Its fossils have been discovered together with remains of *Hipparion* s.s., *Tapirus priscus* (Buday et al. 1964; Holec 1981) and aceratheriine(?) rhinos (Schmidt 1969c; Zervanová 2014).

Because fossils of small mammals, especially rodents, have not been found so far in these uppermost Pannonian fossiliferous horizons, a more detailed and exact correlation with other European sites corresponding to MN13 unit is not possible, yet. In addition, it is not fully excluded that above mentioned fossil record of mastodonts can also stem from a younger period (early Pliocene?). Based on the geological settings at all these four sites, however, the assignment of found mammalian fossil to the latest Miocene is most likely.

Final summary

Based on the currently available data from Miocene terrestrial fossiliferous deposits in the territory of Slovakia, six middle to late Miocene sites with a sufficient fossil record correlated with individual MN units and the ELMMZ (*sensu* Steininger 1999) can be mentioned as local reference localities (LRL; Fig. 4). These are also correlated with chronostratigraphic data of the Central Paratethys area and partly with geochronologic ones if available.

1. DNV-Štokeravská vápenka LRL (48°12'05"N, 17°00'06"E)

Biostratigraphic/Biochronologic correlation: Astaracian, lower part of the MN6 unit;

Geochronologic calibration: base probably at \sim 14.70 Ma and top probably at \sim 13.8 Ma, with a total duration approximately \sim 0.90 Ma;

Chronostratigraphic correlation: upper part of the early Badenian Stage (a terrestrial equivalent of the Devínska Nová Ves Mb. in the karst, Jakubov Fm.), correlated with the upper part of the Langhian Stage in the Mediterranean area.

2. DNV-Sandberg LRL (48°12'02"N, 16°58'29"E)

Biostratigraphic/Biochronologic correlation: Astaracian, upper part of the MN6 unit;

Geochronologic calibration: base at 13.79 Ma and top at 12.76 Ma, with a total duration approximately \sim 1.00 Ma;

Chronostratigraphic correlation: late Badenian Stage (Sandberg Mb., Studienka Fm.), correlated with the lower part of the Serravallian Stage in the Mediterranean area.



Fig. 4. European Miocene chronostratigraphy system correlated with the Central Paratethys stages with the position of Slovak Miocene mammalian sites (created with the TimeScale Creator software, v. 8.0 (2021); modified according to Hilgen et al. 2012). Sites in red are the local referrence localities (LRL); DNV LFC is the Devinska Nová Ves local faunal complex introduced, correlated with the MN6 unit (blue belt) Additionally, both these DNV sites together with DNV– Bonanza (48°12'13"N, 17°00'11"E) form an unique complex of transitional localities within the whole Central Paratethys area. This allows, following the idea of Prof. O. Fejfar, to introduce the term **Devínska Nová Ves local faunal complex** (~14.70–12.76 Ma), corresponding with the MN6 unit.

3. Borský Svätý Jur LRL (48°36'24.46"N, 17°3'2.89"E)

Biostratigraphic/Biochronologic correlation: Vallesian, upper part of the MN9 unit;

Geochronologic calibration: none, but based on indirect correlation, the site age can be assumed at ~ 10.20 Ma (?);

Chronostratigraphic correlation: early Pannonian Stage (Bzenec Fm.), correlated with the lower part of the Tortonian Stage in the Mediterranean area.

4. Pezinok LRL (48°16'40.60"N, 17°16'46.46"E)

Biostratigraphic/Biochronologic correlation: Vallesian, lower part of the MN10 unit;

Geochronologic calibration: 10.95 ± 0.6 Ma for lower part of the outcrop without the mammalian fossil record, which stems from the middle outcrop part with the assumed age of ~9.70–9.60 Ma;

Chronostratigraphic correlation: early Pannonian Stage (Beladice/Volkovce Fm.), correlated with the middle part of the Tortonian Stage in the Mediterranean area.

