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A new record of *Hippotherium* (Perissodactyla: Equidae) from the Late Miocene of the Central Paratethys region (Slovakia)

ANDREJ ČERŇANSKÝ[1, 2], PETER HOLEC[3], MILAN SÝKORA[4] and KLEMENT FORDINÁL[5]

[1]Senckenberg Research Institute and Natural History Museum Frankfurt, Palaeoanthropology and Messel Research, Senckenberganlage 25, D-60325 Frankfurt am Main, Germany
[2]Geological Institute, Slovak Academy of Sciences, Ďumbierska 1, SK-974 01 Banská Bystrica, Slovak Republic; cernansky.paleontology@gmail.com
[3]Department of Biology and Ecology, Faculty of Education, Catholic University in Ružomberok, SK-034 01 Ružomberok, Slovak Republic; petoholec1@gmail.com
[4]Department of Geology and Palaeontology, Faculty of Natural Sciences, Comenius University in Bratislava, Mlynská dolina, SK-842 15 Bratislava, Slovak Republic; sykora@fns.uniba.sk
[5]State Geological Institute of Dionýz Štúr, Mlynská dolina 1, SK-817 04 Bratislava, Slovak Republic; klement.fordinal@geology.sk

Abstract

A new Western Carpathian record of the archaic hipparionine horse, showing morphological characters of the early Central and Western European representatives of the genus *Hippotherium,* is described. The fossil material has been found in the white, cream-coloured limestone of the Hlavina Member – the marginal Upper Miocene deposits of the Rišnovce Depression in the Slovak part of the Danube Basin. The fossiliferous sediments are dated to the Pannonian. The fossil record consists of a mandible fragment with the rarely preserved deciduous dentition and an isolated upper molar of an adult individual. The morphology of the finds is identical to that of the extinct genus *Hippotherium*. The isolated tooth is determined as *H.* cf. *primigenium*. It exhibits a consistent similarity to the early European representatives of these tridactyle horses in the following combination of characters – (1) highly complex enamel plications; (2) multiple pli-caballing; and (3) the distinctly developed lingual hypoconal groove. However, it is possible that these representatives only retained archaic characteristics. The determination of the deciduous teeth of *Hippotherium* is problematic. In the case of the studied material from Hrdovická hill, the mandible with the deciduous teeth belongs most likely to the same species as the single M1-2. However, the material consists of two different ontogenic grown stages. This makes impossible to decide on the basis of such limited material, if both finds represent independent forms, or if the differences could be caused only by ontogenic changes and/or intraspecific variability. Therefore, the mandible is attributed to *Hippotherium* sp. The study extends our knowledge concerning the characteristics of the Central European representatives and the ontogeny of the European *Hippotherium* genus member.

Key words: *Hippotherium*, dentition, ontogeny, Pannonian, Slovakia

Introduction

Fossils material of *Hippotherium* is described from a new site of fossil vertebrates in the Western Carpathians. Slovak members of this taxon are mainly known from the Pannonian sediments as the classical species *Hippotherium primigenium* (Holec, 1981). Horses from the Hrdovická hill locality are different and exhibit many archaic characteristics, identical with the early representatives of European hipparions. The first populations of *Hippotherium* in Europe were extensively studied because of their stratigraphic importance and they are particularly remarkable for the complexly folded enamel plications on their maxillary and mandibular cheek teeth (Bernor and Franzen, 1997; Bernor et al., 2003; Kaiser et al., 2000; Kaiser, 2003; Scott et al., 2005). The first hipparions in the Central Paratethys appeared during the Pannonian (Rögl and Daxner-Höck, 1996) and were found in the Lower Pannonian sediments (Zone C) in the Vienna Basin (Bernor et al., 1988). Similar finds of archaic hipparions have been found in Austria (see in Vangengeim et al., 2006), Germany (Bernor and Franzen, 1997), Spain (Garces et al., 1997), Turkey (Kappelman et al., 2003) and Pakistan (Pilbeam et al., 1996). The appearance of *Hippotherium* in Euroasia from America, called the "Hipparion Datum", is a major event used extensively in biostratigraphy and biochronology as a marker of the beginning of the Late Miocene (MN 9) (e.g. Garces et al., 1997). However, there are different opinions concerning the age of the "Hipparion Datum" in Europe. According to Rögl and Daxner-Höck (1996), hipparions appeared during the Sarmatian in the Eastern Paratethys and later during the Pannonian, in the Central Paratethys.

