

Rhinocerotidae from the Upper Miocene deposits of the Western Pannonian Basin (Hungary): implications for migration routes and biogeography

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Abstract: Although the rhinoceros remains have high biochronological significance, they are poorly known or scarcely documented in the uppermost Miocene deposits of Europe. Several specimens collected from the Upper Miocene (around 7.0 Ma, Turolian) deposits of Kávás (Pannonian Basin, Western Hungary), previously determined as *Rhinoceros* sp., are revised and described in this paper. The postcranial remains of these specimens belong to “*Dihoplus*” *megarhinus* (de Christol) on the basis of the morphological and morphometric characters of humerus, radii, metacarpal and metatarsal elements. An overview of rhinoceros remains from several uppermost Miocene localities and the revision of the rhinoceros material from the Pannonian Basin suggest that “*D.*” *megarhinus* spread during the latest Miocene from the Pannonian Basin towards Italy. The occurrences of this species in Western Hungary and Italy during the latest Miocene further imply that Rhinocerotini species were biogeographically segregated between Western, Southern and Central Europe.

Key words: “*Dihoplus*” *megarhinus*, postcranium, paleobiogeography, biochronology, latest Miocene, Kávás, Pannonian Basin.

Introduction

The occurrences of Rhinocerotidae species have been frequently used as a biochronological tool since the works of Guérin (1980, 1982). However, the temporal and spatial distribution of some species is still debated or remains poorly known, as does their taxonomic status and morphological variability (Guérin 1980, 2004; Groves 1983; Cerdeño 1992, 1995, 1998; Heissig 1999; Pandolfi & Tagliacozzo 2015). During the Late Miocene, only three species belonging to the tribe Rhinocerotini (sensu Heissig 1999=Rhinocerotina in Antoine 2002) have been identified in Europe: *Dihoplus schleiermayeri* (Kaup 1832), *Dihoplus pikermiensis* (Toula 1906) and *Ceratotherium neumayri* (Osborn 1900).

D. schleiermayeri occurs in the Vallesian and lower Turolian deposits (from MN 9 to MN 12) at several Central and Western European localities (Kaup 1832; Guérin 1980; Cerdeño 1992; Heissig 1999). *D. pikermiensis* occurs in the Turolian deposits (?MN 11–MN 13) of the Balkan Peninsula, in particular in Greece and Bulgaria (Geraads 1988; Heissig 1999; Geraads & Spassov 2009). *C. neumayri* has been reported from several fossiliferous localities (MN 10–MN 13) of the Balkan Peninsula, Caucasus, Anatolia and Iran (Osborn 1900; Geraads 1988; Heissig 1999; Geraads & Spassov 2009; Giaourtsakis 2009; Pandolfi 2015a). The co-existence of *C. neumayri* and *D. pikermiensis* is well-documented at Pikermi and Samos and the two species are

constantly present in Greece until the MN 12–MN 13 transition (Heissig 1996). The rhinoceros remains chronologically referred to MN 13 are scarcely documented in Europe (Heissig 1996).

During the Pliocene (MN 14, MN 15, MN 16a) the three aforementioned species were not reported from Europe. The tribe Rhinocerotini is instead represented by four species: “*Dihoplus*” *megarhinus* (de Christol 1834), “*Stephanorhinus*” *miguelcrusafonti* (Guérin & Santafé-Llopis 1978: which is here provisionally retained within the genus *Stephanorhinus*, although cranial remains of this species are unknown and its systematic position appears questionable), *Stephanorhinus jeanvireti* (Guérin 1972: following the ICZN art. 23.12 and 23b, *Rhinoceros elatus* Croizet & Jobert 1828 is synonymous with this species, details are reported in Guérin & Tsoukala 2013, p. 454) and *Stephanorhinus etruscus* (Falconer 1868).

“*D.*” *megarhinus* has been considered a typical Pliocene species (Guérin 1980; Pandolfi 2013) and it has been also recorded in Turkey and Russia (Guérin & Sen 1998; Fukuchi et al. 2009). “*S.*” *miguelcrusafonti* has a restricted geographical and chronological range; it has been recovered at a few early Pliocene Spanish and French localities (Guérin & Santafé-Llopis 1978; Guérin 1980). *S. jeanvireti* has been frequently documented from Late Pliocene localities of France and Italy (Guérin 1972, 1980; Pandolfi 2013), but it has also been recorded in Slovakia (Đurišová 2004; Vlačíky

et al. 2008; Šujan et al. 2013), in Romania (Guérin 1980), in Russia (Titov 2008), and recently in Greece (Guérin & Tsoukala 2013). At the end of the Pliocene, *S. etruscus* has been also recorded in Western Europe (Guérin 1980; Cerdeño 1993; Mazo 1995; Pandolfi 2013; Pandolfi & Marra 2015; Pandolfi et al. 2015a).

The aim of this paper is to describe postcranial rhinoceros remains collected in the Upper Miocene deposits at Kávás (Western Hungary, Fig. 1) and (1) to analyse morphological differences between the Late Miocene and Pliocene species usually assigned to the genera *Dihoplus* and *Stephanorhinus* and (2) to discuss the implications of these findings for migration patterns and biogeography of Rhinocerotidae at the end of the Miocene.

Geological and stratigraphic background

The specimens analysed here were collected from grey, clayey, fine-grained sand or sandstone deposits near the village of Kávás in 1979 (although the name of the collector is missing from the Inventory Book, it was probably Dénes Jánossy). Kávás is located in the western part of the Neogene Pannonian Basin (Fig. 1). The basement of the Neogene infill in this region is represented by Upper Triassic dolomites belonging to the Transdanubian Range (Bakony Mts.). The pre-Neogene basement forms a flat platform at a depth of ca. 1800 m below sea level, separating the Kisalföld sub-basin to the north and the Zala subbasin to the south (Haas et al. 2010).

The Neogene basin fill at Kávás was penetrated by a hydrocarbon exploration well (Nf-3) in the early 1970s. Its 1853 m-thick Neogene sequence started with a 78 m-thick marine unit, consisting of glauconitic calcareous marl with abundant remains of benthic and planktonic foraminifers and pectinid bivalves. The fossils indicate Middle Miocene (Badenian) age. The overlying unit, from 1775 m up to the surface, belongs to the Pannonian. The Pannonian Stage, as used in

Hungary (Pannonian *sensu lato*), corresponds to the Upper Miocene and the Pliocene. Its sedimentary succession was deposited in Lake Pannon, a giant brackish lake, and in the adjacent deltaic and fluvial environments. The Pannonian succession in the Nf-3 borehole can be subdivided into five lithological units, including: (1) marls deposited in a deep lacustrine setting (Endrőd Formation; 1775 to 1623 m), (2) alternation of argillaceous marl and fine-grained sandstone layers, the latter deposited by turbidity currents (Szolnok Formation; 1623 to 1410 m), (3) argillaceous marl and silt with subordinate sandstone layers, deposited on the shelf-margin slope (Algyő Formation; 1410 to 1160 m), (4) alternation of argillaceous marl, sandstone, and lignite layers deposited in shallow lacustrine, deltaic, and paludal environments (Újfalu Formation; 1160 to ca. 400 m), and (5) clay, sand, and fine-grained gravel deposited in flood plains, point bars, and river channels (Zagyva Formation; ca. 400 m to the surface; Fig. 2). The samples collected from the Endrőd and Szolnok formations contained ostracods and cardiid molluscs endemic to Lake Pannon (for a detailed description of the Pannonian formations, see Juhász 1991; Juhász et al. 2007; Sztanó et al. 2013a).

Although the Kávás rhinoceros specimens were originally described as “Lower Pannonian” (this term was traditionally used for the fine-grained deep-water deposits of Lake Pannon), they were obviously recovered from the fluvial succession of the Zagyva Formation, widely outcropping in the vicinity. The clayey sand embedding the bones was deposited in the floodplain of a river that flowed into Lake Pannon several tens of kilometers further to the south.