5. Triblavina LRL (48°12'50.61"N, 17°15'38.47"E)

Biostratigraphic/Biochronologic correlation: Turolian, the lowermost part of the MN11 unit;

Geochronologic calibration: $9.65\pm0.61-8.85\pm0.32$ Ma, the upper datum is supported by biostratigraphic dating (< 8.90 Ma);

Chronostratigraphic correlation: middle Pannonian Stage (Volkovce Fm.), correlated with the upper part of the Tortonian Stage in the Mediterranean area.

Triblavina was chosen as the local reference locality despite the fauna from this site is poorer and less diversified than the assemblage from Krásno (48°35'38.97"N, 18°19'18.15"E). The material from Krásno is still under study and the provided list of fauna is preliminary, while the age of the assemblage of small mammals from Triblavina (MN11) is supported also by authigenic ¹⁰Be/⁹Be dating (Joniak et al. 2020).

6. Šalgovce LRL (48°31'23.51"N, 17°53'40.00"E)

Biostratigraphic/Biochronologic correlation: Turolian, MN12 unit;

Geochronologic calibration: none, but based on the faunal correlation with the MN12 unit, the age of the site could be in the time range of this unit (7.60–6.80 Ma, *sensu* Hilgen et al. 2012);

Chronostratigraphic correlation: late Pannonian Stage (Hlavina Mb., Volkovce Fm.), correlated with the uppermost part of the Tortonian Stage in the Mediterranean area.

All these sites will serve as reference localities for another research of the middle and late Miocene in the territory of Slovakia in the near future. So far, eastern Slovakia remains an unexplored territory, where the potential faunal assemblages can show a relationship with these ones from the Eastern Paratethys area (or Eastern Europe resp.).

Unfortunatelly, to perform a comprehensive magnetostratigraphic calibration on single LRLs is not possible, due to lack of continuous sections. Therefore, the chronological constraining of Slovak Miocene LRL is still weakly established in many cases. In addition, it is also necessary to take into account the fact that some of the proposed correlations are loosely constrained and may need to be further revised since these are only preliminary interpretated. The more comprehensive authigenic ¹⁰Be/⁹Be dating in the region under study would be required in order to provide conclusive arguments on the chronology of presented faunal communities.

The age definition of many sites and their correlation with MN units is often difficult due to the absence of key fossil taxa, especially of small mammals, as well as the absence of significant large mammal taxa that indicate migration events across wide geographical domains. In any case, the available biostratigraphic database for the European Neogene (NOW) suggests the necessity to consider the paleobiogeographical significance of each fossil record and its value for the correlation within both local and extensive geographic areas.

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Supplement

Table S1: Updated list of fossil vertebrates found in the West Carpathian (Slovak part) Miocene sediments correlated with the MN6 unit. Red crosses indicate the type species. *Explanatory notes:* L6.1 – DNV–Štokeravská vápenka, L6.2 – DNV–Bonanza, L6.3 – DNV–Sandberg, L6.4 – DNV–Waitov lom, L6.5 – DNV–Glavica, L6.6 – Horné Strháre.

TAXON	L6.1	L6.2	L6.3	L6.4	L6.5	L6.6
Chondrichthyes						
Aetobatus arcuatus		+	+			
Dasvatis sp		+	?			
Miliohatis sp			+			
Raia sp		+				
Miliobatidae gen et spec indet		+	2			
Rajidae gen et spec indet		+	+			
Notorhynchus primigenius			+			
Araloselachus cuspidatus		+	+			+
Carcharias acutissima		·	+			+
Carcharias sp		+				
Isurus retroflerus		·				+
Isurus sp						+
Otodus magalodon						+
Otodus minor						cf
Odontasnis sp			+			C1.
Negaprion aurobatrodon		+	,			
Sculiorhinus sp		·	9			
Selverna Tyggena			: +			
Sphyrna zygaena Striatolamia magrota			+			
Alopias aviaua			+ +			
Carebarodon hastalis			+			
Calcorhinus minor			т +			т
Gueorminus minor			+			
Lugareus tatus			т +			
Carebarbinus prisous			т +			
Carcharhinus priscus			т +			
Carcharhinus similis			+ +			<u>т</u>
Calcocordo adunous			+			-
Saugting an			+			T
Ostoiehthyos			Т			
Acinenseridae gen et spec indet			+			
Holocantrus sp		+				
Gobius praetiosus		·	+			
Barbus sp			+			
Denter sp			2			
Dinlodus sp.			+			
Trigodon sp.			+			
Tetraodon scillae			+	+		
Cymhium sp			+			
Eninenhelus sp		+	+			
Lates sp		+				
Pagrus sp		·	+			
Phyllodus sp			+			
Saurocenhalus sp.			+			
Scopelus sp			+			
Secranus sp.		+	+			
Sparus auratus			+			
Sparus cinctus			+			
Spherodus sp			+			
Trachurus noetlingi			+			
Trichiurus miocagnicus		+	1			
Trichiurus sp		+	+			
Triala sp.		+	'			
Trisonterus sn			+			
Acanthuridae gen et spec indet		+	+			
Diodontidae gen et spec indet			+			
Holocentridae gen, et spec, indet		+	+			
Labridae gen, et spec, indet		+	+			

