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Original article

Earliest occurrence of "*Dihoplus*" *megarhinus* (Mammalia, Rhinocerotidae) in Europe (Late Miocene, Pannonian Basin, Hungary): Palaeobiogeographical and biochronological implications

La plus ancienne occurrence de « Dihoplus *»* megarhinus *(Mammalia, Rhinocerotidae) en Europe (Miocène supérieur, bassin Pannonien, Hongrie) : implications paléobiogéographiques et biochronologiques*

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ABSTRACT

In 1979, several specimens of Rhinocerotidae were collected from the Late Miocene deposits of the Zala Subbasin, Pannonian Basin, Western Hungary and were inventoried as *Rhinoceros* sp. Based on morphological and metric grounds, this material is here referred to "*Dihoplus*" *megarhinus* (de Christol), a species previously known only from Pliocene localities. This is the earliest record of the species in Europe. Our results support the hypothesis that the origin of "*D*". *megarhinus* took place in Asia and that this species successively dispersed towards Western Europe during the end of the Miocene.

Mots clés :
Rhinocerotidae
« *Dihoplus* » *megarhinus*
Systématique
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RÉSUMÉ

En 1979, plusieurs spécimens de Rhinocerotidae ont été collectés dans les dépôts du Miocène supérieur du bassin de Zala, en Pannonie (Hongrie occidentale), et alors attribués à *Rhinoceros* sp. Sur la base des données métriques et morphologiques, ce matériel est ici attribué à « *Dihoplus* » *megarhinus* (de Christol), une espèce précédemment connue seulement dans des localités du Pliocène. Cette nouvelle découverte est la plus ancienne mention en Europe pour « *D* ». *megarhinus*. Notre analyse suggère que l'origine de « *D* ». *megarhinus* a eu lieu en Asie et que cette espèce s'est probablement dispersée en Europe occidentale dès le Miocène supérieur.

1. Introduction

The tribe Rhinocerotini includes the extant rhinoceroses that are distributed in South-Eastern Asia and Africa. During the Neogene and Pleistocene, this tribe was widely distributed and diversified in Eurasia and Africa. Despite this, the systematic position and the phylogenetic relationships of some species are still debatable, as well as their spatio-temporal distribution is poorly known.

Rhinoceros megarhinus was one of the first extinct rhinoceros species described by palaeontologists. It was named by de Christol (1834) and was generally recorded from several Pliocene localities of Western Europe, Romania, Poland and Turkey (Guérin, 1980;

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Fig. 1. Location map of the Kávás Late Miocene locality, Pannonian Basin, Hungary.
Carte de localisation du gisement de Kávás, Miocène supérieur du bassin Pannonien, Hongrie.

Codrea, 1993; Guérin and Sen, 1998; Pandolfi, 2013). Recently, it was also reported in the latest Pliocene locality of Udunga (Transbaikalia, Russia; Fukuchi et al., 2009).

The aim of this paper is to describe Late Miocene rhinoceros remains originating from Kávás, Zala Subbasin, Western Hungary (Fig. 1), and to discuss the palaeobiogeographical and biochronological implications of this finding.

The Zala Subbasin (Fig. 1) is part of the wider Pannonian Basin and is located north to the "Balaton line", which was interpreted as the eastern continuation of the Periadriatic Lineament (Fodor et al., 1998; Magyar et al., 1999; Haas et al., 2000; Benedek et al., 2004; Dolton, 2006). The specimens we analyse here were collected from grey, clayey, fine-grained sand or sandstone deposits from the village of Kávás in 1979 and were originally inventoried as Early Pannonian remains. This age, however, seems to be too old in some respects and this term was traditionally used for the fine-grained deep-water deposits of Lake Pannon (Pandolfi et al., in press). From the surface of this area, the occurrence of brackish water deposits or any deposit of the Lake Pannon are unknown, so we can rule out the possibility of the Early Pannonian age for the remains under discussion. Instead, these remains were obviously recovered from the fluvial succession of the Zagyva Formation (Pandolfi et al., in press). These (fluvial or lacustrine) sediments were deposited after the filling up of the Lake Pannon. Their age is approximately between 7 and 8 Ma, very similar to the Baltavár locality, which is MN12 (Magyar et al., 2007; Pandolfi et al., in press). It is located near to the Kávás locality (ca. 25 km north-eastwards). Magyar et al. (2007) published the correlations of this area based on magnetic polarity records, biostratigraphy and seismic stratigraphy. On the basis of the seismic correlations and its position, the age of the Kávás locality must be somewhat younger than Baltavár (now Bérbaltavár), because the Late Miocene layers (horizons) are gently deeping southwards (I. Magyar pers. comm., August, 2014; Pandolfi et al., in press). The age of the Kávás locality thus can be estimated as 7.0 (± 0.5) Ma, corresponding to the latest Tortonian/earliest Messinian (see Pandolfi et al., in press for details). In addition, several fossiliferous localities, which yielded some Late Pannonian large mammals (mainly proboscideans), have been reported from the Zala Subbasin and have been chronologically referred to MN12 or MN13 (Gasparik, 2001).

Institutional abbreviations: BSPG, Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; **HNHM**, Hungarian Natural History Museum, Budapest, Hungary; **IGF**, Museo di Storia Naturale, sezione di Geologia e Paleontologia, Florence, Italy; **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; **MFGI**, Geological and Geophysical Institute of Hungary, Budapest, Hungary; **MfN**, Museum für Naturkunde, Berlin, Germany; **MGGC**, Museo di Geologia Giovanni Capellini, Bologna, Italy; **MGPP**, Museo di Geologia e Paleontologia, Padua, Italy; **MNCN**, Museo Nacional de Ciencias Naturales, Madrid, Spain; **MNHN**, Muséum National d'Histoire Naturelle, Paris, France; **MPP**, Museo di Paleontologia, Università di Parma, Parma, Italy; **MPPB**, Museo di Palazzo Poggi, Bologna, 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.

2. Material and methods

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

The specimens from Kávás under consideration belong apparently to the same individual. The main cranial fragment was without an inventory number, and it was also not included under the V.79.117 inventory item in the Inventory Book of the Department of Palaeontology and Geology of HNHM. However, based on its measurements, its morphological characters, its state of preservation and the matrix preserved (light grey sand and sandstone), it appears very probable that the remains have been collected at the same time. During the present study, we discovered that the inventoried fragment of the right maxilla anatomically matched the uninventoried cranial fragment; hence, we can establish that these remains belong indeed to the same individual. This holds for the whole material, because the teeth show a uniform stage of wear. Postcranial remains have been also collected from the same locality but, at present, we cannot confirm if they certainly belong to the same individual described here (Pandolfi et al., in press).

The studied specimens were morphologically compared with the rhinoceros material collected in several Late Miocene and Pliocene localities of Eurasia. The comparisons were based on the material housed in several Museums and Institutions as well as on the specimens published by several authors (Appendix A).

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Dental terminology and anatomical descriptions follow Guérin (1980) and Antoine (2002), whereas the protocol for measurements follows Guérin (1980).

3. Systematic palaeontology

Order PERISSODACTYLA Owen, 1848
Family RHINOCEROTIDAE Gray, 1821
Subfamily RHINOCEROTINAE Gray, 1821
Tribe RHINOCEROTINI Gray, 1821
Genus ***Dihoplus*** Brandt, 1878

Type species: *Rhinoceros schleiermacheri* Kaup, 1832 from the Late Miocene of Eppelsheim, Germany (Kaup, 1832: tab. X, fig. 1; Giaourtsakis and Heissig, 2004: fig. 1.4).

Amended diagnosis: After Geraads and Spassov (2009): large sized two-horned rhinoceros. Nasal septum not ossified. Toothrow rather caudal, nasal notch above anterior premolars. Cranial basis short, post-glenoid apophysis close to the paroccipital process. No P1. Upper premolars primitive, submolariform. Molars with vestigial antecrochet, crista weak or absent, missing on DP3–DP4. Lower i2 present.

Other species: "*D*". *megarhinus* (de Christol, 1834), *D. pikermiensis* (Toula, 1906). *D. ringstroemi* (Arambourg, 1959) is here considered a junior synonym of "*D*". *megarhinus*.

Remarks: The species *Rhinoceros megarhinus* de Christol (1834) was frequently included into the genus *Dicerorhinus* Gloger, 1841 (e.g., Guérin, 1980, 1982), typified by the recent species *Dicerorhinus sumatrensis* (Fisher, 1814) (see Groves, 1983). However, the latter species differs from *R. megarhinus* in having a significantly smaller size, 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 (based on the material observed at MNHN, MSNF, NHML, NMB). The species *R. megarhinus* was recently referred to the genus *Dihoplus* (e.g., Giaourtsakis, 2003; Symeonidis et al., 2006; Lacombat and Mörs, 2008) following the hypothesis proposed by Heissig (1989, 1996, 1999), who recognised an evolutionary lineage from the Late Miocene *D. schleiermacheri* to the Early Pliocene "*D*". *megarhinus*. Deng et al. (2011) also ascribed the species *R. megarhinus* to *Dihoplus*, but in the nine most parsimonious trees obtained by these authors (Deng et al., 2011: fig. S7), the genus *Dihoplus* appeared to be paraphyletic, and *D. megarhinus* clearly did not form a clade with the species *D. pikermiensis* and *D. ringstroemi*. Moreover, the type species of the genus *Dihoplus*, *D. schleiermacheri* was not included in the analysis of Deng et al. (2011). The latter species was considered in a preliminary unpublished analysis reported by Pandolfi et al. (2014) and Pandolfi (2015), but it did not form a clade with *D. megarhinus*, which was included within the paraphyletic genus *Stephanorhinus* Kretzoi, 1942. An inclusion into the latter genus was proposed by Fortelius et al. (1993) and Cerdeño (1995). Nevertheless, de Christol's species does not show the derived morphological characters described as diagnostic for *Stephanorhinus* (e.g., partially ossified nasal septum or loss of anterior teeth: Pandolfi and Tagliacozzo, 2015), whereas the phylogenetic relationships within this genus are yet to be resolved (Giaourtsakis, 2003; Symeonidis et al., 2006; Lacombat and Mörs, 2008; Pandolfi, 2015). Accordingly, we provisionally retain the species *R. megarhinus* within the genus *Dihoplus*.