Age assessments within the Pannonian Stage in NW Hungary are based on correlations of biostratigraphic, magnetostratigraphic, and seismic stratigraphic data (Magyar et al. 2007), and carry a significant uncertainty. The shelf-margin slope below Kávás has an estimated age of 8.9 Ma (Magyar et al. 2007, 2013). The base of the *Prosodacnomys* zone, dated to 8.0 Ma in Tihany (Sztanó et al. 2013b), is inferred

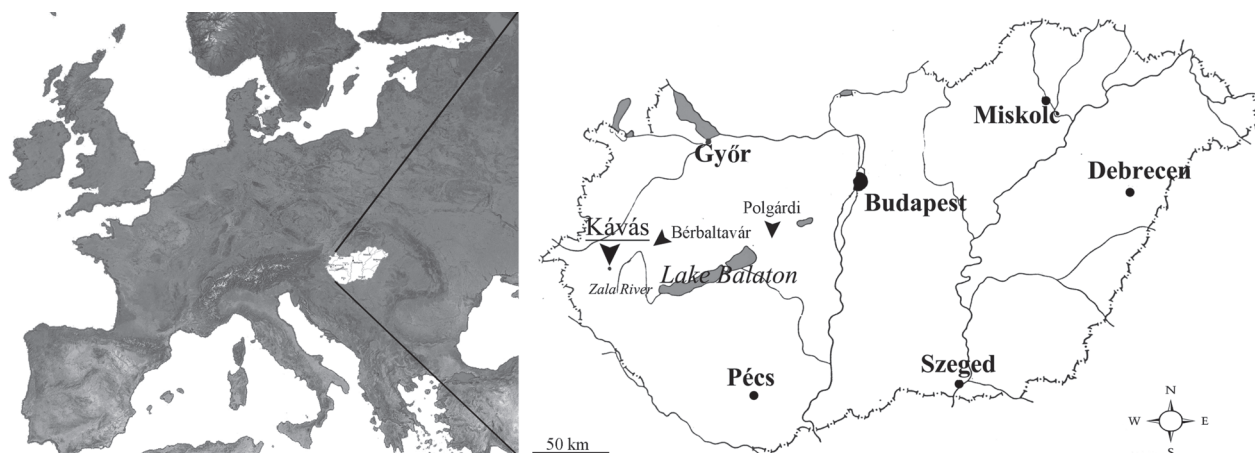


Fig. 1. Location map of Kávás, Pannonian Basin, Western Hungary and other Late Miocene Hungarian localities mentioned in the text.

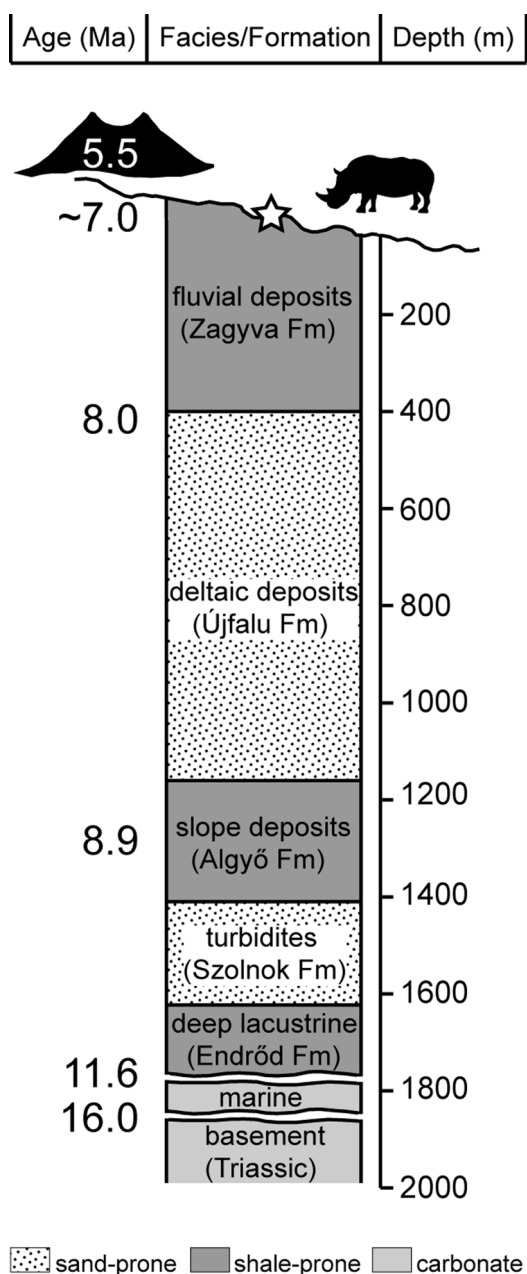


Fig. 2. Stratigraphic position and estimated age of the Kávás outcrop (asterisk) within the Pannonian sequence. The Neogene succession at Kávás is based on a hydrocarbon exploration well.

to be at about 420 m depth in the Nf-3 borehole. Volcanoes of the Little Hungarian Plain Volcanic Field, sitting on the eroded surface of the Zagyva Formation, yield latest Miocene and earliest Pliocene age (e.g. Ság-hegy, 5.5 Ma; Wijbrans et al. 2007). The age of the Kávás locality thus can be estimated as 7.0 Ma (± 0.5 Ma), corresponding to the latest Tortonian/earliest Messinian (i.e., Turolian Land Mammal Age).

The famous Bérbaltavár (better known as Baltavár: Suess 1861; Pethő 1885; Kormos 1914; Benda 1927; Kretzoi 1985, 1987) mammal locality (MN 12 zone: Bernor et al. 2003, 2005; Kaiser & Bernor 2006) is located some 25 km north-

eastward of Kávás. Seismic profiles between the two localities show that the Pannonian layers (horizons) are gently dipping southwards, indicating that Kávás is slightly younger than Bérbaltavár.

Material and methods

The revised Quaternary time scale of Gibbard et al. (2010) is used for chronological references in this text. The bottom and top boundaries of the Pliocene are placed at 5.4 Ma and 2.6 Ma.

The specimens from Kávás collected in 1979 were inventoried as *Rhinoceros* sp. All the specimens have the same registration number V.79.117 in the Inventory Book of the Department of Paleontology and Geology of HNHM. Some cranial elements (Pandolfi et al. 2015b) have the same registration number but it is unclear whether cranial and postcranial remains belong to the same individual. Taphonomic data or photographs of the excavations are not available. However, similarity in dimensions and the existence of left and right bones with the same size and shape suggests that the elements can belong to a single individual. The postcranial elements were morphologically compared with the rhinoceros material collected at several Late Miocene and Pliocene localities of Eurasia and housed in several museums and institutions, as well as with published data (Appendix). The anatomical descriptions follow Guérin (1980) and Antoine (2002), whereas the morphometric approach follows Guérin (1980).

Institutional Abbreviations:

HNHM, Magyar Természettudományi Múzeum (Hungarian Natural History Museum), Budapest, Hungary;
IGF, Museo di Storia Naturale, sezione di Geologia e Paleontologia, Florence, Italy;
MFGI, Magyar Földtani és Geofizikai Intézet (Geological and Geophysical Institute of Hungary), Budapest, Hungary;
MfN, Museum für Naturkunde, Berlin, Germany;
MGGC, Museo di Geologia Giovanni Capellini, Bologna, Italy;
MNCN, Museo Nacional de Ciencias Naturales, Madrid, Spain;
MNHN, Muséum National d'Histoire Naturelle, Paris, France;
MPLBP, Museo di Paleontologia Luigi Boldrini di Pietrafitta, Perugia, Italy;
MPP, Museo di Paleontologia, Università di Parma, Parma, Italy;
MPUR, Museo di Paleontologia, Sapienza, Università di Roma, Rome, Italy;
MSNAF, Museo di Storia Naturale, Accademia dei Fisiocritici, Siena, Italy;
MSNF, Museo di Storia Naturale, sezione di Zoologia, Florence, Italy;
NHML, Natural History Museum, London, England;
NHMW, Naturhistorisches Museum, Wien, Austria;
NMB, Naturhistorisches Museum, Basel, Switzerland.