This is also currently supported by Koufos et al. (2005), who consider the beginning of the Late Miocene as 10.7 Ma in the Eastern Mediterranean. At present, there is no agreement among researchers as to dating the *Hipparion*--datum, and even there is no consensus on the issue within the same regions (Woodburne et al., 1996; Sen, 1997; Agusti et al., 2001; Koufos, 2003). One of the latest known populations of Central European *Hippotherium* is represented by the Baltavar hipparion assemblage (Kaiser and Bernor, 2006).

Gastropods from the Hrdovická hill locality indicate the Pannonian zone H, MN 11 (Fordinál et al., 1996; Fordinál and Nagy, 1997). It seems to be in contradiction with the character of the new *Hippotherium* finds described here. On the other hand, some representatives may have retained their archaic character, such as those in the Dorn-Dürkheim 1 locality (MN 11) in Germany (Bernor and Franzen, 1997; Keiser et al., 2003). The mandible fragment of *Hippotherium* sp. has a rare preservation of the deciduous teeth. This brings new informations about this taxon. The aims of the paper are as follows: to provide a taxonomic assessment, morphological description and measurement of the new fossil material.

Geological settings and methods

The Central Paratethys existed throughout the Early and Middle Miocene. Marine connections to adjacent seas were already strongly narrowed during the latest Middle Miocene. Finally, at 11.6 Ma the western part of that sea became isolated and Lake Pannon formed (Piller, 2006). Lake Pannon was a large, long-lived, brackish lake that occupied the Pannonian Basin System in the Late Miocene and earliest Pliocene. The lake reached its largest areal extent at ca. 9.5 million years ago, as basin subsidence continued due to cooling of the lithosphere. Many intrabasinal ridges and basement highs, including the Transdanubian Range, were partly or completely inundated by this time (Magyar et al., 1999). The lake hosted a highly endemic fauna and flora, of which the molluscs, ostracods, fishes, dinoflagellates, calcareous nannoplankton and some other algal groups are known as fossils (Papp et al., 1985; Stevanović et al., 1990). The fossil material has been found in white, cream-coloured limestone of the Hlavina Member. The Hlavina Member of the Beladice Formation represents the Upper Miocene marginal freshwater lake sediments of the Rišnovce Depression in the Danube Basin (Fordinál et al., 1996; Fordinál and Nagy, 1997). This sediment crops out especially at the Hrdovická hill, where the taxon *Hippotherium* was found. The locality Hrdovická hill is situated in the western part of the Tribeč Mts., about 1 km east of Čeľadince village in the Slovak Republic (Fig. 1).

Fig. 1. Location of the Hrdovická hill site in Slovakia.

Techniques used for the collecting of material include the prospecting. The study is based on fossils housed in the Slovak National Museum in Bratislava. The standard anatomical orientation system is used throughout this paper. The tooth terminology follows that of Churcher and Richardson (1978). The deciduous teeth belong to a juvenile form of approximately 1 to 1.5 years of age, while the upper molar is from the adult individual.

Abbreviations and definitions
dext. – dexter (right),
Index of hypsodonty (HI) = width of tooth x 100/maximal height.
Preflexid index (PrI) = length of preflexid x 100/length of occlusal surface.
Postflexid index (PoI) = length of postflexid x 100/length of the occlusal surface.
Index double knot (DI) = length of double knot x 100/length of the occlusal surface.

Systematic paleontology

Order Perissodactyla Owen, 1848
Suborder Hippomorpha Wood, 1937
Family Equidae Gray, 1821
Hippotherium Kaup, 1833

Hippotherium cf. *primigenium* von Meyer, 1829

Material: Isolated M1-2 dext. (Z 27101) housed in the Slovak National Museum in Bratislava.

Locality and horizon: The Hlavina Member of the Beladice Formation (the Upper Miocene) located at Hrdovická hill in the Tribeč Mts. in the Slovak Republic.