"***Dihoplus***". ***megarhinus*** (de Christol, 1834)
Figs. 2, 3A, 4A–B, 5A, Tables 1–4
Selected synonymy:
1924 *Dicerorhinus orientalis* Ringström p. 5, figs. 1–10, 14–15
1963 *Rhinoceros megarhinus* Cuscani Politi p. 126, plate I–III
1959 *Dicerorhinus orientalis* var. Ringströmi Arambourg p. 73
1993 *Stephanorhinus megarhinus* Fortelius et al. p. 66
1996 "*Dicerorhinus*". *megarhinus* Heissig p. 341
2006 *Dihoplus megarhinus* Symeonidis et al. p. 441
2006 *Dihoplus ringstromi* Deng p. 51, fig. 3
2007 *Lartetotherium megarhinus* Lacombat p. 63
2008 *Dihoplus megarhinus* Lacombat and Mörs p. 160
2009 *Stephanorhinus megarhinus* Fukuchi et al. p. 64, figs. 6–12
2011 *Dihoplus megarhinus* Deng et al. p. 1286
2012 *Dihoplus ringstroemi* Tong p. 556, figs. 1E, 2E, 3E
2013 *Dihoplus megarhinus* Guérin and Tsoukala p. 454

Holotype: MNHN AC2683, skull with mandible described and figured by de Christol (1834: Pl. I, figs 5, 6, 9, 10, 12, 13, 18, 19, 21, 25, 26, 27).

Type locality and horizon: Montpellier (Hérault, France), Early Pliocene.

Amended diagnosis: Large sized two-horned rhinoceros characterised by massive skull with thick and long nasal bones. Nasal septum never ossified. I1 and i2 reduced (vestigial). I2 and i1 absent. Posterior border of the nasal notch ranges from P3–P4 to P4–M1. Occipital face vertical. Nuchal crest marked, transversally developed and with a slightly concave posterior border in dorsal view. Fully closed external auditory pseudomeatus. Mandible with a relatively long symphysis and long horizontal ramus. Ventral border of the horizontal ramus rather straight or slightly curved beneath the molars and curved under the premolars and towards the symphysis. Ectoloph profile slightly convex on the upper premolars. Protocone less developed than the hypocone on P2. Metacone fold faint on P3 and P4. Lingual cingulum generally absent on the upper molars. Mesostyle faint on M1 and M2. Labial and lingual cingula absent or strongly reduced on the lower teeth.

Remarks: *D. ringstroemi* (neither *ringströmi* nor *ringstromi*: ICZN (1999), art. 32.5.2) has been recorded from several Late Miocene (MN12) localities of China and has been usually compared with other European Miocene two-horned rhinoceroses, such as *D. schleiermacheri* and *D. pikermiensis*. Ringström (1924) originally described a nearly complete adult cranium, an adult mandible, several remains of juvenile crania and mandibles, isolated teeth and some postcranial elements from at least 7 Chinese localities in the Provinces of Henan and Shanxi to *Dicerorhinus orientalis* (Schlosser, 1921), a junior synonym of *D. pikermiensis* (Toula, 1906), on the basis of the morphological similarities with the specimens from Pikermi, Samos and Velles. According to Ringström (1924), the dimension is the only difference between the Chinese material and *D. orientalis* from Greece. Moreover, Ringström (1924) referred the juvenile upper toothrows from Taraklia and Novo-Elisavetovka (Late Miocene, Ukraine; Khomenko, 1914; Alexejew, 1916) to *D. orientalis* because the morphological and dimensional similarities with the Chinese material. Arambourg (1959:73) mentioned in a brief footnote that the Chinese material is morphologically similar but larger than that from Southeastern Europe; accordingly he transferred the Chinese specimens to a new taxon named "*D. orientalis* var. *Ringströmi* nov. var.". Based on morphological comparison with specimens collected at Kerassia (Greece), Giaourtsakis et al. (2006) recognised several common features between *D. pikermiensis* and *D. ringstroemi* but reported that the mandible published by Ringström (1924: 12) is "1/3 larger" than the mandibles they have measured and therefore retained the name *D. ringstroemi* "for the Chinese specimens" (Giaourtsakis et al., 2006: 391). Recently Deng (2006: 51) and Tong (2012: 556) reported the following characters in the diagnosis of *D. ringstroemi*: "Larger than *D. orientalis*; skull is long"; the infraorbital foramen is wide; "nasal bone is long and wide and has a domed horn boss"; nasal notch has a U morphology and its ends is above P3/P4; "anterior border of orbit above M2"; strong preorbital tubercle and well-developed lacrimal tubercle; "the skull

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Fig. 2. "*Dihoplus*" *megarhinus* from Kávás. **A**. Skull HNHM V.79.117-1, dorsal view. **B**. Skull HNHM V.79.117-1, left side. **C**. Skull HNHM V.79.117-1, right side. **D**. Skull fragment HNHM V.79.117-4, lateral view. **E**. Left P2-M3 HNHM V.79.117-4, occlusal view. **F**. M2–M3 HNHM V.79.117-2, occlusal view. **G**. Right P2–P3 HNHM V.79.117-3, occlusal view. **H**. Left horizontal ramus of mandible HNHM V.79.117-5, lateral view. **I**. Right p2-m3 HNHM V.79.117-5, occlusal view. **L**. Right horizontal ramus of mandible HNHM V.79.117-6, lateral view. **M**. Left p3-m3 HNHM V.79.117-6, occlusal view. Scale bar equals 10 cm for A–E, H–M. Scale bar equals 2 cm for F–G.

« Dihoplus » megarhinus de Kávás. ***A****. Crâne HNHM V.79.117-1, vue dorsale.* ***B****. Crâne HNHM V.79.117-1, côté gauche.* ***C****. Crâne HNHM V.79.117-1, côté droit.* ***D****. Fragment de crâne HNHM V.79.117-4, vue latérale.* ***E****. P2-M3 gauches HNHM V.79.117-4, vue occlusale.* ***F****. M2–M3 droites HNHM V.79.117-2, vue occlusale.* ***G****. P2–P3 droites HNHM V.79.117-3, vue occlusale.* ***H****. Fragment de mandibule gauche HNHM V.79.117-5, vue latérale.* ***I****. p2-m3 droites HNHM V.79.117-5, vue occlusale.* ***L****. Fragment de mandibule droite HNHM V.79.117-6, vue latérale.* ***M****. p2-m3 gauches HNHM V.79.117-6, vue occlusale. A–E et H–M, échelles : 10 cm. F–G, échelles : 2 cm.*

Table 1

Measurements (in mm) of the skull of "*Dihoplus*" *megarhinus* from Kávás (Hungary), compared with those of "*D*". *megarhinus* from Honan (Late Miocene, China: from Ringström, 1924), Linxia (Late Miocene, China: estimated on the figures provided by Deng, 2006), and from several Pliocene localities of Western Europe (from Guérin, 1980), and with those of *C. neumayri* (Late Miocene, Southeastern Europe, Turkey and Iran: Geraads, 1988; Antoine and Saraç, 2005; Geraads and Spassov, 2009; Giaourtsakis, 2009; Antoine et al., 2012), "*D*". *douariensis* (Late Miocene, Africa: from Guérin, 1966; Giaourtsakis et al., 2009), *D. schleiermacheri* (Late Miocene, Central Europe: Guérin, 1980), *D. pikermiensis* (Late Miocene Southeastern Europe: Geraads, 1988; Geraads and Spassov, 2009), *S. jeanvireti* (Pliocene, Europe: Guérin, 1980; Guérin and Tsoukala, 2013), and *S. etruscus* (Plio–Pleistocene, Europe: Guérin, 1980). L = length; TD = transverse diameter; H = height; f.m. = foramen magnum.

Dimensions (mm) des crânes de « Dihoplus » megarhinus de Kávás (Hongrie), de Honan (Miocène supérieur, Chine : d'après Ringström, 1924), de Linxia (Miocène supérieur, Chine : estimé d'après Deng, 2006), et du Pliocène d'Europe occidentale (d'après Guérin, 1980), et des crânes de C. neumayri (Miocène supérieur, Sud-Est d'Europe, Turquie et Iran : d'après Geraads, 1988 ; Antoine et Saraç, 2005 ; Geraads et Spassov, 2009 ; Giaourtsakis, 2009 ; Antoine et al., 2012), « D ». douariensis (Miocène Supérieur, Afrique : d'après Guérin, 1966 ; Giaourtsakis et al., 2009), D. schleiermacheri (Miocène Supérieur, Europe centrale : d'après Guérin, 1980), D. pikermiensis (Miocène supérieur, Sud-Est d'Europe : d'après Geraads, 1988 ; Geraads et Spassov, 2009), S. jeanvireti (Pliocène, Europe : d'après Guérin, 1980 ; Guérin et Tsoukala, 2013), et S. etruscus (Plio–Pleistocène, Europe : d'après Guérin, 1980). L = longueur ; TD = diamètre transversal ; H = hauteur ; f.m. = foramen magnum.

Measurement	Kávás (HNHM v.79.117)	Western Europe	Honan	Linxia	*C. neumayri*	"*D*". *douariensis*	*D. schleiermacheri*	*D. pikermiensis*	*S. jeanvireti*	*S. etruscus*
L nuchal crest–tip of the nasal bones		700–787.5	745	(715)	680–705	ca. 680	654–667	615–660	637–727	530–648
TD nuchal crest	ca. 211	165–200	188	(174)	ca. 190–235	ca. 208	144–175	ca. 150–215	110–188	101–174
Distance between the frontoparietal crests	(70)	43.5–69		(57)	53–61	68–78	0		48–73.5	34–60.5
H of the occipital face (from the bottom f.m.)			220		220					
H of the occipital face (from the top f.m.)	(170)	167–190			143–ca. 160		145–182	142–155	133–157	117–153
TD at the level of the processus postorbitalis		226–262	236		(230)	262	200		224.5–229	162–200

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Table 2

Measurements (in mm) of the upper teeth of "*Dihoplus*" *megarhinus* from Kávás (Hungary), compared with those of "*D*". *megarhinus* from Lens Lestang (Pliocene, France), Baccinello V3 (latest Miocene, Italy), Udunga (latest Pliocene, Russia: from Fukuchi et al., 2009), Honan (Late Miocene, China: from Ringström, 1924), Linxia (Late Miocene, China: from Deng, 2006), and from several Pliocene localities of Western Europe (from Guérin, 1980), and with those of *C. neumayri* (Late Miocene, Southeastern Europe, Turkey and Iran: Geraads, 1988; Antoine and Saraç, 2005; Geraads and Spassov, 2009; Giaourtsakis, 2009; Antoine et al., 2012), "*D*". *douariensis* (Late Miocene, Africa: from Guérin, 1966; Giaourtsakis et al., 2009), *D. schleiermacheri* (Late Miocene, Central Europe: Guérin, 1980), *D. pikermiensis* (Late Miocene Southeastern Europe: Geraads, 1988; Geraads and Spassov, 2009), *S. jeanvireti* (Pliocene, Europe: Guérin, 1980; Guérin and Tsoukala, 2013), and *S. truscus* (Plio–Pleistocene, Europe: Guérin, 1980). L = length; L × B = length and breadth.