Systematic palaeontology

Order: **Perissodactyla** Owen 1848
 Family: **Rhinocerotidae** Gray 1821
 Tribe: **Rhinocerotini** Gray 1821
 Genus: *Dihoplus* Brandt 1878

Type Species: *Rhinoceros schleiermacheri* Kaup 1832 from the Late Miocene of Eppelsheim, Germany.

“Dihoplus” megarhinus (de Christol 1834)
 (Figs. 3-4, Table 1)

Note: *Rhinoceros megarhinus* de Christol 1834 has sometimes been reported as a synonym of *Rhinoceros leptorhinus*

Cuvier 1822. However, the Cuvier’s name was based on the inaccurate description of heterogeneous material belonging to two or three different taxa (Guérin et al. 1969).

The species *Rhinoceros megarhinus* was typically assigned to the genus *Dicerorhinus* Gloger 1841 (Guérin 1980, 1982; Guérin & Sen 1998; Guérin & Tsoukala 2013), represented by the recent species *Dicerorhinus sumatrensis* (Fisher 1814) (see Grooves 1983). However, as noted by Pandolfi (2013) and Pandolfi et al. (2015b), *D. sumatrensis* differs from *R. megarhinus* in having the posterior border of the nasal notch at the level of P2, the dorsal profile of the skull less concave, the occipital face oblique inclined forward, the external auditory pseudomeatus open, the protocone and the hypocone separated on the upper premolars and the metacone fold well developed on the upper premolars (cranial material of *D. sumatrensis* housed at MNHN, MSNF,

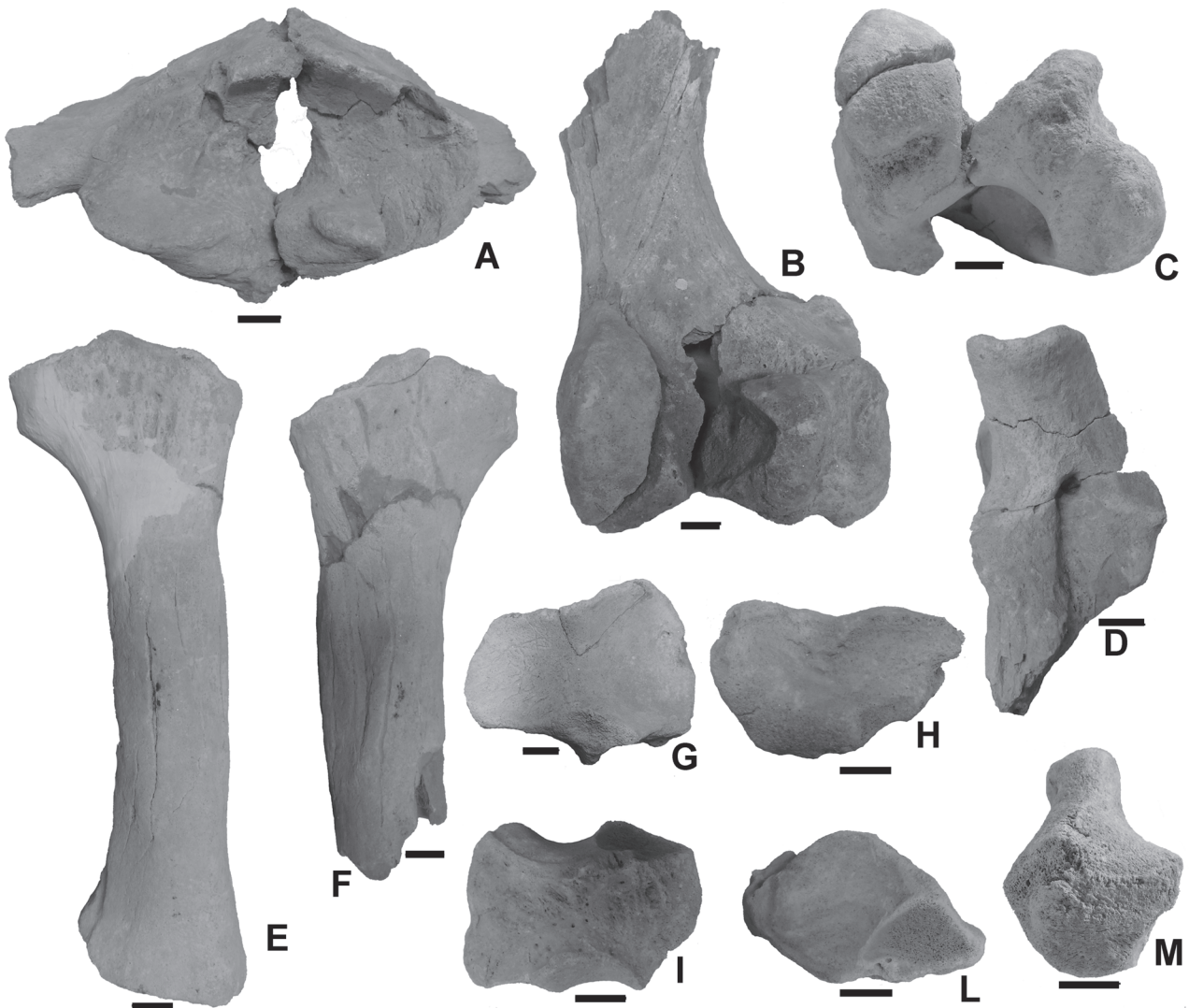


Fig. 3. *“Dihoplus” megarhinus* from Kávás. **A** — atlas HNHM V.79.117-7, anterior view; **B** — humerus HNHM V.79.117-8, anterior view; **C** — humerus HNHM V.79.117-8, distal view; **D** — ulna fragment HNHM V.79.117-9, proximal articular surface view; **E** — radius HNHM V.79.117-10, anterior view; **F** — radius HNHM V.79.117-11, anterior view; **G** — radius HNHM V.79.117-11, proximal view; **H** — radius distal epiphysis HNHM V.79.117-12, distal view; **I** — scaphoid HNHM V.79.117-13, medial view; **L** — scaphoid HNHM V.79.117-13, proximal view; **M** — magnum HNHM V.79.117-15, anterior view. Scale bars=2 cm.

NHML and NMB: Pandolfi 2013; Pandolfi et al. 2015b). The species *Rhinoceros megarhinus* was recently assigned to the genus *Dihoplus* (e.g., Lacombe & Mörs 2008) following the hypothesis proposed by Heissig (1989, 1996, 1999) who suggested an evolutionary lineage leading from *Dihoplus schleiermayeri* to “*Dicerorhinus*” *megarhinus*. Deng et al. (2011) ascribed the species *R. megarhinus* to *Dihoplus*, but in the parsimonious trees figured by these authors (Deng et al. 2011: fig. S7), the genus *Dihoplus* was paraphyletic and *D. megarhinus* clearly did not form a clade with the species *Dihoplus pikermiensis* and *Dihoplus ringstroemi*. Moreover, the type species of the genus *Dihoplus*, *D. schleiermayeri*, was not included in the analysis of Deng et al. (2011). The latter species was considered in the unpublished analysis reported by Pandolfi et al. (2014) and Pandolfi (2015a) but it did not form a clade with *D. megarhinus* which was included within the paraphyletic genus *Stephanorhinus* Kretzoi 1942. An assignment to the latter genus was proposed by Groves (1983), Fortelius et al. (1993) and Cerdeño (1995). Nevertheless, de Christol’s species does not show the typical morphological characters described as diagnostic for *Stephanorhinus* (e.g., ossified nasal septum or loss of anterior teeth), and the phylogenetic relationships within this genus are yet to be resolved. In agreement with Pandolfi et al. (2015b), we provisionally retain the species *R. megarhinus* within the genus *Dihoplus*.