Description: The upper right isolated molar M1-2 is characterized by closed fossettes with rich enamel

Tab. 1
Dimensions of the isolated M1-2 dext. (in mm)

	mm
Height of crown on the mesostyle	37.8
Height of crown on the protocone	26.7
Lenght of crown	23.4
Width of the occlusal surface	23.4
Lenght of the protocone	6.1
Dimension of the occlusal surface	547.56
Index of tooth	0
Index of protocone	0.26
Abrasion stage	I
Enamel formula	5-3-7-5-3/2

plication in their borders (Fig. 2). The crown is relatively high (Tab. 1) and the roots are missing. However in these animals, the height of the tooth is strongly correlated with the wear. The parastyle is strong and somewhat larger than the mesostyle. The metastyle is not distinctive. The enamel wall of the occlusal surface between the mesostyle and the metastyle is almost straight, and the cement here forms only a very thin layer. The mesial wall is moderately convex and almost without the cement, while the distal wall is flat and is completely lacking in cement. The lingual wall is concave and also the shortest one, with a very thin layer of the cement on its surface. It is mostly situated in the vicinity of the occlusal surface. The enamel formula is 5-3-7-5-3/2. The plis are narrow and deep. The protocone is elliptical and isolated. The hypocone is elliptical with a deep distal hypoconal groove and a clear lingual hypoconal one. The pli--caballin is multiple. There is a narrow furrow between the prefossette and the postfossette which is deep and wide towards the protocone.

Comparison: A single P3-4 dext. described by Holec (1981) from the Pannonian Zone E of Pezinok locality is compared with M1-2 dext. from Hrdovická hill. The studied M1-2 has a smaller occlusal surface and thinner cement on the buccal side. The enamel on the buccal wall between the parastyle and the metastyle is regularly concave without undulation. The protoloph undulation is more complicated and deeper. The protocone is smaller and there are three folds in the tooth from the Hrdovická hill locality in comparison to one in the Pezinok tooth.

The upper molar RLB 9111, described as *Hippotherium* aff. *primigenium* from zone F of the Austrian locality of Götzendorf (in Bernor et al., 1993; figs. 7A, B), has distinctly less plicated enamel in comparison to that from the Hrdovická hill locality. Its pre – and postfossette patterns are only poorly developed, the protocone is elongated and the pli-caballin is double.

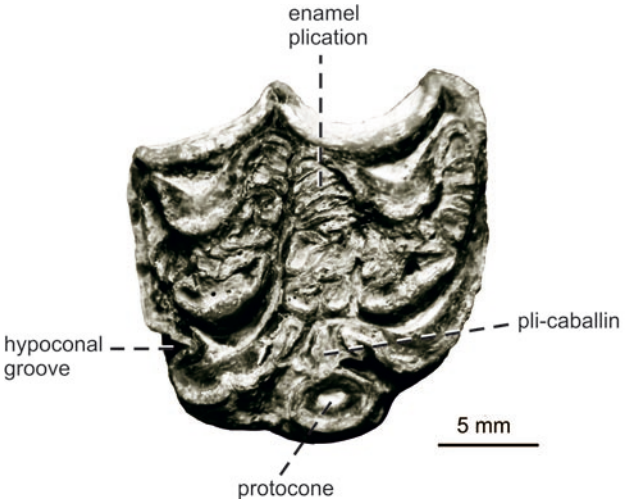

Fig. 2. *Hippotherium* cf. *primigenium* (von Meyer, 1829) from the Hrdovická hill site; occlusal surface of the isolated M1-2 dext., occlusal view.

The premolar and molar finds described by Kaiser and Bernor (2006) from the Late Miocene sediments (MN 12) of the Hungarian locality of Balvatar have complex plications of pre- and postfossettes. However, the pli-caballin varies from being highly reduced on M2, P2 and P4, single on M2 and double on P3.

The occlusal morphology of the isolated molar from the Hrdovická hill locality has a conservative character which allies closely with German hipparions from Eppelsheim (MN 9), Höwenegg (MN 9), but also with Dorn Dürkenheim (MN 11), where the representatives retained their archaic characters (Bernor and Franzen, 1997). Similar features of the highly plicated pre – and postfossettes and multiple pli-caballin are also present in the Valesian MN 9 hipparion assemblage from Hungarian site of Rudabánya, where Bernor et al. (2003) introduced the name *Hippotherium intrans*. The highly complex enamel plications are not as distinctive as in the Hrdovická hill find, and the Rudabánya hipparions represented a more advanced population of *H. primigenium* lineage (see Bernor et al., 1993).

Hippotherium sp.