Dimensions (mm) des dents jugales supérieures de « Dihoplus *»* megarhinus *de Kávás (Hongrie), de Lens Lestang (Pliocène, France), de Baccinello V3 (Miocène supérieur terminal, Italy), d'Udunga (Pliocène supérieur terminal, Russie : d'après Fukuchi et al., 2009), de Honan (Miocène supérieur, Chine : d'après Ringström, 1924), de Linxia (Miocène supérieur, Chine : d'après Deng, 2006) et du Pliocène d'Europe occidentale (d'après Guérin, 1980), et des dents jugales supérieures de* C. neumayri *(Miocène supérieur, Sud–Est d'Europe, Turquie et Iran : d'après Geraads, 1988 ; Antoine et Saraç, 2005 ; Geraads et Spassov, 2009 ; Giaourtsakis, 2009 ; Antoine et al., 2012), «* D *».* douariensis *(Miocène supérieur, Afrique : d'après Guérin, 1966 ; Giaourtsakis et al., 2009),* D. schleiermacheri *(Miocène supérieur, Europe centrale : d'après Guérin, 1980),* D. pikermiensis *(Miocène Supérieur, Sud–Est d'Europe : d'après Geraads, 1988 ; Geraads et Spassov, 2009),* S. jeanvireti *(Pliocène, Europe : d'après Guérin, 1980 ; Guérin et Tsoukala, 2013), et* S. etruscus *(Plio–Pleistocène, Europe : d'après Guérin, 1980). L = longueur ; L × B = diamètre transversal et largeur.*

Measurement	Kávás (HNHM v.79.117)	Lens Lestang (NHML M40834)	Baccinello V3 (NMB nn)	Western Europe	Udunga	Honan	Linxia	*C. neumayri*	*"D". douariensis*	*D. schleiermacheri*	*D. pikermiensis*	*S. jeanvireti*	*S. etruscus*
L P2–M3	(280)	264.74	(257)	255–274			(270)	247–274	264–284	267	240–272	248–253.5	215–245
L P2–P4	130	118.09	(115)	105.5–128			(101)	117–132	134.8–136.1	131	111–123	114–117	100–137
L M1–M3	(155)	156.1	(149)	142–162.5			(168)	134–161	156.8	148	134–153	120–149	126.5–145
P2 L × B	39.4–41.1 × 48.2–49			35–40 × 40–46				36.1–41 × 41.8–44	30–38.5 × 38–47.6	32–39 × 33.5–43		31–37 × 35–41	29–35 × 32–42.5
P3 L × B	46.9–47.3 × 57–57.25			39.5–48 × 48–59	43.6 × 42.5			43.6–50 × 53.6–58	42–(45.7)x56.5–(62.3)	36.5–45 × 46–56.5		40–43 × 45–53.5	35–43.5 × 42–54
P4 L × B	50.75 × 65			43–51 × 53–67	47–47.8 × 45.1–46.1			48–50.2 × 59–63	43–47.8 × 62.5–72.2	43–50 × 53–64		40.5–46.5 × 46–58.5	37–49 × 45–63
M1 L × B				49–64 × 55.5–70	49.1–53.7 × 48.4–50.1	64 × 66		52.5–58 × 61–63.4	52–58.8 × 63–70	47.5–61.5 × 54.5.70.5		48.5–56 × 50–58	45–54 × 48–60.5
M2 L × B	64 × 74			53.5–65.5 × 59.5–73	54–59.3 × 47.7–61.2	62 × 63		59–63 × 64–67.3	53–61 × 67–71	52–61.5 × 60–72		51–56 × 51.5–63.5	45.5–57 × 48–65.5
M3 L × B	64.8 × 65.95			57–65.5 × 56–66		66 × 64		50–66.9 × 57.6–61.2	50–63.4 × 59–64	52–61 × 44–58		53–61.5 × 46–59	47–59 × 46–56.5

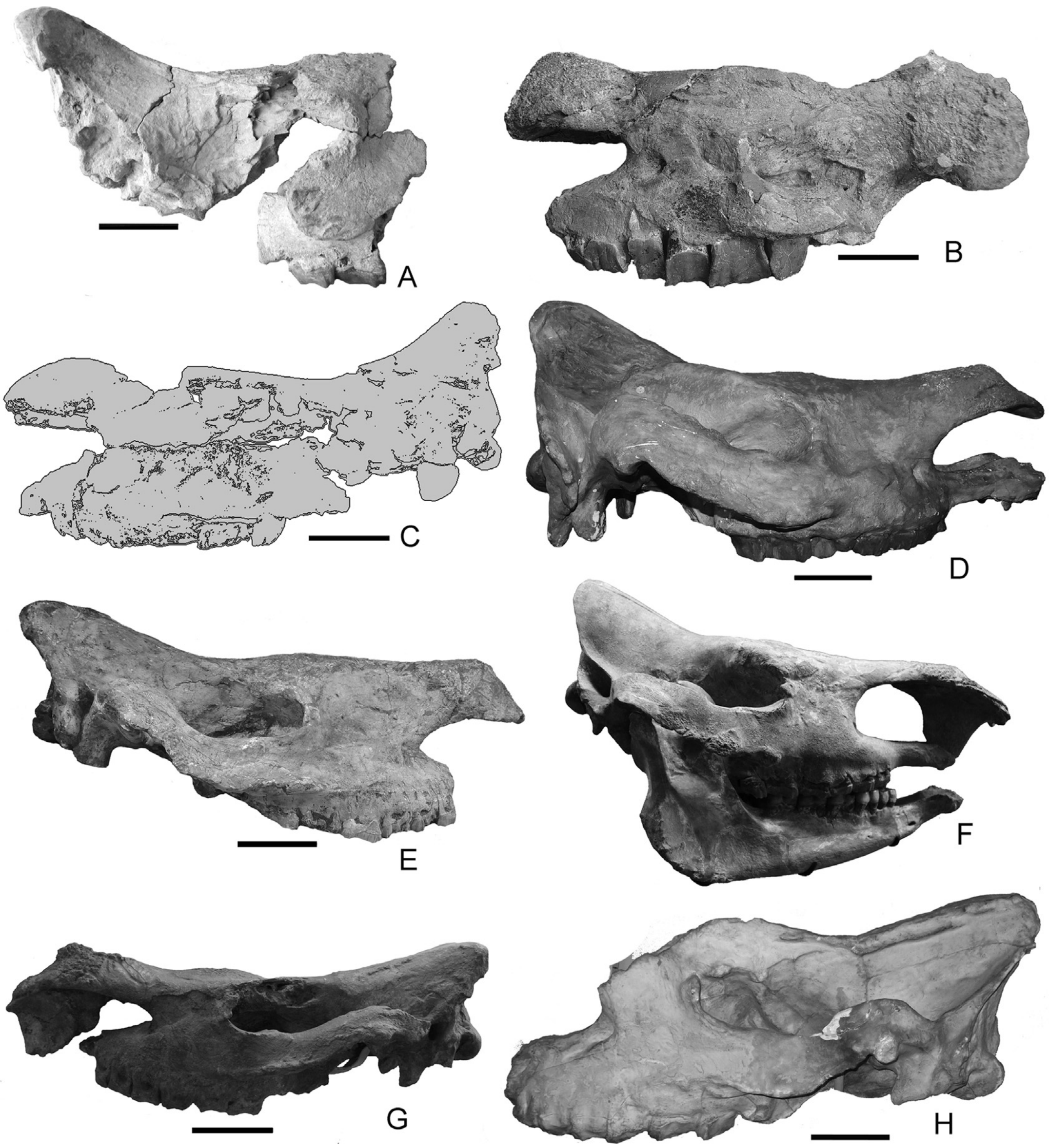

Fig. 3. Skulls of selected Rhinocerotini, lateral view. **A**. Re-assembled skull of "*Dihoplus*" *megarhinus* from Kávás, Hungary (HNHMV.79.117-1 and 2). **B**. Skull of *Ceratotherium neumayri* from Maragheh, Iran (NHMW 2014/0424/0001 ex mar0381). **C**. Skull of "*Diceros*" *douariensis* from Kuseralee, Ethiopia (re-drawn from Giaourtsakis et al., 2009). **D**. Skull of *Dihoplus schleiermacheri* from Eppelsheim, Germany (cast NHML M2781). **E**. Skull of *Dihoplus pikermiensis* from Pikermi, Greece (NHML M10143). **F**. Skull of *Stephanorhinus jeanvireti* from Vialette, France (NMB Vt621). **G**. Skull of *Stephanorhinus etruscus* from Upper Valdarno, Italy (IGF 756). **H**. Skull of "*Dihoplus*" *megarhinus* from Lens Lestang, France (cast NMB Fp16). Scale bar equals 10 cm.