Table S1 (continued)

TAXON	L6.1	L6.2	L6.3	L6.4	L6.5	L6.6
Serranidae gen. et spec. indet.		+				
Sparidae gen. et spec. indet.		+	+	+		
Sphyraenidae gen. et spec. indet.			+			
Tetraodontidae gen. et spec. indet.		+				
Triglidae gen. et spec. indet.		+	+			
Perciformes indet.		+	+			
Osteichthyes indet.		+				
Amphibia						
Bergmannia wettsteini	+					
Salamandra broilii	+					
Salamandra sansaniensis		+				
Triturus roehrsi	+					
Voigtiella ludwigi	+					
Urodela indet.	+	+				
Latonia gigantea	+					
Eopelobates bayeri	+	+				
Bufo priscus		+				
Bufo sp.	+	+				
<i>Hyla</i> sp.	+	+				
Anura indet.		+				
Amphibia indet.	+	+				
Reptilia						
Psephophorus polygonus			+			
Trionyx sensu lato			+			
Trionyx sp.			+	+		
Testudinata indet.	+		+			
Euleptes klembarai	+					
Ophisaurus spinari	+					
Ophisaurus sp.		+				
Colubrinae gen. et spec. indet.	+	+				
Elapidae gen. et spec. indet.	+					
Neonatrix sp.	+	+				
<i>Vipera</i> sp.	+					
Ohidia indet.	+	+				
Gavialosuchus sp.			+			
Reptilia indet.	+					
Aves						
Miogallus altus	+					
Phalacrocorax intermedius	+					
Tyto sanctialbani	+					
Passeriformes indet.	+					
Aves indet.	+					
Proboscidea						
Prodeinotherium bavaricum	?					
Deinotherium levius	?		cf.			
Zygolophodon turicensis	+	+	+			
Sirenia						
Metaxytherium medium			+			
Primates						
Pliopithecus antiquus			+			
Pliopithecus vindobonensis	+					
Griphopithecus suessi			+			
Lagomorpha						
Lagomorpha gen. et spec. indet.			+			
Rodentia						
Blackia miocaenica	+					
Spermophilinus bredai	+	+				
Sciuridae gen. et spec. indet.		+				
Keramidomys carpathicus	+	+				
<i>Eomyops</i> sp.	+					
Eomyidae gen. et spec. indet.	+	+				
Myoglis meini	+	+				
Microdyromys complicatus	+					
Muscardinus sansaniensis	+	+				

Table S1 (continued)