Material: The right mandible fragment with deciduous teeth dp2-dp4 (Z 27102) housed in the Slovak National Museum in Bratislava.

Locality and horizon: The Hlavina Member of the Beladice Formation (the Upper Miocene) located at Hrdovická hill in the Tribeč Mts. in the Slovak Republic.

Description: Lower teeth: dp2-dp4 dext. There are three lower deciduous teeth in situ in the lower jaw fragment, whose only roots of dp3 are partly visible (Fig. 3). The layer of cement is very thin, or absent. The occlusal surface of all three crowns is anteroposteriorly elongated and slightly mediolaterally compressed (Tab. 2). The enamel wall is surrounding the metaconid, the metastylid and also the protoconid and the hypoconid is undulating. The ectoflexid in dp2 extends deeply toward the isthmus and almost touches the linguaflexid. The ectoflexid of dp3 is not so extended. The double knot is relative short

Tab. 2
Dimensions of the right deciduous teeth dp2, dp3, and dp4 (in mm)

	dp2	dp3	dp4
Lengt of tooth	32	28.5	29.6
Width of tooth	13.5	11.2	10.4
Hight of the tooth crown (in the lingual side)	18.4	20	23.9
Lenght of double knot	10.7	11.6	11.5
Lenght of preflexid	9.8	10.2	10.2
Lenght of postflexid	10.8	13.3	10.3
Index of hypsodonty (HI)	73.36	39.29	43.51
Preflexid index (PrI)	30.62	35.78	29.58
Postflexid index (PoI)	33.75	46.66	34.79
Index of double knot (DI)	33.43	40.7	38.85
Lenght of teeth row		93.6	

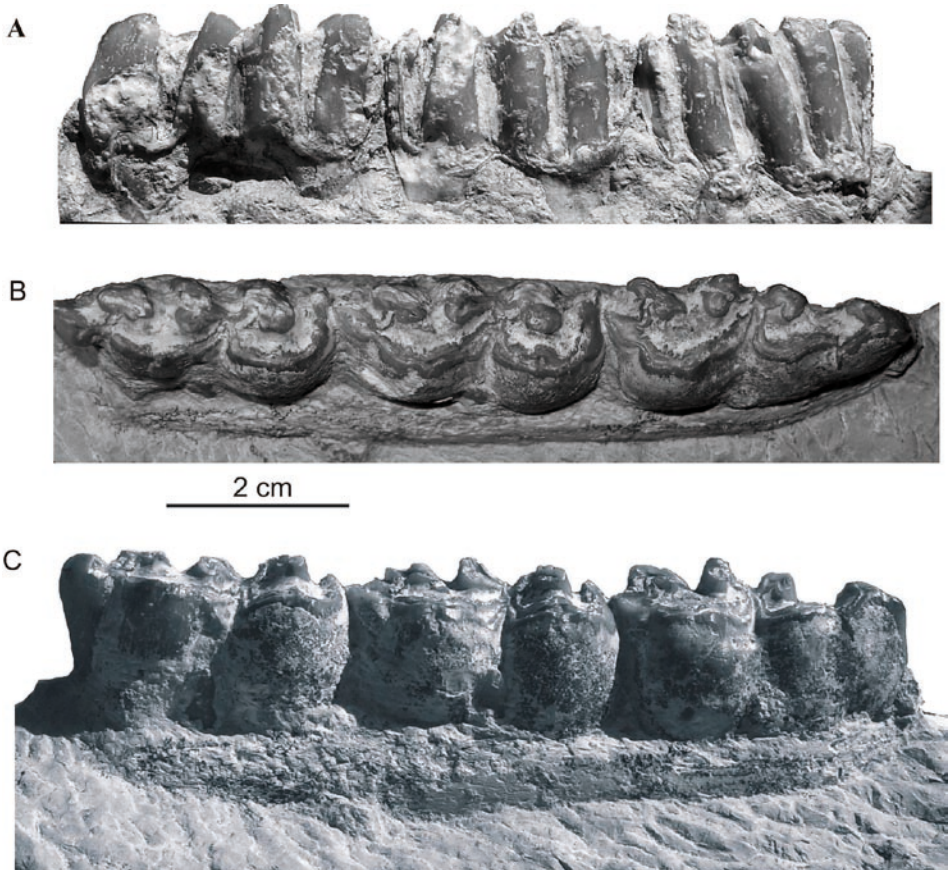

Fig. 3. *Hippotherium* sp. from the Hrdovická hill site; the right mandible fragment with the deciduous dentition dp2-dp4. A – linqual view; B – occlusal view; C – buccal view.

in proportion to the length of the occlusal surface (see index of double knot DI). Their walls are undulosed and the linguaflexid is shallow and U-shaped. The paraconid in dp2 represents a single cone in front of the tooth and an individual hypoconulid is present in dp4.