Crânes de quelques Rhinocerotini, vue latérale. **A**. *Crâne restauré de* « Dihoplus » megarhinus *de Kávás, Hongrie (HNHMV.79.117-1, 2).* **B**. *Crâne de* Ceratotherium neumayri *de Maragheh, Iran (NHMW 2014/0424/0001 ex mar0381).* **C**. *Crâne de* « Diceros » douariensis *de Kuseralee, Éthiopie (re-dessiner d'après Giaourtsakis et al., 2009).* **D**. *Crâne de* Dihoplus schleiermacheri *d'Eppelsheim, Allemagne (moulage NHML M2781).* **E**. *Crâne de* Dihoplus pikermiensis *de Pikermi, Grèce (NHML M10143).* **F**. *Crâne de* Stephanorhinus jeanvireti *de Vialette, France (NMB Vt621).* **G**. *Crâne de* Stephanorhinus etruscus *de Valdarno supérieur, Italie (IGF 756).* **H**. *Crâne de* « Dihoplus » megarhinus *de Lens Lestang, France (moulage NMB Fp16). Échelles : 10 cm.*

roof is concave, but the occiput is not too raised"; "frontal horn boss small"; "parietal crests are broadly separated"; "subaural channel closed"; "the occipital surface is inclined anteriorly, and the occipital crest bears a wide notch at the midline"; "I2 and i1 absent, I1 and i2 reduced"; "P1 lost"; "in the upper premolars, the protocone is not constricted, the antecrochet is absent, the crochet is narrow, the parastyle is weak, and the paracone rib is weak or absent"; "protocone is not constricted, the parastyle is wide and projected, the antecrochet is wide and short, and the crochet is well developed"; M1 and M2 "have a marked paracone rib, and M3 has a triangular occlusal surface".

However, the above mentioned characters can be observed on several specimens referred to "*D*". *megarhinus* and collected at Montpellier (France; type locality), Lens Lestang (France), Saint-Laurens (France) and other Italian localities (see comparison section). The skulls from Montpellier and Lens Lestang, described and compared in the following chapter, are larger and longer than those referred to as *D. pikermiensis* (Guérin, 1980: 450, tab. 84; Geraads, 1988: 17, tab. 1). The nasal bones of "*D*". *megarhinus* are long and very similar in morphology to those of *D. ringstroemi* (Ringström, 1924: figs. 1–2; Guérin, 1980: Pl. 10; Deng, 2006: fig. 3). The nasal notch in "*D*". *megarhinus* has a U-shaped morphology in lateral view and its posterior border is at the level of P3–P4, as well as in the figured skulls of *D. ringstroemi* (Ringström, 1924: figs 1–2; Guérin, 1980: Pl. 10; Deng, 2006: fig. 3). The anterior border of the orbital cavity is at the same level in both species. The dorsal profile

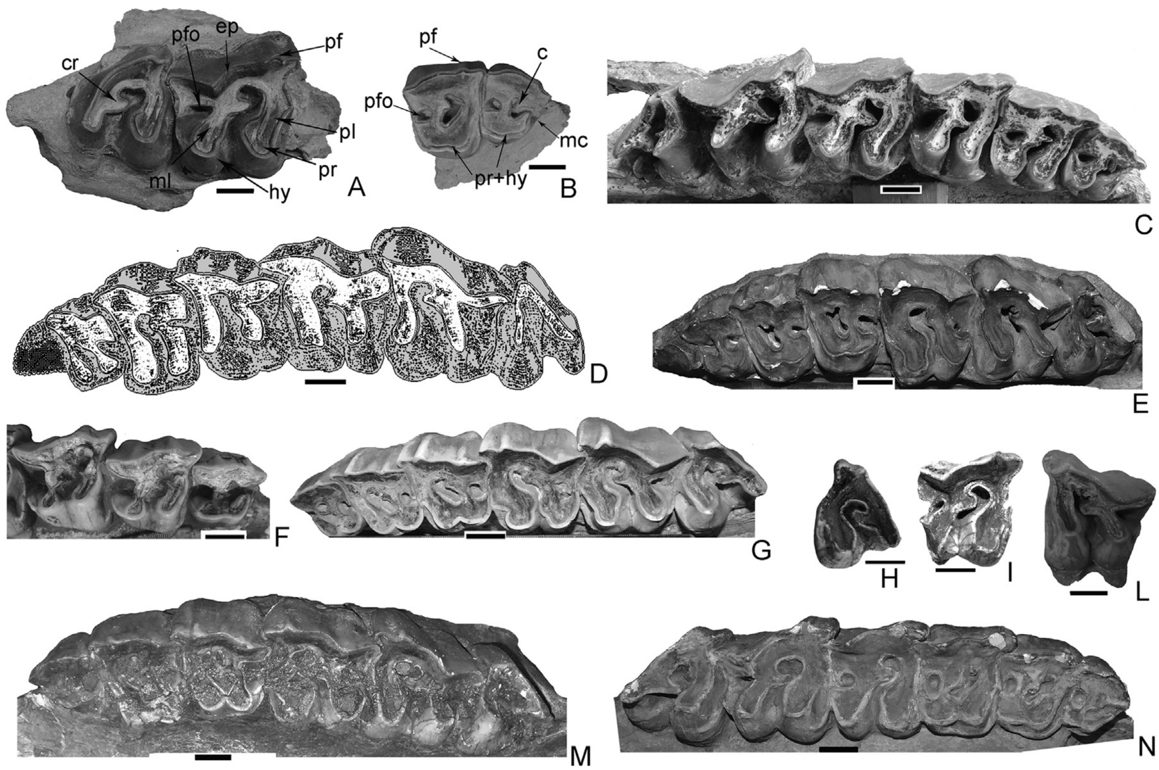

Fig. 4. Upper teeth of selected Rhinocerotini, occlusal view. **A**. M2–M3 of "*Dihoplus*" *megarhinus* from Kávás, Hungary (HNHMV.79.117-2). **B**. P2–P3 of "*Dihoplus*" *megarhinus* from Kávás, Hungary (HNHMV.79.117-3). **C**, P2–M3 of *Ceratotherium neumayri* from Maragheh, Iran (NHMW 2014/0424/0001 ex mar0381). **D**. DP1–M3 of "*Diceros*" *douariensis* from Douaria, Tunisia (re-drawn from Guérin, 1966). **E**. DP1–M3 of *Dihoplus schleiermacheri* from Eppelsheim, Germany (cast NHML M2781). **F**. P2–P3 of *Dihoplus pikermiensis* from Pikermi, Greece (NHML M10142). **G**. P2–M3 of *Dihoplus pikermiensis* from Pikermi, Greece (NHML M10144). **H**. M3 of *Stephanorhinus jeanvireti* from Vialette, France (NMB Vt145). **I**. M2 of *Stephanorhinus jeanvireti* from Vialette, France (NMB Vt209). **L**. M2 of *Stephanorhinus jeanvireti* from Rákoscsaba, Hungary (HNHM v.79.112). **M**. P2–M3 of *Stephanorhinus etruscus* from Capitone, Italy (MPUR 1500). **N**. P2–M3 of "*Dihoplus*" *megarhinus* from Lens Lestang, France (cast NHML 40834). Scale bar equals 2 cm. c = crista; cr = crochet; ep = ectoloph; hy = hypocone; mc = mesial cingulum; ml = metaloph; pf = paracone fold; pfo = post-fossette; pl = protoloph; pr = protocone; pr + hy = protocone and hypocone joined.

Jugales supérieur de Rhinocerotidae, vue occlusale. ***A****. M2–M3 de* « Dihoplus » megarhinus *de Kávás, Hongrie (HNHMV.79.117-2)* ***B****. P2–P3 de* « Dihoplus » megarhinus *de Kávás, Hongrie (HNHMV.79.117-3).* ***C****. P2–M3 de* Ceratotherium neumayri *de Maragheh, Iran (NHMW 2014/0424/0001 ex mar0381).* ***D****. DP1–M3 de* « Diceros » douariensis *de Douaria, Tunisie (re-dessiner d'après Guérin, 1966).* ***E****. DP1–M3 de* Dihoplus schleiermacheri *de Eppelsheim, Allemagne (moulage NHML M2781).* ***F****. P2–P3 de* Dihoplus pikermiensis *de Pikermi, Grèce (NHML M10142).* ***G****. P2–M3 de* Dihoplus pikermiensis *de Pikermi, Grèce (NHML M10144).* ***H****. M3 de* Stephanorhinus jeanvireti *de Vialette, France (NMB Vt145).* ***I****. M2 de* Stephanorhinus jeanvireti *de Vialette, France (NMB Vt209).* ***L****. M2 de* Stephanorhinus jeanvireti *de Rákoscsaba, Hongrie (HNHM v.79.112).* ***M****. P2–M3 de* Stephanorhinus etruscus *de Capitone, Italie (MPUR 1500).* ***N****, P2–M3 de* « Dihoplus » megarhinus *de Lens Lestang, France (moulage NHML 40834). Échelles : 2 cm. c = crista ; cr = crochet ; ep = ectolophe ; hy = hypocône ; mc = cingulum antérieur ; ml = metalophe ; pf = pli du paracône ; pfo = post-fossette ; pl = protolophe ; pr = protocône ; pr + hy = protocône et hypocône reliés.*

Table 3
Measurements (in mm) of the mandible of "*Dihoplus*" *megarhinus* from Kávás (Hungary), compared with those of "*D*". *megarhinus* from Val di Pugna and Palaia (Early Pliocene, Italy: from Pandolfi, 2013), Montpellier (Early Pliocene, France), Honan (Late Miocene, China: from Ringström, 1924) and from several Pliocene localities of Western Europe (from Guérin, 1980), and with those of *C. neumayri* (Late Miocene, Southeastern Europe, Turkey and Iran: Geraads, 1988; Antoine and Saraç, 2005; Geraads and Spassov, 2009; Giaourtsakis, 2009; Antoine et al., 2012), "*D*". *douariensis* (Late Miocene, Africa: from Guérin, 1966; Giaourtsakis et al., 2009), *D. schleiermacheri* (Late Miocene, Central Europe: Guérin, 1980; Giaourtsakis et al., 2006), *D. pikermiensis* (Late Miocene Southeastern Europe: Geraads, 1988; Giaourtsakis et al., 2006; Geraads and Spassov, 2009), *S. jeanvireti* (Pliocene, Europe: Guérin, 1980; Guérin and Tsoukala, 2013), and *S. etruscus* (Plio–Pleistocene, Europe: Guérin, 1980). L = length; H = height.