Material: HNHM V.79.117; 16 post-cranial remains, one atlas, one distal epiphysis of humerus, one proximal fragment of ulna, two proximal epiphysis of radius, one distal epiphysis of radius, one damaged scaphoid, one damaged pyramidal, one fragment of magnum, two fragmentary second metacarpal, one damaged third metacarpal, one fourth metacarpal, a fragmentary pelvis, one third cuneiform, one proximal half of fourth metatarsal.

Description and comparison

Atlas: The atlas HNHM V.79.117-7 is poorly preserved and the transverse processes are partially damaged (Fig. 3A). In dorsal view, the dorsal tubercle is relatively large, the two alar foramina are partially damaged but appear large. The posterior border of the bone is concave. In ventral view, the ventral tubercle is developed and extends posteriorly. In anterior view, two deep articular surfaces for the occipital condyles are present (Fig. 3A); they are externally delimited by a marked edge. In posterior view, the articular surfaces for the axis are flat.

In the atlas of *D. schleiermayeri* from Eppelsheim (NHML 1284) the anterior articular surfaces are more distally separated than in the studied specimen. In anterior view, the atlas of *S. etruscus* (specimens from Capitone and Upper Valdarno: Appendix) differs from the studied specimen in having a more rounded proximal-lateral border of the articular surface and in being less massive. A relatively well preserved atlas of “*D.*” *megarhinus* from Montpellier (NHMB Mp922) displays the same morphological characters described for the atlas from Kávás. Unfortunately, no atlas of “*S.*” *miguelcrusafonti* is known, and we had no opportunity

to observe directly any atlas attributed to *S. jeanvireti* or *D. pikermiensis*.

Humerus: Only a distal epiphysis of a humerus V.79.117-8 is kept at HNHM. The trochlea is anteriorly damaged (Fig. 3B–C). In anterior view, the medial border of the medial lip of the trochlea is slightly convex whereas the lateral border of the lateral lip is straight (Fig. 3B–C). The lateral tuberosity is well developed and large, the medial tuberosity is much smaller. The lateral epicondylar crest is relatively short, marked and well developed. The trochlear fossa is transversally elongated. In posterior view, the lateral epicondylar crest is well developed, the olecranon fossa is wide and deep. The lateral epicondyle is large and well developed and the medial epicondyle is massive. In distal view, the medial lip of the trochlea has a convex medial border; the posterior border of the trochlea is regularly concave and the medial epicondyle extends posteriorly (Fig. 3B–C). The lateral tuberosity is well developed and rounded.

In distal view, the humeri of *D. pikermiensis* (Appendix) display a smaller and less anterior-posteriorly developed lateral tuberosity. The studied specimen has a larger olecranon fossa than in *S. jeanvireti* (Appendix) and the bone is more massive than in *S. jeanvireti* and *S. etruscus* (Appendix). No morphological data are available on the humeri of “*S.*” *miguelcrusafonti* and *D. schleiermayeri*. The humeri of “*D.*” *megarhinus* from Monte Giogo (MPP: Simonelli 1897) and Val di Pugna (MSNAF 7100) have a marked antero-posterior crest in the lateral side of the distal epiphysis, a large olecranon fossa and massive epicondyles as in the studied specimen. The humerus of “*D.*” *megarhinus* from Saint-Laurent (Guérin et al. 1969: figs. 18–19) displays a sinuous medial border of the medial lip of the distal trochlea and the posterior-medial epicondyle is massive as well as in the specimen from Kávás. The specimens of “*D.*” *megarhinus* from Montpellier (Appendix) share several morphological characters with those from Kávás: e.g., the posterior-lateral epicondyle on the humerus is well developed and larger than the medial one, the lateral epicondylar crest is well evident. The dimensions of the distal epiphysis of the humerus from Kávás are slightly larger than those of “*D.*” *megarhinus* from several Pliocene localities (Table 1).

Ulna: The ulna is represented by a fragment of a proximal epiphysis HNHM V.79.117-9 (Fig. 3D). In anterior view, the medial and lateral sides of the articular surface for the humerus are concave. The articular surfaces for the radius are not evident due to the bad preservation. The sigmoid incisure is relatively high, flat, and distally delimited by a deep foramen (Fig. 3D).

The ulna of *D. schleiermayeri* differs from the studied specimen in having, in anterior view, a more asymmetrical articular surface (Guérin 1980: fig. 34C). With respect to the specimen from Kávás, the proximal articular surface of the ulna of *D. pikermiensis* (Appendix) is more transversally developed and the medial lip is more concave. The proximal articular surface of the ulna of *S. jeanvireti* (Appendix) appears to be more slender than that of the studied specimen and the medial lip is higher and more concave. In *S. etruscus* (Appendix) the sigmoid incisure is shorter than in Kávás and the proximal articular surface is more symmetrical in ante-

Table 1: Measurements (in mm) of the postcranial remains of “*Dihoplus*” *megarhinus* from Kávás (Zala subbasin, Hungary), compared with those of “*D.*” *megarhinus* from Montpellier (Early Pliocene, France), Udunga (latest Pliocene, Russia), and with the minimal and maximal values given by Guérin (1980). **DTD** — distal transverse diameter; **DAPD** — distal antero-posterior diameter; **DTDth** — distal transverse diameter of the trochlea; **TDof** — transverse diameter of the olecranon fossa; **PTD** — proximal transverse diameter; **PAPD** — proximal antero-posterior diameter; **TD** — transverse diameter; **lxH** — breadth and height; **L** — length; **DTDmax** — maximal distal transverse diameter.

Measurement	Kávás (HNHM v.79.117)	Montpellier (NMB various specimens)	Western Europe (from Guérin, 1980)	Udunga (from Fukuchi et al., 2009)
Humerus DTD	171	153.44–160.16	144–166	154.4–158.9
Humerus DAPD	137.2	125.1–132.96	100–135	99.5–120.8
Humerus DTDth	120.1	98.61–126.43		
Humerus TDof	53.5	43.65–55.76		
Radius PTD	120.4	108.13–111.19	94.5–116	96.1–110.6
Radius PAPD	85–86.1	70.52–80.10	61–82	66.8–82
Scaphoid TD	58.7	61.6	50–72.5	47.5–65.1
Magnum TD	51		44.5–61	51.1–60.4
Pyramidal lxH	54.7×63	53.64×65.75	49–65.5×53–64	41.9–65.6×52.9–71.6
MCII PTD	55.9–59.3	53.46–57.52	39–58.5	49.5–58.1
MCIII PAPD	50.5	53.98–57.22	48–58	44.5–58.2
MCIV PTD	48.5	53.02	48–54	42–67.3
MCIV PAPD	46.1	44.63	36.5–47	39.5–53.2
Third cuneiform lxH×L	57.1×29.9×57.7		48.5–57×29.5–35×47–61	51.3–60.6×28–35.2×54.7–66.6
MTIV L	167.5		164–182	
MTIV DTDmax	40.5		39–42	

rior view. The morphological characters of the studied specimen are also evident in a fragmentary ulna of “*D.*” *megarhinus* from Montpellier (NMB Mp1008).

Radius: Two proximal halves of radius, HNHM V.79.117-10 and HNHM V.79.117-11 (Fig. 3E–G), and a fragmentary distal epiphysis, HNHM V.79.117-11, are preserved (Fig. 3H).