Comparison: The lack of any certainly determined comparative material or bibliographical data makes comparisons extremely difficult. A material of *Hippotherium* described by Koufos (1984) as *H. macedonicum* from the early Late Miocene of Greece has also preserved deciduous dentition. However, *H. macedonicum* is a small-sized hipparion which is completely different from *H. primigenium*. Its ectostylid is more developed and usually double, while the occlusal surfaces of the deciduous teeth from the Hrdovická hill locality are distinctly anteroposteriorly elongated and more slender.

Discussion and stratigraphy comments

Hipparions, such as those described here, belong to the archaic forms of the group of *H. primigenium*. The determination of the deciduous teeth of *Hippotherium* is problematic. There is no certainly determined comparative material or bibliographical data. In the case of the studied material from Hrdovická hill, the mandible with the deciduous teeth belongs most likely to the same species as the single M1-2. However, the isolated material lacks enough diagnostic features to support this, thus enabling determination to the species level somewhat questionable. Besides this, the material consists of two different ontogenic grown stages. The deciduous teeth belong to the juvenile form approximately 1 to 1.5 years of age. This makes impossible to decide on the basis of such limited material if both finds represent independent forms or if the differences could be caused only by ontogenic changes and/or intraspecific variability. In horses, there are different loading patterns on the cutting edges of upper and lower teeth. A basic requirement for translatory chewing is anisodonty, the differential width of the occluding teeth that allows one toothrow to move across the other while maintaining occlusal contact (see e.g. Fortelius, 1985; Kaiser and Fortelius, 2003). For all these reasons, it is better to attribute the mandible fragment to *Hippotherium* sp.

The isolated molar from the Hrdovická hill in Tribeč Mts. exhibits a large similarity to the early European hipparions, and mainly to those from the Pannonian Zone C (terms after Papp, 1951) in the following combination of characters:

1. Recent research on the European *Hippotherium* has shown that the earliest locally occurring members of this clade had highly complex enamel plications (Bernor and Franzen, 1997; Bernor et al., 2003; Kaiser et al., 2000; Kaiser, 2003; Scott et al., 2005). The richly plicated enamel

of M1-2 from the Hrdovická hill is a particularly notable character of *Hippotherium* evolved in Central and Western Europe, following the "Hipparion Datum".

2. The pli-caballin is multiple, and this feature is present in the early European hipparions, especially those in Central and Western Europe (Koufos, pers. comm.). According to Bernor and Lipscomb (in Bernor et al., 1993), a multiple pli-caballin is a typical feature of the Pannonian C *Hippotherium primigenium* and this feature is consistently double in Pannonian D and later *H. primigenium*.

3. The presence of a strongly developed lingual hypoconal groove. It is regarded as an archaic feature within *Hippotherium* members (Koufos, pers. comm.).

This is in contradiction with the stratigraphy of the locality based on the record of mollusc assemblage indicating zone H. Based on the gastropod assemblage consisted of *Fortuna clairi* Schlickum-Strauch, *Tropidomphalus doderleini* (Brusina), *Helicigona wenzi* Soos, *Bathyomphalus moedlingensis* (Sauerzopf) and *Planorbis confusus* Soos, the age of fossiliferous sediments is consigned to the Upper Pannonian Zone H (Fordinál et al., 1996; Fordinál and Nagy, 1997) (for the stratigraphic range of the gastropods see Sauerzopf, 1953, and Lueger, 1981). The species *Fortuna clairi* Schlickum-Strauch has been described from the Pliocene sediments of Germany (Schlickum and Strauch, 1972), from the Upper Pannonian sediments (Zone H) of the Vienna Basin (Lueger, 1981) and from the Slovak Republic (Fordinál, 1996). The species *Tropidomphalus doderleini* (Brusina) was described only from the Pannonian sediments of the Zone G-H in the Vienna Basin (Lueger, 1981), the Slovak Republic (Fordinál, 1996) and from the upper Pannonian sediments of Hungary (Bartha, 1959). This range is also supported by new studies from Austria, where the species was not found in localities older than Zone G-H (Harzhauser and Binder, 2004; Harzhauser and Temper, 2004). The species *Bathyomphalus moedlingensis* (Sauerzopf) is known only from the sediments of the Zone H of Austria and the Slovak Republic (Sauerzopf, 1953; Fordinál, 1998; Harzhauser and Binder, 2004).