Dimensions (mm) des mandibules de « Dihoplus » megarhinus *de Kávás (Hongrie), de Val di Pugna et Palaia (Pliocène inférieur, Italie : d'après Pandolfi, 2013), de Montpellier (Pliocène inférieur, France), de Honan (Miocène supérieur, Chine : d'après Ringström, 1924) et du Pliocène d'Europe occidentale (d'après Guérin, 1980), et des mandibules de* C. neumayri *(Miocène supérieur, Sud–Est d'Europe, Turquie et Iran : d'après Geraads, 1988 ; Antoine et Saraç, 2005 ; Geraads et Spassov, 2009 ; Giaourtsakis, 2009 ; Antoine et al., 2012),* « D ». douariensis *(Miocène supérieur, Afrique : d'après Guérin, 1966),* D. schleiermacheri *(Miocène supérieur, Europe centrale : d'après Guérin, 1980 ; Giaourtsakis et al., 2006),* D. pikermiensis *(Miocène supérieur, Sud–Est d'Europe : d'après Geraads, 1988 ; Giaourtsakis et al., 2006 ; Geraads et Spassov, 2009),* S. jeanvireti *(Pliocène, Europe : d'après Guérin, 1980 ; Guérin et Tsoukala, 2013), et* S. etruscus *(Plio–Pleistocène, Europe : d'après Guérin, 1980). L = longueur ; H = hauteur.*

Masurement	Kávás (HNHM v.79.117)	Val di Pugna, Palaia	Montpellier (NHML M40805 and NMB MP1)	Western Europe	Honan	*C. neumayri*	*"D". douariensis*	*D. schleiermacheri*	*D. pikermiensis*	*S. jeanvireti*	*S. etruscus*
L horizontal ramus	> 535			515–606	(558)[a]	(510)–550	503	520–610.9	532–630	497–535	430–509
H below m3	118–120	96.5–105	115.5	87–127	115	85–108	89–90	89.5–110	101.4–107.6	90–105	79–105
L symphysis			133.38	101–149	132	121–143	97	142.2–144	123.8–151	114–133	92–123

[a] The value of 635 mm for the length of the mandible reported by Ringström (1924) is questionable. If the height of the horizontal ramus is of 115 mm below m3, proportionally, the length of the mandible seems to be approximately of 558 mm.

Table 4

Measurements (in mm) of lower teeth of "*Dihoplus*" *megarhinus* from Kávás (Hungary), compared with those of "*D*". *megarhinus* from Val di Pugna and Palaia (Early Pliocene, Italy: from Pandolfi, 2013), Montpellier (Early Pliocene, France), Udunga (latest Pliocene, Russia: from Fukuchi et al., 2009), Honan (Late Miocene, China: from Ringström, 1924), and from several Pliocene localities of Western Europe (from Guérin, 1980), and with those of *C. neumayri* (Late Miocene, Southeastern Europe, Turkey and Iran: Geraads, 1988; Antoine and Saraç, 2005; Geraads and Spassov, 2009; Giaourtsakis, 2009; Antoine et al., 2012), "*D*". *douariensis* (Late Miocene, Africa: from Guérin, 1966; Giaourtsakis et al., 2009), *D. schleiermacheri* (Late Miocene, Central Europe: Guérin, 1980; Giaourtsakis et al., 2006), *D. pikermiensis* (Late Miocene Southeastern Europe: Geraads, 1988; Giaourtsakis et al., 2006; Geraads and Spassov, 2009), *S. jeanvireti* (Pliocene, Europe: Guérin, 1980; Guérin and Tsoukala, 2013), and *S. etruscus* (Plio–Pleistocene, Europe: Guérin, 1980). L = length; L × B = length and breadth.

Dimensions (mm) des jugales inférieur de « Dihoplus » megarhinus *de Kávás (Hongrie), de Val di Pugna et Palaia (Pliocène inférieur, Italie : d'après Pandolfi, 2013), de Montpellier (Pliocène inférieur, France), d'Udunga (Pliocène supérieur terminal, Russie : d'après Fukuchi et al., 2009), de Honan (Miocène supérieur, Chine : d'après Ringström, 1924) et du Pliocène d'Europe occidentale (d'après Guérin, 1980), et des jugales inférieur de* C. neumayri *(Miocène supérieur, Sud–Est d'Europe, Turquie et Iran : d'après Geraads, 1988 ; Antoine et Saraç, 2005 ; Geraads et Spassov, 2009 ; Giaourtsakis, 2009 ; Antoine et al., 2012),* « D ». douariensis *(Miocène supérieur, Afrique : d'après Guérin, 1966),* D. schleiermacheri *(Miocène supérieur, Europe centrale : d'après Guérin, 1980 ; Giaourtsakis et al., 2006),* D. pikermiensis *(Miocène supérieur, Sud–Est d'Europe : d'après Geraads, 1988 ; Giaourtsakis et al., 2006 ; Geraads et Spassov, 2009),* S. jeanvireti *(Pliocène, Europe : d'après Guérin, 1980 ; Guérin et Tsoukala, 2013), et* S. etruscus *(Plio–Pleistocène, Europe : d'après Guérin, 1980). L = longueur ; LxB = diamètre transversal et largeur.*

Measurement	Kávás (HNHM v.79.117)	Val di Pugna and Palaia	Montpellier (NHML M40805)	Montpellier (NMB MP1031)	Western Europe	Udunga	Honan	*C. neumayri*	*"D". douariensis*	*D. schleiermacheri*	*D. pikermiensis*	*S. jeanvireti*	*S. etruscus*
L p2–m3	(288)	ca. 244.65–254.81	272.31	(261.53)	228–293			247–278	265	247.5–310.1	ca. 252–270.5	234–246	210–251.1
L p2–p4	125.2	106.63	118.14	(116)	101–136			102–119		102.5–129	107–116.8	97–106.5	87–108
L m1–m3	(158)	ca. 139–144.97	158.09	151.8	134–165			144.2–158.9		139–177	135.8–156	127–140	121–143
p2 L × B	33.4 × 21.8	28.6–31.88 × 17.92–19.05			29.5–43 × 16.5–25	29.7–30 × 14.1–18.1	32 × 26	30.7–32 × 16.7–22.3	26 × 16–18.5	26–37 × 18.5–26	33.2 × 22.9	27–32 × 16.5–21	25–33 × 16–22
p3 L × B	41.55 × 30.7	37.6–40.05 × 24.6–25.83			35–44 × 22–31.5		38 × 34	34–43 × 28.2–29.3	34.5–35.5 × 33–36	34.5–41.5 × 26–30	37.3–37.5 × 24.2–29.5	33–38 × 23–34	31.5–37.5 × 21.5–29
p4 L × B	44.7–44.95 × 35–35	39.41–42.52 × 28.7–30.51			37.5–48 × 27.5–38	39.7 × 26.1	46 × 39	40.6–49 × 30.8–33.1	40–43 × 28.5–38	38–48 × 27–34.5	38.2–44.3 × 28.5–33.5	37–40.5 × 24–31	35–42.5 × 22–31
m1 L × B	50.4–53.6 × 38.45	44.22–48.85xca. 29.6–32.2			38.5–53 × 29–40	40.8–40.9 × 28	44 × 42	(43)–52 × 31.2–34	48.5–49 × 28.5–30.5	43–55.5 × 30.5–38.5	43.2–46.5 × 29.8–37.2	40–47 × 25–34	36–50 × 26.5–33
m2 L × B	58 × 36.1	49–52.24 × 30.61–32.73			43–57.5 × 31–39	51.9–52 × 32.5–33.1	52 × 43	49.8–56 × 32–37.8	51.5–55.5 × 29–35.5	47.5–58.5 × 31–40	47.9–52.3 × 34.3–35.5	43–53.5 × 27–34.5	40–54 × 27–34
m3 L × B	58 × 34	49.12 × 35			48–62 × 29.5–37	52–54.9 × 31.4–31.6	ca. 58 × 40	52–56.2 × 29–33.8	53–54 × 27–27.5	46–55 × 29–36.5	44.3–51.3 × 31.4–34.2	43.5–54 × 26–33	41–52 × 26–33

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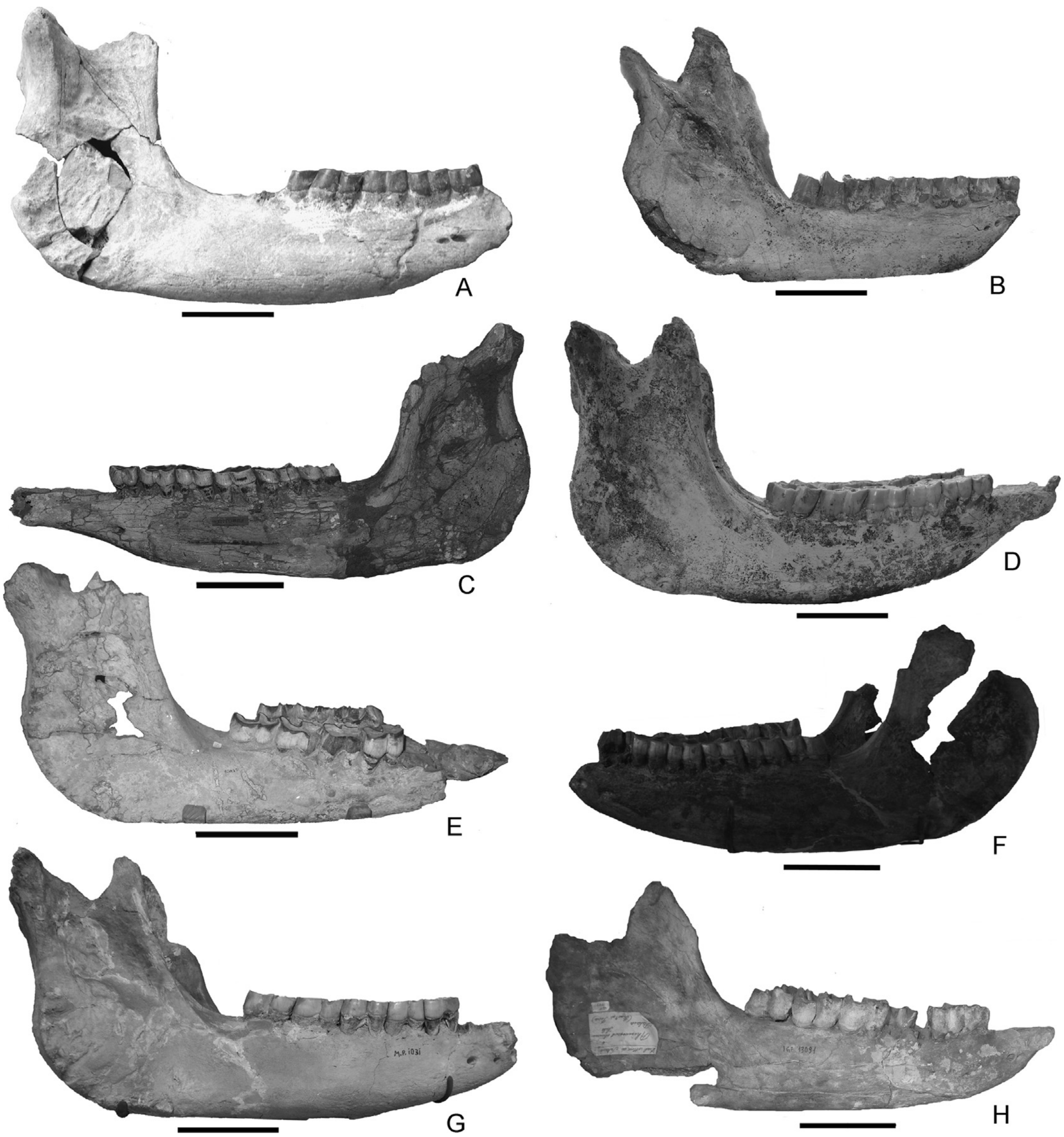