In the proximal epiphysis, in anterior view, the coronoid process is prominent, the bicipital tuberosity is slightly depressed, and the posterior proximal apophysis is evident (Fig. 3E–F). In posterior view, a long and very narrow medial articular surface for the radius is present on the specimen HNHM V.79.117-10 whereas it is absent on HNHM V.79.117-11. A larger, slightly concave and subtriangular lateral articular surface for the radius is present on both specimens. This surface is slightly smaller and laterally delimited by a marked groove on HNHM V.79.117-11.

In proximal view, the medial and lateral articular surfaces are subquadrangular (Fig. 3G). The medial border of the proximal surface is convex, whereas the anterior border is concave only at the level of the coronoid apophysis (Fig. 3G). The lateral border is straight and oblique on HNHM V.79.117-11. The angle between the posterior border of the medial articular surface and that of the lateral one is obtuse.

On the distal epiphysis of HNHM V.79.117-12, in anterior view, the articular surface for the scaphoid is partially observable, whereas the medial and lateral styloid processes are not preserved (Fig. 3H). The distal border of the articular surface for the semilunar is convex. In distal view, the distal articular surface is well developed, its posterior medial portion extends backwards. The anterior border of the epiphysis is concave at the level of the extensor carpi radialis. The articular surface for the semilunar is concave whereas that for the scaphoid is anteriorly concave and posteriorly convex.

Compared with the studied material, “*S.*” *miguelcrusafonti* from the Pliocene of Spain displays a rounded proximal-medial articular surface on the radius and a less developed posterior apophysis on the proximal epiphysis (Guérin & Santafé-Llopis 1978: pl. 5A–B). The studied specimens differ from the Pliocene *S. jeanvireti* (Appendix), which displays, in proximal view, a less obtuse angle between the posterior borders of the medial and lateral articular surfaces. The remains of the latest Pliocene–Early Pleistocene *S. etruscus* (Appendix) are smaller than those collected at Kávás, the proximal lateral surface on the proximal epiphysis of the radius is less developed and its lateral border is convex. In *D. pikermiensis* (Appendix) the proximal-lateral articular surface for the ulna is slightly more developed, the anterior border of the proximal epiphysis has a concavity in the middle, the proximal-lateral articular surface for the humerus extends forward and its anterior border is at the same level than that of the proximal-medial surface. The radius of “*D.*” *megarhinus* from Montpellier (Appendix) shares with the specimens from Kávás a convex medial border of the proximal epiphysis and a concave anterior border at the level of the coronoid apophysis. In some specimens from Montpellier the posterior-medial articular surface for the ulna is not evident. The distal epiphysis of a radius from Val di Pugna (MSNAF 4754) is very damaged, but resembles the specimens from Kávás in having, in distal view, a straight lateral border of the articular surface and a slightly concave posterior border of the lateral half; moreover, the external tuberosity of the anterior face is rounded and large. These features are also more evident in “*D.*” *megarhinus* from Montpellier than in any other Pliocene species (Guérin 1972: fig. 2B). The dimensions of the proximal epiphyses from Kávás are slightly larger than those of “*D.*” *megarhinus* from several Pliocene localities (Table 1).

Scaphoid: The scaphoid HNHM V.79.117-13 is partially damaged on its anterior-proximal border (Fig. 3I-L). In medial view, the posterior border of the bone is straight whereas the anterior one is convex in its proximal half (Fig. 3I). In lateral view, the bone is very damaged, the articular surface for the semilunar is not evident. In the same view, the distal articular surfaces are evident. They are composed by a small anterior articular surface for the semilunar connected with a larger one for the magnum. In dorsal view, the articular surface is anteriorly damaged and transversally covers the proximal face of the bone.

The scaphoid of *D. schleiermachi* from Eppelsheim (NHML 1281) differs from the studied specimen in being shorter and in having, in medial view, a convex posterior-distal border. The scaphoid of "*S.*" *miguelcrusafonti* differs from that of Kávás in having, in medial view, a larger and higher distal articular surface (Guérin 1980: fig. 63B). In *S. jeanvireti* the anterior tuberosity is more marked and developed and the proximal articular surface is not evident in medial view. The scaphoid of *S. etruscus* is shorter and appears massive. The scaphoid from Kávás resembles those of "*D.*" *megarhinus* from Montpellier in the morphology of the anterior tuberosity, of the posterior border of the bone and in the development of the distal articular surface. The unique dimension obtained from the scaphoid falls within the dimensional range of "*D.*" *megarhinus* (Table 1).

Pyramidal: The pyramidal HNHM V.79.117-14 is very damaged and only the lateral half of the bone is well preserved. In anterior view, the proximal-lateral border is convex, whereas the lateral-distal one is concave. A relatively large tuberosity is present on the lateral border. In proximal view, the proximal articular surface is concave anterior-posteriorly and convex lateral-medially. In distal view, the distal articular surface is flat and subtrapezoidal.

The distal articular surface on the pyramidal of "*S.*" *miguelcrusafonti* (Appendix) is smaller with rounded angles; this surface is more rounded in *S. jeanvireti* than in the studied specimen. The pyramidal of *S. etruscus* is smaller and shorter than the studied specimen. Unfortunately, pyramidals certainly attributable to *D. schleiermachi* or *D. pikermiensis* have not been found in the visited collections and any useful morphological character cannot be obtained from the figures published by Guérin (1980: fig. 36E). The pyramidal of "*D.*" *megarhinus* from Montpellier displays the same morphology described for the Kávás specimen. The dimensions of the pyramidal fall within the dimensional range of "*D.*" *megarhinus* (Table 1).

Magnum: Only the anterior face of the magnum HNHM V.79.117-15 is preserved (Fig. 3M). In anterior view, the anterior face of the bone is pentagonal. The distal border is convex, and the medial border has a slight concavity in its distal half (Fig. 3M).

The magnum of "*S.*" *miguelcrusafonti* (Appendix) is very damaged; the preserved portion of the anterior face appears less massive than in the studied specimen. The anterior face of the magnum of *S. jeanvireti* is proportionally higher and transversally shorter than that from Kávás whereas the magnum of *S. etruscus* is generally smaller. The magnum of "*D.*" *megarhinus* from Montpellier is massive and displays

a well developed anterior tuberosity as in the specimen from Kávás. The unique dimension obtained from the magnum falls within the dimensional range of "*D.*" *megarhinus* (Table 1).

Second Metacarpal: In proximal view, the articular surface for the trapezoid of the second metacarpal HNHM V.79.117-16 has rounded angles (Fig. 4A); it is larger in its anterior half than in the posterior one. A developed tuberosity occurs at the posterior end of the proximal epiphysis (Fig. 4A). In lateral view, the articular surface for the magnum is long; its proximal border is not regularly convex and it is separated from the proximal articular surface by a marked edge. The articular surface for the third metacarpal (small, narrow and long) is separated from that for the magnum by a very bland edge. The distal border of the lateral articular surface is concave and it is delimited by a marked groove. On the specimen HNHM V.79.117-17 the proximal articular surface is rounded, concave lateral-medially and slightly convex anterior-posteriorly; it is transversally elongated in its anterior half but does not reach the lateral and medial borders of the proximal epiphysis (Fig. 4A-B).

In *D. schleiermachi* the lateral articular surface on the proximal epiphysis is separated in two facets by a bland groove and, in proximal view, the proximal articular surface is more rounded (Guérin 1980: fig. 39B). The MCII of *D. pikermiensis* differ from the studied specimen in having a less developed anterior-lateral tuberosity, a much wider proximal articular surface and a flat proximal-lateral articular surface. The proximal articular surface on the MCII of "*S.*" *miguelcrusafonti* from Layna (MNCN) is narrower whereas the lateral articular surface is more concave proximal-distally. The specimen from Kávás differs from the Pliocene *S. jeanvireti* which displays a flat proximal-lateral articular surface and from *S. etruscus* which displays little developed medial and lateral tuberosities on the proximal epiphysis. The MCII of "*D.*" *megarhinus* from Montpellier share several morphological characters with those from Kávás: e.g., the proximal-lateral articular surface is concave and the anterior-medial tuberosity is well evident in proximal view. The dimensions of the MCII from Kávás are close to the maximal values of "*D.*" *megarhinus* (Table 1).