There are two possible explanations for that: (1) The horse material from Hrdovická hill represents an archaic representative belonging to the early European *Hippotherium* members. From this viewpoint, the stratigraphy of the locality is questionable, because it is questionable that the evolution of gastropods in isolated lakes and forests should form the main basis for an exact determination of the age. On the other hand, we could interpret the finds of the archaic *Hippotherium* as having been redeposited from older, and perhaps already non-existent, Lower Pannonian sediments in this area. Freshwater Lower Pannonian sediments have not been found yet in the Slovak part of the Danube Basin. Proof concerning the existence of some mode of transport is contained in the fact that a lot of fragments of terrestrial gastropods living in ambient forests at this time were also found in sediments of this lake. This is also supported by the marginal flat character of the sedimentary environment. (2) The other possibility is that the horse material belongs stratigraphically to the Pannonian zone H (MN 11). The same morphological character is present in the material from the locality of Dorn-Dürkheim in Germany, MN zone 11 described by Keiser et al. (2003), especially on the specimen SMF-DD81 (P3; plate 1, fig. 2). Here, the population retained their archaic characteristics (Bernor and Franzen, 1997). It appears that some or even all the archaic features of cheek teeth typical for the "Hipparion Datum" may have also persisted in some populations (or individuals) during the Upper Pannonian. From this viewpoint, these morphological features which are considered important in the identification of the Pannonian C *Hippotherium* certainly require revision. Anyhow, the exact dating of the material from Hrdovická hill remains unresolved.

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References

Agusti, J., Cabrera, L., Garcés, M., Krijgsman, W., Oms, O. & Parés, J. M., 2001: A calibrated mammal scale for the Neogene of Western Europe. *State of the Art. Earth Sci. Rev., 52, 247 – 260.*

Bartha, F., 1959: Finomrétegtani vizsgálatok a Balaton környéki felsö-pannon képzödményeken. *Magy áll. földt. Intéz. Évk., 48, 3 – 191.*

Bernor, R. L., Kovar-Eder, J., Lipscomb, D., Rögl, F., Sen, S. & Tobien, H., 1988: Systematic, stratigraphic and paleoenvironmental contexts of first appering Hipparion in the Vienna Basin, Austria. *J. Vert. Pal., 8, 4, 427 – 452.*

Bernor, R. L., Mittmann, H. W. & Rögl, F., 1993: Systematics and chronology of the Götzendorf "Hipparion" (Late Miocene, Pannonian F, Vienna Basin). *Ann. Naturhist. Mus. (Wien), 95, 101 – 120.*

Bernor, R. L. & Frantzen, J., 1997: The hipparionine horses from the Turolian age (Late Miocene) locality of Dorn Dürkheim, Germany. *Cour. Forsch. Inst. Senckenberg, 30, 117 – 185.*

Bernor, R. L., Armour-Chelu, M., Kaiser, T. M. & Scott, R. S., 2003: An evaluation of the late MN 9 (Late Miocene, Vallesian age) Hipparion assemblage from Rudabánya (Hungary): Systematic background, functional anatomy and paleoecology. *In: Nieves Lopéz-Martínez, N., Peláez-Campomanes, P., & Hernándes Fernándes, M. (eds.): Sorrounding Fossil Mammals: Dating, Evolution and Paleoenvironment. Coloquios de Paleontología. Vol. Extraordinario No. 1 en homenaje al Dr. Remmert Daams, 35 – 45.*

Churcher, C. S. & Richardson, M. L., 1978: Equidae. *In: Maglio, V. J., & Cooke, H. S. B. (eds.): Evolution of African Mammals. Cambridge, MA: Harvard University Press, 379 – 422.*

Fordinál, K., 1996: Terrestrial gastropods of the Upper Pannonian in the northern part of the Danube Basin. *Slovak Geol. Mag., 1, 5 – 16.*