Fig. 5. Mandibles of Rhinocerotidae, lateral view. **A**. Re-assembled mandible of "*Dihoplus*" *megarhinus* from Kávás, Hungary (HNHMV.79.117-5). **B**. Mandible of *Ceratotherium neumayri* from Maragheh, Iran (NHMW 2014/0424/0001 ex mar0381). **C**. Mandible of *Dihoplus schleiermacheri* from Eppelsheim, Germany (NHML M375); **D**. Mandible of *Dihoplus pikermiensis* from Pikermi, Greece (NHML M10150). **E**. Mandible of *Stephanorhinus jeanvireti* from Monte San Pietro, Italy (MGGC 9354). **F**. Mandible of *Stephanorhinus etruscus* from Upper Valdarno, Italy (IGF 755). **G**. Mandible of "*Dihoplus*" *megarhinus* from Montpellier, France (NMB Mp1031). **H**. Mandible of "*Dihoplus*" *megarhinus* from Palaia, Italy (IGF 5566v). Scale bar equals 10 cm.

Mandibules de Rhinocerotidae, vue latérale. ***A****. Restauré mandibule de* « Dihoplus » megarhinus *de Kávás, Hongrie (HNHMV.79.117-5).* ***B****. Mandibule de* Ceratotherium neumayri *de Maragheh, Iran (NHMW 2014/0424/0001 ex mar0381).* ***C****. Mandibule de* Dihoplus schleiermacheri *de Eppelsheim, Allemagne (NHML M375).* ***D****. Mandibule de* Dihoplus pikermiensis *de Pikermi, Grèce (NHML M10150).* ***E****. Mandibule de* Stephanorhinus jeanvireti *de Monte San Pietro, Italie (MGGC 9354).* ***F****. Mandibule de* Stephanorhinus etruscus *de Valdarno supérieur, Italie (IGF 755).* ***G****. Mandibule de* « Dihoplus » megarhinus *de Montpellier, France (NMB Mp1031).* ***H****. Mandibule de* « Dihoplus » megarhinus *de Palaia, Italie (IGF 5566v). Échelles : 10 cm.*

of the skull and the morphology of the occiput are also very similar in "*D*". *megarhinus* and *D. ringstroemi*, but in the specimen from Kávás, the occiput is slightly more raised than in *D. ringstroemi*. In addition, "*D*". *megarhinus* and *D. ringstroemi* share the following characters: distant frontoparietal crests, fully closed external auditory pseudomeatus, concave profile of the nuchal crest (= "grande crête occipitale" or "chignon" in Guérin, 1980 and "protubérance occipitale externe" in Antoine, 2002) in dorsal view, absence of I2 and i1, reduced i2. The presence of a reduced I1 in "*D*". *megarhinus* has been never reported in previous contributions probably because a preserved praemaxilla is known only on the skull from Montpellier (Gervais, 1851: Pl. 2). The praemaxilla is absent on the skulls from Millas (Maurette, 1910: Pl. 1), Lens Lestang (Falconer, 1868; this work) and Saint-Laurent (Guérin et al., 1969: figs. 1–2). According to Falconer (1868: 382), the praemaxilla was present on the skull from Monte Zago, but unfortunately this specimen was destroyed during the World War II and no morphological characters can be currently observed. Moreover, the presence of reduced upper incisors cannot be observed from the pictures of the same skull reported by Cuvier (1836: Pl. 47, fig. 6). During a visit to the NMB collection, one of the authors (LP) recovered an unpublished maxilla and praemaxilla referable to "*D*". *megarhinus*. The specimen (without collection number) was collected at Baccinello V3, latest Miocene in age (MN13; Rook et al., 2011). The upper teeth are morphologically very similar to those from Kávás and Lens Lestang as well as to several remain from Montpellier; therefore, the Baccinello specimen can be surely ascribed to "*D*". *megarhinus*. Fortunately, the specimen preserved the right side of the praemaxillae with a small and rounded I1, very similar to that observed in *D. pikermiensis*.

Moreover, the characters described for the upper teeth of *D. ringstroemi* (e.g., absence of P1, of a protocone constriction and of an antecrochet on the premolars, paracone fold weak on upper premolars, marked paracone fold on upper molars, small crista on M3) are also known and observed in the specimens of *"D". megarhinus* previously discussed (see also Guérin, 1980). In terms of dimensions, the Chinese material is similar to that collected from several European localities (Tables 1–4).

Based on these evidences, *D. ringstroemi* is here considered as junior synonym of *"D". megarhinus*.

Studied material: HNHM V.79.117, including a fragmentary skull and three fragments of maxillae (belonging to one right and one left maxilla).

4. Description and comparison

4.1. Skull

Description: In dorsal view, the cranial fragment HNHM V.79.117-1 displays a well-developed boss of the frontal horn, distant frontoparietal crests and a concave posterior border of the nuchal crest (Fig. 2A). In lateral view, the dorsal profile of the skull is concave, the boss of the frontal horn is evident, the external auditory pseudomeatus is fully closed, the area between the temporal and nuchal crest is depressed and the occipital face is vertical (Fig. 2B–C). In occipital face view, the nuchal crest is well developed and its dorsal profile is straight. A fragment of skull with a small portion of the orbital cavity and the M2–M3 (HNHMV.79.117-2 which is a fragment of the skull HNHM V.79.117-1) suggests that the anterior border of the orbit was located at the level of the anterior half of M2. On the specimen HNHM V.79.117-3, the posterior border of the nasal notch is at the level of P3–P4 (Fig. 2D).

Comparison: Compared to HNHM V.79.117, the skulls of *Ceratotherium neumayri* (Osborn, 1900) display a rather straight dorsal profile, a forked nuchal crest, an inclined backward occipital face and the posterior border of the nasal notch between P2 and P3 (Fig. 3B; Appendix A). Contrary to the studied material, *"Diceros" douariensis* Guérin, 1966 has an open external auditory pseudomeatus (Giaourtsakis et al., 2009), the insertion for the frontal horn is less developed, and the occipital face is lower (Fig. 3C; Giaourtsakis et al., 2009: fig. 14.1). The studied material differs from *D. schleiermacheri* in that the frontoparietal crests are very close, the posterior border of the nuchal crest is straight and transversally less developed, the posterior border of the nasal notch is at the level of P2, and the external auditory pseudomeatus is partially closed (Fig. 3D). The dorsal profile of the skull is more concave in the specimen NHML M49660 ascribed to *D. pikermiensis* (Geraads, 1988; Giaourtsakis et al., 2006). Nevertheless, this feature could be amplified by a lateral deformation of the skull. Other specimens collected at Pikermi and housed at NHML do not display such a markedly concave profile of the skull (Fig. 3E). In this species, the posterior border of the nasal notch terminates generally at the level of P2–P3 (Fig. 3E), the insertion for the frontal horn is less developed and the frontoparietal crests are relatively closer (exception made for the specimen NHMW 2009z-0085-0001 which is dorso-ventrally compressed). The studied specimens differ from the Pliocene *S. jeanvireti* (Guérin, 1972), which displays a less transversally developed nuchal crest and a less concave dorsal profile of the skull (Fig. 3F). The skulls of the latest Pliocene–Early Pleistocene *S. etruscus* (Falconer, 1868) are smaller and less massive than the specimen collected at Kávás; moreover in *S. etruscus*, the dorsal profile of the skull is straight (Fig. 3G) and the occipital face is less developed transversally. The specimens HNHM V.79.117 are morphologically and metrically close to those of the Pliocene European *"D". megarhinus* (de Christol, 1834; Falconer, 1868; Capellini, 1894; Simonelli, 1897; Guérin et al., 1969; Guérin, 1980; Pandolfi, 2013: (tab. 1)). In the skull from Lens Lestang (cast housed at NHML and NMB; Falconer, 1868; Fig. 3H), as well as in the studied specimen, the dorsal profile is concave and the occipital face is vertical, the external auditory pseudomeatus is fully closed, the anterior border of the orbital cavity is at the level of M2, the posterior border of the nasal notch is at the level of P4, the frontoparietal crests are distant despite the deformation of the skull and the posterior border of the nuchal crest is concave (Fig. 3H). Nevertheless, in the skull from Lens Lestang the occipital face appears less elevated than in the studied specimen (Fig. 3H). The skull from Kávás is morphologically similar to that from Saint-Laurent (Guérin et al., 1969: 83, fig. 1, 85, fig. 4, 93, fig. 6). In the latter specimen, the dorsal profile of the skull is more concave, the occipital face is vertical and elevated, the nuchal crest is transversally developed, the frontoparietal crests are distant, and the insertion for the frontal horn is wide and marked. The skull of *"D". megarhinus* from Montpellier (Guérin, 1980) is similar to those from Lens Lestang and Kávás. The skull HNHM V.79.117 shares the following characters with *"D". megarhinus* from China: the dorsal profile of the skull is relatively concave, the posterior border of the nasal notch is at the level of P3–P4, the anterior border of the orbital cavity is at the level of M2, the external auditory pseudomeatus is fully closed, the occipital face is vertical, the frontoparietal crests are distant, the posterior border of the nuchal crest is concave. Nevertheless, on the studied material, the occipital face is slightly more elevated and transversally expanded, and the insertion of the frontal horn is much wider.