Third Metacarpal: The proximal half of the third metacarpal HNHM V.79.117-18 is badly preserved (Fig. 4C-E). In anterior view, the proximal-medial tuberosity is prominent and the proximal border of the proximal articular surface is concave. In proximal view the articular surface for the magnum is subtrapezoidal, with a convex medial border, and a slightly concave anterior border (Fig. 4C). This surface is separated from that for the uncinat, smaller and subtriangular, by a strong saliency. In lateral view, the anterior-proximal and the posterior articular surfaces are well separated by a marked groove (Fig. 4E). The anterior-proximal surface is subtrapezoidal and is proximally joined with that for the uncinat. The posterior surface is subelliptical, with the maximal axes parallel to the posterior border of the diaphysis.

The studied material differs from *D. schleiermachi* in which the posterior-lateral articular surface on the MCIII is rounded and larger than the anterior-lateral one and the proximal articular surface on the MCIII is less developed trans-

versally (Appendix). In *D. pikermiensis* (Appendix) the posterior-lateral articular surface is wider and well developed, the articular surface for the uncinata is less developed and the medial border of the proximal epiphysis is less expanded anterior-posteriorly. Compared with the studied material "*S. miguelcrusafonti*" displays a less developed proximal-medial tuberosity on MCIII (Guérin & Santafé-Llopis 1978). The studied specimen differs from *S. jeanvireti* which has a convex anterior border and a subtriangular lateral articular surface. The MCIII of *S. etruscus* differs from that of Kávás in having a small and subelliptical proximal-lateral articular

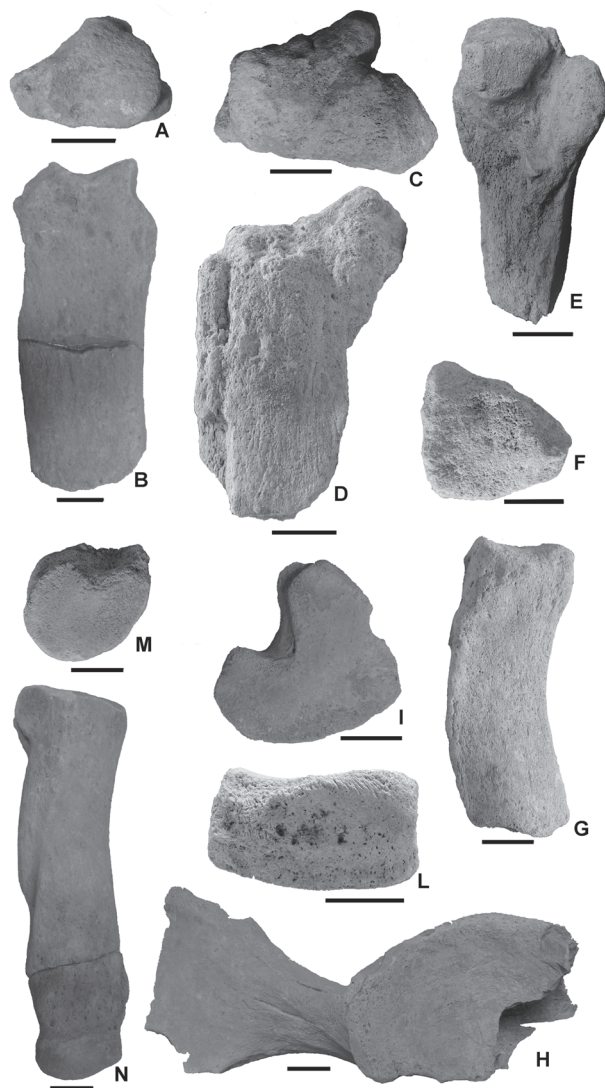


Fig. 4. "*Dihoplus*" *megarhinus* from Kávás. **A** — MCII HNHM V.79.117-16, proximal view; **B** — MCII HNHM V.79.117-16, anterior view; **C** — MCIII HNHM V.79.117-18, proximal view; **D** — MCIII HNHM V.79.117-18, anterior view; **E** — MCIII HNHM V.79.117-18, lateral view; **F** — MCIV HNHM V.79.117-19, proximal view; **G** — MCIV HNHM V.79.117-19, anterior view; **H** — pelvis HNHM V.79.117-20, acetabular view; **I** — third cuneiform HNHM V.79.117-21, proximal view; **L** — third cuneiform HNHM V.79.117-21, anterior view; **M** — MTV HNHM V.79.117-22, proximal view; **N** — MTV HNHM V.79.117-22, anterior view. Scale bars=2 cm.

surface and a well developed and subtriangular posterior-lateral surface. The MCIII of "*D. megarhinus*" from Montpellier share several characters with the studied specimen: the anterior border of the proximal epiphysis is usually slightly concave but is also straight in some specimens, the posterior-lateral articular surface is subelliptical but appears slightly wider than that from Kávás.

Fourth Metacarpal: On the fourth metacarpal HNHM V.79.117-19, in proximal view, a broad articular surface for the uncinata is present (Fig. 4F-G). The latter surface is subtriangular, its medial border is slightly convex, whereas the anterior one is straight. In medial view, the two articular surfaces for the third metacarpal are badly preserved and only a rather rounded posterior one is evident. In posterior-lateral view, the proximal articular surface slightly extends over the posterior-lateral border of the proximal epiphysis giving two small, elongated and narrow surfaces, distally delimited by two marked depressions. MCIV of *D. schleiermacheri* has never been reported from Eppelsheim (Guérin 1980).

In respect to the studied specimen, the proximal epiphysis of *D. pikermiensis* and *S. jeanvireti* are transversally longer and anterior-posteriorly shorter; both species display, however, a different shape of the proximal epiphysis. In "*S. miguelcrusafonti*" the posterior border of the proximal epiphysis displays a marked groove and the proximal articular surface is less developed than the proximal epiphysis (Guérin 1980: fig. 71B). The proximal epiphysis of *S. etruscus*, in proximal view, is rather similar to that of the studied specimen but its posterior border is generally straight and the lateral articular surface is partially evident. The shape of the proximal epiphysis of the specimen from Kávás is similar to that of the MCIVs of "*D. megarhinus*" from Montpellier. The dimensions of the MCIV from Kávás fall within the values of "*D. megarhinus*" (Table 1).

Pelvis: The pelvis is represented only by a fragment of acetabulum and ischium HNHM V.79.117-20. The proximal border of the acetabulum is regularly convex, whereas the posterior-proximal border is straight (Fig. 4H). The preserved portion of the articular cavity is deep and surrounded by a sharp edge.

The posterior-proximal border of the acetabulum from Montpellier is straight as well as that from Kávás and similar to the specimen from Rio Secco (MGGC 9350). *S. etruscus* differs from the studied specimen in being smaller and in having a more rounded acetabulum. In *S. jeanvireti* the angle between the dorsal border of the acetabulum and the dorsal border of the ischium is more obtuse.

Third Cuneiform: In anterior view, the anterior face of the third cuneiform HNHM V.79.117-21 is rectangular (Fig. 4I-L). The proximal border is slightly concave on its medial half and slightly convex in its lateral half. The distal border is slightly convex. The medial and lateral borders are straight, and the angle between the distal border and the medial one is approximately of 90°. In proximal view, the proximal articular surface is wide and subtriangular. The medial face of the bone is badly preserved; the anterior and posterior articular surfaces for the second metatarsal are subsquare and the anterior one is slightly higher. In posterior-lateral view, two articular surfaces are present. The posterior-proximal

one is elliptical whereas the anterior-distal one is triangular, wide and flat.