Fordinál, K., 1998: Freshwater gastropods of Upper Pannonian age in the northern part of the Danube Basin. *Slovak Geol. Mag., 4, 293 – 300.*

Fordinál, K., Nagy, A. & Fejdiová, O., 1996: Upper Pannonian freshwater sediments from the surroundings of Čeľadince (western margin of the Tríbeč Mts., Slovakia). *Miner. Slov., 28, 307 – 311.*

Fordinál, K. & Nagy, A., 1997: Hlavina Member – marginal Upper Pannonian sediments of the Rišnovce depression. *Miner. Slov., 29, 401 – 406.*

Fortelius, M., 1985: Ungulate cheek teeth: Developmental, functional, and evolutionary interrelations. *Acta Zool. Fennica, 180, 1 – 76.*

Garces, M., Cabrera, L., Agusti, J. & Pares, M. J., 1997: Old World appearance datum of *Hipparion* horses: Late Miocene large mammal dispersal and global events. *Geology, 25, 19 – 22.*

Harzhauser, M. & Binder, H., 2004: Synopsis of the late Miocene mollusc fauna of the classical sections Richardhof and Eichkogel in the Vienna Basin. *Arch. Molluskenkde, 133, 109 – 165.*

Harzhauser, M. & Temper, P. M., 2004: Late Pannonian wetland ecology of the Vienna Basin based on molluscs and lower vertebrate assemblages (Late Miocene, MN 9, Austria). *Cour. Forsch. Inst. Senckenberg, 246, 55 – 68.*

Holec, P., 1981: Occurrences of *Hipparion primigenium* (H. v. Meyer, 1829) (Mammalia, Equidae) remnants in the Neogene of the West Carpathians (Slovakia, Czechoslovakia). *Geol. Carpath., 32, 427 – 447.*

Kaiser, T. M., 2003: The dietary regiments of two contemporaneous populations of *Hippotherium primigenium* (Perissodactyla, Equidae) from the Vallesian (Upper Miocene) of South Germany. *Palaeogeogr. Palaeoclimatol. Palaeoecol. (Amsterdam), 198, 381 – 402.*

Kaiser, T. M., Solounias, N., Fortelinius, M., Bernor, R. L. & Schrenk, F., 2000: Tooth mesowear analysis on *Hipparion primigenium* from the Vallesian Dinotheriensande (Germany). A blind test study. *Carolinea, 58, 103 – 114.*

Kaiser, T. M. & Fortelius, M., 2003: Differential mesowear in occluding upper and lower molars: Opening mesowear analysis for lower molars and premolars in hypsodont horses. *J. Morphology, 258, 67 – 83.*

Kaiser, T. M., Bernor, R. L., Scott, R. S., Franzen, J. L. & Solounias, N., 2003: New Interpretations of the Systematics and Palaeoecology of the Dorn-Dürkheim Hipparions (Late Miocene, Turolian Age [MN11]), Rheinhessen, Germany. *Senckenberg. lethaea, 83, 103 – 133.*

Kaiser, T. M., & Bernor, R. L., 2006: The Balvatar Hippotherium: A mixed feeding Upper Miocene hipparion (Equidae, Peryssodactyla) from Hungary (east-central Europe). *Beitr. Paläont., 30, 241 – 267.*

Kappelman, J., Duncam, A., Feshea, M., Lunkka, J. P., Ekart, D., McDowell, F., Ryan, T. & Swisher III, C. C., 2003: Chronology of the Sinap Formation. *In: Fortelius, M., Kappelman, J., Sen, S. & Bernor, R. L. (eds.): Geology and Paleontology of the Miocene Sinap Formation, Turkey, Columbia Univ. Press, New York, 41 – 66.*

Koufos, D. G., 1984: A new *Hipparion* (Mammalia, Perissodactyla) from the Vallesian (Late Miocene) of Greece. *Paläont. Z. (Stuttgart), 58, 307 – 317.*

Koufos, D. G., 1984: A new *Hipparion* (Mammalia, Perissodactyla) from the Vallesian (Late Miocene) of Greece. *Paläontol. Z., 58, 307 – 317.*