4.2. Upper teeth

Description: The specimen HNHM V.79.117-4 retains almost the complete upper toothrow, however the last two molars are poorly preserved, the specimen HNHM V.79.117-3 is composed by P2 and P3 while HNHM V.79.117-2 by M2 and M3 (Fig. 2E–G). Labial and lingual cingula are absent on both premolars and molars whereas mesial and distal cingula are evident on the molars. The P2 HNHM V.79.117-4 is at the same stage of wear as in specimen HNHM V.79.117-3 (Fig. 2E, G); the occlusal profile of the ectoloph is slightly convex, the paracone fold is faint, the parastyle is large and short, a medifossette is present on HNHM V.79.117-4 and a crista on HNHM V.79.117-3, the post-fossette is circular, the hypocone is more developed than the protocone, the metaloph is slightly oblique, the protoloph is joined with the ectoloph by a narrow "bridge" on HNHM V.79.117-4 and is not joined with the ectoloph on HNHM V.79.117-3. At this stage of wear, the protocone and hypocone on P2 and P3 are lingually joined (Fig. 2E, G). The profile of the ectoloph on P3 is rather straight, the paracone fold is weak and the parastyle is short; a small crochet is present only on HNHM V.79.117-3 (Fig. 2G), the post-fossette is circular and the metaloph is slightly oblique (Fig. 2). The P4 HNHM V.79.117-4 is morphologically similar to P3 but the metacone fold is faint, and the protocone is joined with the hypocone by a lingual bridge. The protocone constriction is weak on the molars (Fig. 2E–F). The M1 HNHM V.79.117-4 is much worn down and lacks the ectoloph. A hint of the crochet is still detectable; the post-fossette is small and the metaloph is constricted. M2 is much damaged on HNHM V.79.117-4 and only a portion of the protoloph is preserved. The M3 is represented only by the roots on the specimen HNHM V.79.117-4. In the specimen HNHM V.79.117-2, M2 and M3 are relatively worn down (Fig. 2F). The paracone fold is strong on M2 and M3; the mesostyle is faint on M2; the parastyle fold is marked on both the teeth, the parastyle is developed on M2. The posterior profile of the ectoloph, in occlusal view, is concave on M2; a single crochet is present on M2 and M3, whereas crista and antecrochet are absent on both teeth at this stage of wear. On M2, the post-fossette is wide and the distal cingulum is continuous; the metaloph is short and both metaloph and protoloph are slightly oblique. M3 has a triangular outline in occlusal view.

Comparison: The upper teeth of *C. neumayri* differ from Kávás specimens by having backwards bent protolophs, molariform upper premolars and a more wavy profile of the ectoloph in occlusal view (Fig. 4C). The premolars of "*D*". *douariensis* are molariform and have a strong and continuous lingual cingulum, whilst the M1 has a flat lingual side of the protocone which also displays a lingual groove on the type material from Douaria (Guérin, 1966: fig. 8; Fig. 4D). In *D. schleiermacheri*, DP1 is present, a crista occurs on the upper premolars and the metacone fold is present on the upper premolars (Fig. 4E). A reduced lingual cingulum is usually present on the upper premolars of *D. pikermiensis*; in addition, the metacone fold is marked on upper premolars and the protocone constriction is marked on M1–M2 (Fig. 4F–G). Contrary to the studied material, the M2 of "*S*". *miguelcrusafonti* (Guérin and Santafé-Llopis, 1978) from the Pliocene of Spain displays a well-developed crochet and a crista, whereas the P3 displays separated protocone and hypocone, double crochet, crista, accessory folds and a wide post-fossette (Guérin and Santafé-Llopis, 1978). *S. jeanvireti* has protocone and hypocone separate on P2 and P3 (Guérin, 1972, 1980; Guérin and Tsoukala, 2013: figs. 5–7) and the paracone fold is smaller and narrower on M2 than in the studied specimens (Fig. 4H–L). In *S. etruscus*, the lingual cingulum is usually present on the upper premolars, the crista is usually present on the upper premolars and on M1 and M2 (Fig. 4M). In "*D*". *megarhinus* from China, as in the studied specimens, the lingual cingulum is absent on the upper premolars, P1 is absent and the protocone is less developed than the hypocone on P2 (Ringström, 1924: figs. 1–2; Deng, 2006: fig. 3). However, a small crista is present on the M3 of "*D*". *megarhinus* from Linxia (Deng, 2006: fig. 3) whereas this fold is absent on the studied M3. In the cheek teeth from Lens Lestang (cast housed at NHML and NMB; Falconer, 1868; Fig. 4N), as well as in the studied material, the post-fossette is small and rounded on the teeth, the protoloph is not joined with the ectoloph on the right P2 and weakly joined with the ectoloph on the left P2, the protocone is less developed than the hypocone on P2, P3 and P4 are subsquare, the metaloph is constricted on P3 and P4, the crochet is weakly developed on P3 and P4, the protocone is weakly constricted on M1 and the antecrochet and the crista are absent on M1 and M2. Nevertheless, in the skull from Lens Lestang a small crista occurs on the left M3 and a reduced lingual cingulum is evident on the upper premolars (Fig. 5N). On the teeth from Saint-Laurent, the lingual cingulum is absent on the premolars (Guérin et al., 1969: 111). The upper teeth of the skull from Montpellier are quite similar to those from Lens Lestang and Kávás but display the following differences: the crochet on P3 is slightly more developed, a weak crista occurs on P3 and P4, the crochet is replaced by three weak enamel folds on P4 and a weak crista occurs on M2 (Guérin, 1980: Pl. 10, Pl. 15). The presence of the lingual cingulum on the upper premolars is a variable character on the specimens from Montpellier (Guérin et al., 1969: 112). Thirty-seven isolated teeth from Montpellier (Appendix A) are morphologically similar to those from Lens Lestang and Kávás (Appendix A), but a few of them display some other characters: a crista is present on two P3, a weak metacone fold is evident on one P4, a weak double crochet occurs on one M2, a weak crista occurs on three M2 and on two M3. The dimensions of the upper teeth are close to the maximal values of "*D*". *megarhinus* given by Guérin (1980) (Table 2).

4.3. Mandible

Description: The right horizontal ramus HNHM V.79.117-5 is relatively long and high, the ventral border is slightly convex and two mental foramina occur at the level of p2–p3. The height of the horizontal ramus decreases below the premolars (Fig. 2H). The fragment of the left horizontal ramus HNHM V.79.117-6 displays the same morphology as HNHM V.79.117-5 (Fig. 2L). The vertical ramus HNHM V.79.117-5 was reconstructed and it appears at a straight angle with the horizontal ramus (Fig. 5A). The coronoid apophysis is broken but it appears relatively well developed sagittally. The sygmoidal incisure is relatively wide but not deep. The articular condyle is not too strong and it is damaged on the medial side. The mandibular foramen is below the alveolar arc and the masseteric and temporal fossae are relatively shallow.

Comparison: The mandibles of *C. neumayri* display a slightly convex lower border of the horizontal ramus, which inclines abruptly upwards below p3–p2 and an inclined backward vertical ramus (Fig. 5B). The posterior border of the symphysis is at the level of p3 or behind it in *C. neumayri*, whereas on the specimen HNHM V.79.117-5, the symphysis terminates at the level of p2–p3 (Fig. 2I). "*D*". *douariensis* differs from the specimens collected at Kávás by having a concave anterior border of the vertical ramus in lateral view (Guérin, 1966: fig. 7), an horizontal ramus inclined abruptly upwards below p3–p2, and the posterior border of the symphysis at the level of p3. The mandible of *D. schleiermacheri* differs from the studied specimens in having a well-developed lower incisors and a rather straight ventral border of the horizontal ramus (Fig. 5C). In *D. pikermiensis*, the ventral border of the horizontal ramus of the mandible is regularly convex (Fig. 5D). With respect to the studied specimen, *S. jeanvireti* has a straight and relatively less high horizontal ramus beneath the molars. Moreover, the height of the horizontal ramus gradually decreases under the premolars and towards the symphysis (Fig. 3F, 5E), whereas *S. etruscus* displays a convex ventral border of the horizontal ramus (Fig. 5F). The mandible collected at Kávás is rather similar to that of "*D*". *megarhinus* from Honan (Ringström, 1924: figs. 3–4). In the re-assembled specimen from Kávás (Fig. 5A), the anterior border of the vertical ramus appears rather straight than in "*D*". *megarhinus* from Quaidam Basin (IVPP V13799: Deng and Wang, 2004: fig. 2), but this difference could be related with a provisional restoration of the specimen. The ventral border of the horizontal ramus of the mandible from Saint-Laurent is slightly straight; in addition, the height of the horizontal ramus decreases below the premolars (Guérin et al., 1969: 99, fig. 8, 107, fig. 13). The mandibles of "*D*". *megarhinus* from Montpellier (NHML M40805 and NMB various specimens) and from other Italian localities (e.g., Palaia: Pandolfi, 2013) have a straight ventral border of the horizontal ramus beneath the molars, which curves gradually under the premolars and towards the symphysis, resembling the specimen from Kávás (Fig. 5G–H). The height of the horizontal ramus behind the m3 on the specimens from Kávás falls into the range given by Guérin (1980) for "*D*". *megarhinus* (Table 3).

4.4. Lower teeth

Description: On the specimen HNHM V.79.117-5, the toothrow is represented by p2–m1 and a fragment of m2, whereas on the specimen HNHM V.79.117-6 p3, m2 and m3 are preserved and p3 and m1 are damaged (Fig. 2). Labial cingula are absent on all the teeth and the external rugosities are absent on the premolars. The external groove is developed until the neck and the paralophid reaches the lingual rim. The trigonid is angular, forming an acute dihedron in occlusal view. The metaconid and the entoconid are not constricted (Fig. 2). The lingual valleys have a V-shaped morphology, but the posterior valley of m2 is U-shaped. Lingual cingula are absent on the teeth. On p2, the paralophid is straight, without constriction, the paraconid is developed and the posterior valley is lingually open (Fig. 2).