The anterior face of the third cuneiform in *D. schleiermachi* is proportionally higher and transversally shorter than that of the studied specimen (Guérin 1980: fig. 50C). The third cuneiform of "*S.*" *miguelcrusafonti* is rather similar to the studied specimen but, in distal view, the anterior-medial side of the face appears less developed anterior-posteriorly. The studied specimen differs from *S. jeanvireti* which displays a concave lateral border and a convex medial border of the anterior face. The dorsal border of the anterior face in *S. etruscus* is more concave, whereas the distal border is more convex than in the studied specimen; moreover the anterior face in *S. etruscus* appears higher and transversally shorter. The dimensions of the third cuneiform from Kávás fall within the values of "*D.*" *megarhinus* (Table 1).

Fourth Metatarsal: In anterior view, the medial border of the fourth metatarsal HNHM V.79.117-22 is sinuous (Fig. 4M-N). The insertion of the muscle interossei is long and reaches the distal half of the diaphysis. In proximal view, the articular surface is rounded, its posterior border has a concavity in the middle and is delimited by a marked groove (Fig. 4M). The two articular surfaces for the third metatarsal, on the medial face of the bone, are of about the same size; the anterior one is subtrapezoidal, whereas the posterior one is rounded. These two surfaces are separated by a marked groove. Moreover, the anterior surface is proximally joined with the proximal articular surface.

The MTIV of *D. schleiermachi* displays, in proximal view, a well developed posterior tuberosity and, in medial view, the posterior articular surface for the third metatarsal is joined with the proximal articular surface (Guérin 1980: fig. 55E). In *D. pikermiensis* the proximal articular surface is rounded and the two medial articular surfaces are partially evident in proximal view. In respect to the studied specimen, the proximal articular surface of *S. jeanvireti* is less rounded and less developed than the proximal epiphysis. The proximal articular surface in *S. etruscus* is triangular and smaller than that of the specimen from Kávás. In "*D.*" *megarhinus* from Montpellier, as in the studied specimen, the proximal articular surface is rounded, the anterior medial surface for the third metatarsal is joined with the proximal epiphysis and the posterior medial surface is rounded (Guérin 1972: fig. 20B). The dimensions of the MTIV from Kávás fall within the values of "*D.*" *megarhinus* (Table 1).

Discussion and conclusions

Although there are numerous localities with Turolian land mammal remains from Hungary, remains of land mammals tend to be sparse. However, a few localities contain specimen-rich land mammal assemblages dominated by large-sized mammals. Kretzoi (1982) gave a detailed list of the so-called *Hipparion*-fauna localities from the Late Miocene of the Carpathian Basin and sketched the biochronological correlation among the most important localities (Kretzoi 1982, 1985, 1987). Kretzoi established the Sümegium and the Hatvanium (these two stages approximately correspond

to the MN 12) and the Bértalavárium (approximately corresponds to the MN 13; Bértalavár is the recent name of a small village that was called Baltavár earlier). He placed Baltavár and Polgárdi, the two faunistically-richest late Turolian land mammal localities of Western Hungary, into the Bértalavárium. This correlation was used later by Kordos (1992) and Gasparik (2001). Kretzoi (1983) also sketched a biostratigraphic chart using *Hipparion* species as biostratigraphic-index forms. However, Kaiser & Bernor (2006) revised the Baltavár "hipparions" and pointed out that Baltavár is older than was believed earlier. Its age is MN 12 rather than MN 13 and Polgárdi belongs to MN 12 or MN 13. This result fits well with older opinions because Baltavár assemblages are compositionally very similar to the world-famous Píkermi fauna. A similar dating has been inferred by Gasparik (2004) on the basis of proboscidean material: MN 12 for Baltavár and MN 13 for Polgárdi. The proboscidean record from Baltavár is still under revision because the two species that have been described here (cf. *Tetralophodon longirostris* Kaup 1832 and cf. *Mammuth borsoni* Hays 1834) show some characteristics which indicate that these specimens must probably be reassigned to other species [*Tetralophodon atticus* (Wagner 1857) and *Mammuth obliquelophus* (Mucha 1980)], as was suggested by Markov (2008).

Latest Miocene (MN 12 or 13) rhinoceroses are poorly documented in Western Hungary and are represented by rare remains. As far as the rhinocerotid remains from the above mentioned localities are concerned, "*Dihoplus*" *megarhinus* was not described from any of them, but two other species, identified as *Aceratherium incisivum* and *D. schleiermachi*, were found (Kretzoi 1952, 1982; Kordos 1992). The latter species has been reported at Baltavár (MN 12) (*Rhinoceros pachygnathus* in Pethó 1885; Giaourtsakis 2009). However, a fragment of hemimandible with p4-m3 (L.sz.Ob-331) housed at the Geological Museum of the MFGI displays morphological characters (a short paralophid and a mesial-lingual cingulum) that suggest a similarity to *Aceratherium*. Some specimens housed at the MFGI can be ascribed to *Aceratherium* sp. (an isolated DP4 v13.00339.1; an isolated lower molar v13.00335.1) or Rhinocerotidae indet. (an isolated and much worn M3 v13.00376.1) whereas only a calcaneum (v13.00340.1) and perhaps a fragment of juvenile mandible with dp1-dp2 can be identified as *Dihoplus*. Nevertheless, the calcaneum (v13.00340.1) differs from *D. schleiermachi* in having a more developed tuber calcanei and, in posterior view, a clearly evident articular surface for the cuboid. Moreover, the values of the transverse diameter of the sustentaculum tali (DT=98 mm) and of the anterior-posterior diameter of the tuber calcanei (DAP=88 mm) are larger than those reported for *D. schleiermachi* by Guérin (1980) and are close to the maximal values of "*D.*" *megarhinus* (Guérin 1980: tab. 108). Unpublished remains of a rhinoceros housed at the NMB have been collected at Polgárdi and include indeterminable fragments of teeth and fragments of bones. Among the other remains, a damaged proximal epiphysis of radius morphologically resembles the specimens from Kávás and can be assigned as "*D.*" cf. *megarhinus*.

"*D.*" *megarhinus* has usually been documented in the Pliocene deposits (Guérin et al. 1969; Guérin 1980; Pandolfi 2013), but its presence has been also suggested in latest Miocene, MN 13 (late Messinian), localities of Baccinello V3 (Toscana, Italy: Hürzeler & Engesser 1976; Pandolfi 2013; Pandolfi et al. 2015b) and Monticino Quarry (Emilia-Romagna, Italy: De Giuli 1989; Pandolfi 2013; Pandolfi et al. 2015b). The record of Kávás, which is older than the above mentioned Italian records, strongly reinforces the occurrence of "*D.*" *megarhinus* during the Miocene in Europe and suggests a critical revision of several findings usually identified as *Dihoplus* sp. (Novo Elisavetovka, Ukraine, MN 12: Alexejewa 1916; Giaourtsakis et al. 2006; Pandolfi et al. 2015b), *Stephanorhinus* sp. (Moncucco, Northern Italy, MN 13: Angelone et al. 2011) or *Dihoplus schleiermacheri*? (Verduno, Northern Italy, MN 13: Colombero et al. 2014).

Moreover, the occurrences of "*D.*" *megarhinus* throughout the latest Miocene suggest that this species spread from the Pannonian Basin towards Italy during the MN 13. The latter hypothesis is also supported by the dispersal pattern of the genus *Hippotherium* recently suggested by Bernor et al. (2011). According to these authors, *Hippotherium* is not documented from the Baccinello area until the base of the MN 13 and it may have emigrated from the Pannonian area.