Koufos, G. D., 2003: Late Miocene mammal events and biostratigraphy in the Eastern Mediterranean. *In: Reumer, J. W. E. & Wessels, W. (eds.): Distribution and Migration of Tertiary Mammals in Eurasia, 343 – 372.*

Koufos, D. G., Kostopoulos, D. S. & Vlachou, Th. D., 2005: Neogene/Quaternary mammalian migrations in Eastern Mediterranean. *Belg. J. Zool., 135, 2, 181 – 190.*

Lueger, J. P., 1981: Die Landschnecken im Pannon und Pont des Wiener Beckens. I. Systematik, II Fundorte, Stratigraphie, Faunenprovinzen. *Denkschr. Österr. Akad. Wiss., math.-naturwiss. Kl., 120, 1 – 124.*

Magyar, I., Geary, D. H. & Müller, P., 1999: Paleogeographic evolution of the Late Miocene Lake Pannon in Central Europe. *Palaeogeogr. Palaeoclimatol. Palaeoecol. (Amsterdam), 147, 151 – 167.*

Papp, A., 1951: Das Pannon des Wiener Beckens. *Mitt. Geol. Gesell. (Wien), 39 – 41.*

Papp, A., Jámbor, Á. & Steininger, F. F. (eds.), 1985: Chronostratigraphie und Neostratotypen, Miozän der Zentralen Paratethys 7, Pannonien. *Akadémiai Kiadó, Budapest, 1 – 636.*

Pilbeam, J., Morgan, M., Barry, J. C. & Flynn, L., 1996: Europenean MN Units and the Siwalik Faunal Sequence of Pakistan. *In: Bernor, R. L., Fahlbusch, V. & Mittman, H. W. (eds.): The Evolution of Western Euroasian Neogene mammal faunas. Columbia Univ. Press, New York, 96 – 105.*

Piller, W. E., 2006: The central Paratethys: An example for the isotopic evolution of an epicontinental sea. *In: Allison, P. A., Wells, M. R. & Pratt, B. R. (eds.): Epi-continental Seas in the Geological Record: The Limitations of the Uniformitarian Paradigm II. The Geological Society of America (GSA), 38, 7, 540.*

Rögl, F. & Daxner-Höck, G., 1996: Late Miocene Paratethys correlations. *In: Bernor, R. L., Fahlbusch, V. & Mittman H. W. (eds.): The Evolution of Western Euroasian Neogene mammal faunas. Columbia Univ. Press, New York, 96 – 105.*

Sauerzopf, F., 1953: Die Planorbiidae aus dem Pannon des Alpenostrandes. *Burgenländische Heimatbläter, (Eisenstadt), 15, 49 – 66.*

Scott, R. S., Bernor, R. L. & Raba, W., 2005: Hipparionine horses of the Greater Pannonian Basin: Morphometric evidence from the Postcranial Skeleton. *In: Bernor, R. L., Kordos, L. & Rook, L. (eds.): Multidisciplinary Research at Rudabánya. Palaeontogr. italica, 90, 195 – 210.*

Schlickum, W. R. & Strauch, F., 1972: Zwei neue Landschneckengattungen aus dem Neogen Europas. *Arch. Moll. (Frankfurt a. M.), 102, 71 – 76.*

Sen, S., 1997: Magnetostratigraphic calibration of the European Neogene mammal chronology. *Palaeogeogr. Palaeoclimatol. Palaeoecol. (Amsterdam), 133, 181 – 204.*

Stevanović, P. M., Nevesskaya, L. A., Marinescu, F., Sokać, A. & Jámbor, Á. (eds.), 1990: Chronostratigraphie und Neostratotypen, Neogen der Westlichen ("Zentrale") Paratethys 8, Pontien. *Jazu and Sanu, Zagreb Beograd, 1 – 952.*

Vangengeim, E. A., Lungu, A. N. & Tesakov, A. S., 2006: Age of the Vallesian Lower Boundary (Continental Miocene of Europe). *Stratigraphy and Geological Correlation, 14, 655 – 667.*

Woodburne, M. O., Bernor, R. L. & Swisher, III, C. C. 1996: An appraisal of the stratigraphic and phylogenetic bases for the *"Hipparion"* Datum in the Old World. *In: Bernor, R. L., Fahlbusch, V. & Mittmann, H. W. (eds.): The Evolution of Western Eurasian Neogene Mammal Faunas, Columbia Univ. Press, New York, 124 – 136.*

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