TAXON	L6.1	L6.2	L6.3	L6.4	L6.5	L6.6
Bransatoglis astaracensis	+	+				
Miodvromvs hamadrvas	+					
Gliridae gen, et spec, indet.	+	+				
Eumvarion weinfurteri	+					
Eumvarion latior	+	cf				
Eumvarion sp		+				
Democricetodon vindobonensis	+	+				
Megacricetodon schaubi	cf					
Megacricetodon gregarius	+					
Megacricetodon sp.		?				
Lartetomys zanfei	cf	+				
Cricetidae gen, et spec, indet.	+	+				
Neocometes brunonis	+	+				
Anomalomys gaudryi	+					
Rodentia indet		+	+			
Eulipotyphla						
Lantanotherium sansaniense	+	aff.				
Postpalerinaceus intermedius	+					
Erinaceidae gen, et spec, indet.		+				
Dinosorex zapfei	+	cf.				
Viretia gracilidens	+					
Lartetium dehmi	+					
Soricidae gen. et spec. indet.	+	+				
Plesiodimylus chantrei	+	+				
Plesiodimylus similis	+					
Proscapanus sansaniensis	cf.					
Talpa minuta	+	+				
Gerhardstorchia meszaroshi		+				
Desmanella sp.	+					
Desmanodon sp	+					
"Scaptonyx" edwardsi	+					
Urotrichus dolichochir	?					
Desmaninae gen, et spec, indet.		+				
Talpidae gen, et spec, indet.	+	+				
Eulipotyphla indet.	+	+				
Chiroptera						
Rhinolophus delphinensis	+					
Rhinolophus grivensis	+					
Megaderma lugdunensis	+					
Paleptesicus priscus	+					
Miniopterus fossilis	+					
Chiroptera indet.	+	+				
Carnivora						
Viverridae gen. et spec. indet.		+				
Styriofelis turnauensis	+		+			
Miopanthera lorteti			cf.			
Amphicyon major	+					
Amphicyon sp.			+			
Pseudocyon steinheimensis	+					
"Tomocyon" sp.	+					
Pseudarctos bavaricus bavaricus			+			
Hemicyon sansaniensis	+					
Hemicyon goeriachensis			+			
Ursavus brevirhinus	+		+			
Alopecocyon goeriachensis	+					
Devinophoca claytoni		+				
Devinophoca emryi		+				
Devinophoca sp.			+			
Phocidae gen. et spec. indet.				+		
Potamotherium miocenicum			+			
Lartetictis dubia			+			
Trocharion albanense	+	+	+			
Mustelidae gen. et spec. indet.	+	+	+			
Carnivora indet.		+				

Table S1 (continued)

TAXON	L6.1	L6.2	L6.3	L6.4	L6.5	L6.6
Cetartiodactyla						
Mesocetus hungaricus			+			
Mesocetus sp.					+	
Squalodon sp.						+
Schizodelphis sulcatus			cf.			
Aureliachoerus aurelianensis	+					
Hyotherium soemmeringi	+		+			
Conohyus simorrensis			+			
Listriodontinae gen. et spec. indet.			+			
Taucanamo sansaniense			+			
Albanohyus pygmaeum			+			
Dorcatherium vindobonense	+		+			
Dorcatherium naui			+			
Palaeomeryx magnus	+		+			
Lagomeryx parvulus		+	+			
Lagomeryx sp.		+				
Dicrocerus elegans	+		+			
Heteroprox larteti	+		+			
Cervidae gen. et spec. indet.						+
Cervoidea indet.			+			
Eotragus clavatus	+					
Tragocerinae gen. et spec. indet.			+			
Perissodactyla						
Tapirus telleri			+			
Hoploaceratherium tetradactylum	cf.					
Dicerorhinus steinheimensis			?			
Rhinocerotidae gen. et spec. indet.	+		+			
Anisodon grande	+					
Anchitherium aurelianense			+			

Table S2: Updated list of fossil vertebrates found in the West Carpathian (Slovak part) Miocene sediments correlated with the MN7+8 unit. Red cross indicates the type species. *Explanatory notes:* L7+8.1 – Dúbravka–Pole, L7+8.2 – Rohožník, L7+8.3 – Handlová, L7+8.4 – Nováky, L7+8.5 – Bánovce nad Bebravou, L7+8.6 – Horné Ozorovce, L7+8.7 – Svinná, L7+8.8 – Košice–Bankov.