The occurrences of "*D.*" *megarhinus* in Western Hungary (MN 12 and 13) and Italy (MN 13) also suggests a biogeographic segregation of Rhinocerotini species in Europe during the latest Miocene. In fact, *D. schleiermacheri* is the sole Rhinocerotini species in Western Europe during the latest Miocene (Guérin 1980; Cerdeño, 1992; Heissig 1996, 1999) whereas *D. pikermiensis* and *C. neumayri* represented the two rhinocerotine species during the Turolian (late Tortonian-Messinian, approximately 9-5.3 Ma) in Southeastern Europe (Geraads 1988; Geraads & Spassov 2009). *D. schleiermacheri*, *D. pikermiensis* and *C. neumayri* became extinct at the end of the Miocene (Guérin 1980; Heissig, 1996, 1999) whereas "*D.*" *megarhinus* occurred in southern France (MN 14), in Turkey (MN 15) and elsewhere too in Europe (Guérin 1980; Radulescu & Samson 1985; Guérin & Sen 1998; Pandolfi 2013).

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Appendix

Source for postcranial comparison material. Institutional abbreviations are reported in the text. nc = no code.

Bibliographic Source

"Dihoplus" megarhinus

Locality: Montpellier, Saint-Laurens, Monte Zago, Rio Secco, Val di Pugna-Fangonero.

References: Simonelli (1897); Guérin et al. (1969); Guérin (1980); Pandolfi (2013).

"Stephanorhinus" miguelcrusafonti

Locality: Layna, Perpignan.

References: Guérin & Santafé-Llopis (1978).

Stephanorhinus jeanvireti

Locality: Vialette, Villafranca d'Asti.

References: Guérin (1972, 1980).

Stephanorhinus etruscus

Locality: Senèze, Capitone, Upper Valdarno

References: Ambrosetti (1972); Guérin (1972, 1980); Pandolfi & Petronio (2011).

Dihoplus schleiermacheri

Locality: Eppelsheim.

References: Guérin (1980).

Direct Observations

HNHM

Stephanorhinus jeanvireti

Ajnásko: Humerus b.801; Pyramidal b.918, b.828; MC2 b.807; MC4 b.806.

IGF

Stephanorhinus jeanvireti

Montopoli: two anterior and two posterior limbs 1075.

Stephanorhinus etruscus

Upper Valdarno: Assembled skeleton 716, 3098, 2293v; Almost complete anterior limb 731; Humerus 730, 717, 2209v, 14840, 488v; Radius 2211v, 2212v, 2214v, 4566v, 4567v, 488v; Ulna 4566v, 4567v; MC2 1355v; MC3 1355v, 2231v, 488v; MC4 2232v, 488v; MT4 2233v, 487v.

MFGI

Stephanorhinus jeanvireti

Pula: Radius v.18511, v.18514, v.18515.

Dihoplus schleiermacheri

Pannonian Basin: Radius v.11117; MC3 v.11110.

MfN

Dihoplus schleiermacheri

Eppelsheim: Radius MbMa28312; MC3 MbMa28313, MbMa 28307.

Dihoplus pikermiensis

Pikermi: Humerus MbMa24815, MbMa24817; MC2 MbMa28279; MC3 MbMa28281, MbMa28283.

MGGC

"Dihoplus" megarhinus

Rio Secco: Pelvis 9350.

Montegiogo: Atlas 9372.

Monte Zago?: Complete anterior limb (cast) nc.

Stephanorhinus jeanvireti

Monte Pastore: Humerus nc.

MNCN

Dihoplus schleiermacheri

Venta del Moro: Third Cuneiform 11817.

"Stephanorhinus" miguelcrusafonti

Layna: Pyramidal 23785; Magnum 23783; MC2 70374; MT4 23767.

Stephanorhinus etruscus

Cullar de Baza I: Scaphoid 13141; Pyramidal 13143; MC2 13144.

El-Rincon: Humerus 41874; Radius 41869; MC3 41870; MT4 41871.

Huésca: Humerus 19206; MC3 55139; Pelvis 19207.

La Puebla de Valverde: MC2 32751; MC4 54888.

MPLBP

Stephanorhinus etruscus

Pietrafitta: Two almost complete mounted skeletons.

MPUR

Stephanorhinus etruscus

Capitone: Almost complete skeleton 1500.

MSNAF

"Dihoplus" megarhinus

Val di Pugna-Fangonero: Humerus 7100; Radius 4754.

Stephanorhinus etruscus

Castelnuovo di Baradenga Scalo: Humerus 7141; Ulna 7139; Scaphoid 7128; Magnum 7126; MC2 7130; MC3 7138.

NHML

Dihoplus schleiermacheri

Eppelsheim: Atlas 1284; Scaphoid 1281; MC3 1282.

Dihoplus pikermiensis

Pikermi: Humerus M11282b, 11363a, M48268, M11367; Radius M48168, M48129, M11288, M48253, M48154; MC2 M11303a, M11303b, M11298a, M48188, M48195; MC3 M11301a, M11301b, M48181; MC4 M11297, M48187; MT4 M11327.

NHMW

Stephanorhinus jeanvireti

Hajnáčka: Humerus 1878-46-30; Radius 1878-46-33; Pyramidal 1878-46-40; MC2 1878-46-42, 1878-46-42b; MC3 1878-46-42, 1878-46-42b; MC4 nc.

Dihoplus pikermiensis

Samos and Pikermi: Humerus 1860/0032/0048; Radius 1863/0001/0025, 1860/0032/0056; Ulna 1863/0001/0024; Scaphoid 2009z0089/0001; MC2 1860/0032/0079, 1860/0032/0078, 1860/0032/0083b; MC3 1863/0001/0030, 1860/

0032/0079, 1860/0032/0082, 1860/0032/0078; MC4 1860/0032/0078, 1860/0032/0079; MT4 1911/0005/0493.

NMB

"Dihoplus" megarhinus

Montpellier: Atlas Mp922; Humerus Mp528, Mp817; Radius Mp816, Mp106, Mp731, Mp1032, Mp329, Mp453; Ulna Mp1008; Scaphoid Mp814, Mp324; Pyramidal Mp815; MC2 Mp985, Mp526, Mp646; MC3 Mp131, Mp647, Mp455, Mp525; MC4 Mp733; Pelvis Mp103, Mp333.

Stephanorhinus etruscus

Saint Vallier: MT4 Stv365, Stv243.

Senèze: Atlas Se1711; Humerus Se1703, Se1711; Radius Se1711, Se1703; Ulna Se1711; Scaphoid Se1703, Se1711; Pyramidal Se1711; Magnum Se1703, Se1711; MC2 Se1711,

Se1703; MC3 Se1703, Se1756 (four specimens), Se1711; MC4 Se1711; Pelvis Se1711; Third Cuneiform Se1711; MT4 Se1703, Se1711.

Upper Valdarno: Humerus Va1680; Radius Va1337; Third Cuneiform Va612.

Stephanorhinus jeanvireti

Villafranca d'Asti: Humerus Vj89, nc, nc; Radius nc; Pyramidal Vj242; MC2 nc; MC3 Vj90, nc; MC4 nc; MT4 nc.

Vialette: Humerus nc, nc, nc; Radius Vt42, Vt621, Vt620; Ulna Vt621, Vt42; Scaphoid Vt620; Pyramidal Vt620; Magnum nc; MC2 Vt621, Vt621b, Vt620; MC3 Vt621, Vt621b, Vt930; MC4 Vt621, Vt621b, Vt620; Pelvis nc, nc; Third Cuneiform Vt624, nc; MT4 Vt624, nc.

Perrier-Les Étouaires: Humerus Prr327, Prr429; Radius Prr109, Prr52; Magnum Prr56; MC3 Prr55.