TAXON	L7+8.1	L7+8.2	L7+8.3	L7+8.4	L7+8.5	L7+8.6	L7+8.7	L7+8.8
Chondrichthyes								
Galeocerdo aduncus		+						
Proboscidea								
Prodeinotherium bavaricum							+	
Gomphotherium angustidens						+		
Zygolophodon turicensis			+	+				
"Mastodontidae" gen. et spec. indet.								+
Primates								
Primates indet.				+				
Carnivora								
Lophocyon carpathicus								+
Cetartiodactyla								
Pelocetus sp.		+						
Pomatodelphininae gen. et spec. indet.		+						
Dicrocerus sp.		+						
Perissodactyla								
Hoploaceratherium tetradactylum				cf.				
Aceratheriinae gen. et spec. indet.					+			
Brachypotherium brachypus	cf.							
Lartetotherium sp.	+							

Table S3: Updated list of fossil vertebrates found in the West Carpathian (Slovak part) Miocene sediments correlated withthe MN9 unit. *Explanatory notes:* L9.1 – Borský Svätý Jur, L9.2 – Fulianka, L9.3 – Perín.

TAXON	L9.1	L9.2	L9.3
Osteichthyes			
Trewasciaena dobrogiaca	+		
Sparidae gen. et spec. indet.	+		
Amphibia			
Rana sp.	+		
Amphibia indet.	+		
Reptilia			
Nicoria sp.	?		
Testudo csakvarensis	+		
Testudo sp.	+		
Geoemydidae gen. et spec. indet.	+		
Trionychidae gen. et spec. indet.	+		
Emydinae gen. et spec. indet.	+		
Lacerta sp.	+		
Pseudopus sp.	+		
Sauria indet.	+		
Natricinae gen. et spec. indet.	+		
Colubrinae gen. et spec. indet.	+		
Colubridae gen. et spec. indet.	+		
Colubroidea indet.	+		
Aves			
Aves indet.	+		
Proboscidea			
Deinotherium levius	+	+	
Tetralophodon longirostris			+
Lagomorpha			
Eurolagus sp.	+		
Spermophilinus bredai	+		
Eomyops catalanicus	+		
Keramidomys indieri Museardinus hispaniaus	т 		
Muscurainus nispanicus Climilus lissioneis	T of		
Graphiurops austriacus	сі. т		
Gliridaa gan at spag indat	+		
Stangofhar sp	+		
Furovenomys minutus	+		
Eurovenomys minutus Funvarion leemani	+		
Megacricetodon minutus	+		
Democricetodon sp	+		
Neocricetodon n. sp.	+		
Microtocricetus mollasicus	+		
Rodentia indet.	+		
Eulipotyphla			
Schizogalerix voesendorfensis	+		
Lantanotherium sanmigueli	+		
Erinaceidae gen. et spec. indet.	+		
Crusafontina endemica	+		
Dinosorex engesseri	cf.		
Paenelimnoecus repenningi	cf.		
Soricidae gen. et spec. indet.	+		
Desmanella sp.	+		
Proscapanus minor	cf.		
Talpa sp.	+		
Talpidae gen. et spec. indet.	+		
Chiroptera			
Myotis sp.	+		
Vespertilionidae gen. et spec. indet.	+		
Chiroptera indet.	+		
Carnivora			
Ictitherium viverrinum	+		
<i>Eomellivora</i> sp.	+		

Table S3 (continued)

TAXON	L9.1	L9.2	L9.3
Cetartiodactyla			
Suidae gen. et spec. indet.	+		
Cervidae gen. et spec. indet.	+		
Ceratiodactyla indet.	+		
Perissodactyla			
Aceratherium sp.			+
Dihoplus schleiermacheri	cf.		
Hippotherium primigenium	cf.		

Table S4: Updated list of fossil vertebrates found in the West Carpathian (Slovak part) Miocene sediments correlated with the MN10 unit. *Explanatory notes:* L10.1 – Pezinok, L10.2 – Dubná skala.

TAXON	L10.1	L10.2
Osteichthyes		
Sparidae gen. et spec. indet.	+	
Proboscidea		
Deinotherium giganteum	+	
Rodentia		
Spermophilinus sp.	+	
Albanensia sp.	+	
Eomyops catalanicus	+	
Keramidomys sp.	+	
Graphiurops austriacus	+	
Paraglirulus sp.	+	
Euroxenomys minutus	+	
Neocricetodon sp.	+	
Microtocricetus mollasicus	+	
Progonomys hispanicus	+	
Anomalomys gaillardi	+	
Eulipotyphla		
Plesiodimylus chantrei	cf.	
Dinosorex engesseri	cf.	
Blarinella dubia	cf.	
Paenelimnoecus sp.		+
Perissodactyla		
Hippotherium primigenium	+	

Table S5: Updated list of fossil vertebrates found in the West Carpathian (Slovak part) Miocene sediments correlated with the MN11 unit. *Explanatory notes:* L11.1 – Triblavina, L11.2 – Krásno, L11.3 – Hrdovická brázda, L11.4 – Závada.

TAXON	L11.1	L11.2	L11.3	L11.4
Proboscidea				
"tetralophodont gomphothere" indet.				+
Rodentia				
Spermophilinus turolensis		+		
Spermophilinus sp.	+			+
Blackia miocaenica		+		
Hylopetes sp.		+		
Pliopetaurista bressana		cf.		
Miopetaurista sp.		+		
Keramidomys ermannorum	+	cf.		
Keramidomys sp.	+			
<i>Eomyops</i> sp.	+	+		
Graphiurops austriacus		+		
Glirulus lissiensis		+	+	
Myomimus dehmi	+	cf.		
Vasseuromys pannonicus	+			
Muscardinus sp.		+		
Neocricetodon skofleki		cf.		
Neocricetodon sp.	+			
Collimvs sp.		+		
Apodemus lugdunensis	+	+	+	
Epimeriones austriacus	+	+		
Anomylomys sp.		+		
Eozapus intermedius	+	+		
Eulipotyphla				
Schizogalerix sp.		+		
Lantanotherium sanmigueli	+	+		
Erinaceidae gen. et spec. indet.		+		
Plesiodimylus chantrei	cf.			
Crusafontina kormosi	aff.	+		
Blarinella dubia	cf.	cf.		
Paenelimnoecus repenningi	cf.	cf.		
Anourosoricini gen. et spec. indet.			+	
Soricidae gen. et spec. indet.		+		
Archaeodesmana vinea	cf.			
Archaeodesmana sp.		+		
Desmanella sp.	+	+		
Talpidae gen. et spec. indet.	+	+	+	
Chiroptera				
Vespertilionidae gen. et spec. indet.		+		
Chiroptera indet.		+		
Carnivora				
Feliformia indet. I		+		
Feliformia indet. II		+		
Caniformia indet.		+		
Carnivora indet.		+		
Cetartiodactyla				
Hippopotamodon major		cf.		
Bovoidea indet.		+		
Cervoidea indet.		+		
Perissodactyla				
Tapiriscus pannonicus		cf.		
Dihoplus schleiermacheri		cf.		
Hippotherium primigenium			cf.	
<i>Hippotherium</i> sp.			+	

Table S6: Updated list of fossil vertebrates found in the West Carpathian (Slovak part) Miocene sediments correlated with theMN12 unit. Explanatory notes:L12.1 – Šalgovce, L12.2 – Topoľčany–Kalvária, L12.3 – Prusy, L12.4 – Sereď–Šintava.

TAXON	L12.1	L12.2	L12.3	L12.4
Proboscidea				
Konobelodon atticus		?	?	?
Anancus sp.		+		
Rodentia				
Spermophilinus sp.	+			
Neopetes hoeckarum	+			
Pliopetes hungaricus	+			
Pliopetaurista dehneli	+			
Eomyops sp.	+			
Muscardinus dacicus	cf.			
Neocricetodon skofleki	+			
Neocricetodon fahlbuschi	cf.			
Apodemus lugdunensis	+			
Epimeriones austriacus	+			
Eulipotyphla				
Erinaceidae gen. et spec. indet.	+			
Crusafontina kormosi	+			
Amblycoptus sp.	+			
Blarinella dubia	cf.			
Soricidae gen. et spec. indet.	+			
Archaeodesmana sp.	+			
Talpidae gen. et spec. indet.	+			
Chiroptera				
Chiroptera indet.	+			
Perissodactyla				
Tapirus priscus		+		
Hipparion s. s.		+		