Comparison: The morphology of the lower teeth is quite conservative in Late Miocene–Pliocene Rhinocerotini. The lower teeth of *C. neumayri* are rather hypsodont in respect to those of the studied material. p1 occurs on the unique know mandible of "*D*". *douariensis* (Guérin, 1966). Labial and lingual cingula are absent on "*S*". *miguelcrusafonti* (Guérin and Santafé-Llopis, 1978) and "*D*". *douariensis*, whereas in *S. etruscus* a lingual cingulum occurs on lower teeth (Guérin, 1980, 2004). The lower teeth from Montpellier ("*D*". *megarhinus*) display the same characters described for HNHM V.79.117. Lingual and labial cingula are absent on the lower teeth of *D. schleiermacheri* and of *D. pikermiensis* (NHML), but mesial cingula occur on lower molars of *D. pikermiensis*. The dimensions of the teeth from Kávás (Table 4) fall into the range of "*D*". *megarhinus* given by Guérin (1980).

5. Discussion

The presence of the frontal horn, the short metaloph on the upper molars, the slight protocone constriction on the upper teeth, the absence of well-developed labial and lingual cingula, the absence of a well-developed antecrochet on the upper teeth, the less developed protocone than hypocone on P2, and the long paralophid on the lower teeth enable to ascribe the studied specimens to Rhinocerotini. The relative dimensions and proportions of the studied specimens as well as their morphology (concave dorsal profile of the skull, high occipital face, low-crowned teeth, absence of P1, submolariform premolars, absence of crista and antecrochet on the upper molars) suggest an attribution to the genus *Dihoplus*. Based on morphological comparison, the Late Miocene rhinoceros remains collected in the Zala Subbasin (Pannonian Basin, Hungary) can be referred to "*D*". *megarhinus*.

This is the earliest record of this species in Europe.

According to Hürzeler and Engesser (1976) and Guérin (1980), a fragmentary tibia comparable in size to that of "*D*". *megarhinus* has been recovered from Baccinello V3, latest Miocene in age (Tuscany, central Italy). More recently, Guérin (2003) ascribed this remain to *D.* cf. *douariensis*. According to Pandolfi (2013), the tibia (cast housed at NMB) is quite different from those of "*D*". *megarhinus* from Montpellier, but the specimen is damaged and badly preserved. However, the discovery of a maxilla (NMB nn) surely referable to "*D*". *megarhinus* confirms the occurrence of this species in the latest Miocene faunal assemblage of Italy. Furthermore, two upper teeth ascribed to *D.* cf. *megarhinus* have been also recovered from the latest Miocene deposits of Monticino Quarry (Brisighella, Emilia-Romagna) (De Giuli, 1989; Engesser, 1989; Rook et al., 1991, 1999). These teeth share several morphological features with "*D*". *megarhinus* but also display some advanced traits (e.g., double crochet, crista) that lack in the specimens from Baccinello V3, Kávás and other localities; these features are instead present in a few specimens from Montpellier.

Alexejew (1916) ascribed to *R. pachygnathus* a right upper milk toothrow from the Turolian (MN12) locality of Novo-Elisavetovka (Ukraine). This specimen was ascribed to *D. orientalis* by Ringström (1924) and it was recently referred to *Dihoplus* sp. by Giaourtsakis et al. (2006). According to these authors, "this toothrow does not show any significant morphological difference in respect to the Eastern Mediterranean specimens of the genus" (Giaourtsakis et al., 2006: 381). We agree with the viewpoint of Giaourtsakis et al. (2006), but an attribution to "*D*". *megarhinus* cannot be ruled out either. The same goes for the upper milk toothrow collected at Taraklia (Khomenko, 1914; Ringström, 1924).

Fukuchi et al. (2009) ascribed over 500 specimens collected in the Pliocene (MN15–16a) locality of Udunga (Transbaikalia) to *S. megarhinus*. According to Fukuchi et al. (2009), the specimens from Udunga are more closely related to the European sample of the species than to the Turkish one reported by Guérin and Sen (1998). A dispersal of *S. megarhinus* directly from Europe was therefore suggested (Fukuchi et al., 2009). Within the material reported by Fukuchi et al. (2009), a praemaxilla displays an alveolus for a small and reduced upper incisor (I1) and no trace of ossification between the praemaxilla and the nasal can be observed. Both characters suggest an attribution to the genus *Dihoplus*. The isolated upper molars have a marked paracone fold, a single crochet and also a crista which is very close to the anterior end of the crochet (Fukuchi et al., 2009: fig. 6). On the basis of the material figured by Fukuchi et al. (2009), the occurrence of "*D*". *megarhinus* during the latest Pliocene is confirmed in the Transbaikalia. In Italy, "*D*". *megarhinus* was reported in several Pleistocene fossiliferous localities but these records are related to nomenclatural misidentifications with other species (Pandolfi, 2013). Breda et al. (2010) ascribed to *S.* cf. *megarhinus* a few rhinoceros remains recovered at the early Middle Pleistocene site of Boxgrove (England) (Breda et al., 2010: 140–144, figs. 6–7). According to Pandolfi (2013), the morphology of the fragmentary skull from Boxgrove (M82542; Breda et al., 2010: 140–144, figs. 6–7) partially resembles that of *S. etruscus*. Moreover, several morphological features of the teeth from Boxgrove (M82482-97; Breda et al., 2010: fig. 6) can be observed in some specimens of *S. etruscus* from Upper Valdarno and Capitone (Pandolfi, 2013), but further additional morphological comparisons are needed to better identify these remains.

The rhinoceros remains from Meyrargues (France), previously ascribed to *D. mercki*, can be referred to "*D*". *megarhinus* (Bonifay, 1961; Guérin, 1980). These deposits were usually referred to the Pleistocene, but according to Bonifay (1961), "l'origine de ces éléments reste assez obscure" (Bonifay, 1961: 1). Finally, Koenigswald (1988, 1991) reported the occurrence of *D.* cf. *megarhinus* in the Pleistocene deposits at Gross-Rohrheim (Germany). The morphology of the teeth figured by Koenigswald (1988, 1991: fig. 8) is very similar to that of the specimens from Boxgrove and most probably they belong to the same undefined species.

6. Conclusions

The new Late Miocene record of "*D*". *megarhinus* enable us to draw a new palaeobiogeographic scenario and hypothesis for the dispersal pattern of this species in Eurasia.

Due to the strong morphological and metric similarities, the Late Miocene (MN12) Chinese *D. ringstroemi* named by Arambourg (1959) is here considered a junior synonym of "*D*". *megarhinus* established by de Christol (1834). This suggests that "*D*". *megarhinus* could have spread from Asia to Eastern Europe during the Late Miocene. The Turolian rhinoceros from Taraklia (Khomenko, 1914) and Novo-Elisavetovka (Alexejew, 1916), referred as *D. orientalis* by Ringström (1924) and later as *Dihoplus* sp. (Giaourtsakis et al., 2006; see previous chapter), could support this hypothesis, but new findings are needed for a more precise specific attribution. However, a similar dispersal pattern has been also recorded for other Rhinocerotidae taxa, such as *S. kirchbergensis*, *C. tologojensis*, *C. antiquitatis* and the genus *Elasmotherium* (Guérin, 1980, 2010; Antoine, 2002; David and Eremeico, 2003; Kahlke and Lacombat, 2008; Deng et al., 2011; Tong, 2012; Tong et al., 2014).

The de Christol's species is here reported for the first time from the Pannonian Basin, in fossiliferous deposits biochronologically referable to MN12–13 transition (around 7.0 Ma: Pandolfi et al., in press). At the end of the Miocene (MN13), "*D*". *megarhinus* was recorded in Italy and later, during the Early and Late Pliocene (MN14 and MN15), in several Western European localities (Montpellier, Lower Valdarno, Lens Lestang, Saint-Laurens: Guérin, 1980; Pandolfi, 2013). During the second half of the Pliocene, this species was also spread in Turkey (MN15: Guérin and Sen, 1998). The latest Pliocene record from Udunga (MN15–MN16a) could represent the persistence of this species in Asia and not just the dispersal of "*D*". *megarhinus* in Asia from Europe as suggested by Fukuchi et al. (2009). The Russian finding, however, is the

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youngest occurrence of the species in Eurasia, whereas the reported Pleistocene occurrences of "*D*". *megarhinus* (e.g., Boxgrove, Gross-Rohrheim) are not supported on a morphological ground.

Disclosure of interest

The authors declare that they have no conflicts of interest concerning this article.

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Appendix A. Appendix A Source for comparison material.

Taxon	Direct observation	Locality	References
"*Dihoplus*" *megarhinus*	NHML, NMB	Lens Lestang, Millas, Montpellier, Saint-Laurens (France)	Gervais, 1851; Falconer, 1868; Maurette, 1910; Guérin et al., 1969; Guérin, 1980
"*Dihoplus*" *megarhinus*	IGF, MGGC, MPP, MPPB, MSNAF, NMB	Baccinello, Monte Giogo, Monte Zago, Rio Secco, Val di Pugna-Fangonero, Valdarno Inferiore (Italy)	Azzaroli, 1962; Cuscani Politi, 1963a, 1973; Guérin, 1980; Pandolfi, 2013
"*Dihoplus*" *megarhinus*	BSPG, IVPP	Honnan, Linxia, Quaidam (China)	Ringström, 1924; Deng and Wang, 2004; Deng, 2006
"*Stephanorhinus*" *miguelcrusafonti*	MNCN	Layna (Spain)	Guérin and Santafé-Llopis, 1978; Guérin, 1980
Stephanorhinus jeanvireti	NMB	Perrier-Les Étouaires, Vialette (France)	Guérin, 1972, 1980
Stephanorhinus jeanvireti	IGF, MGGC, NMB	Dusino, Monte Pastore, Monte Pugnalsco, Monte San Pietro, Montopoli, Pradalbino, Villafranca d'Asti (Italy)	Sacco, 1895; Guérin, 1972, 1980; Pandolfi, 2013
Stephanorhinus etruscus	MNHN, NMB	Perrier-Les Étouaires, Saint-Vallier, Senéze (France)	Guérin, 1972, 1980, 2004; Lacombat, 2005, 2006
Stephanorhinus etruscus	IGF, MGGC, MGPP, MSNAF, MPUR	Capitone, Castelnuovo di Barardenga Scalo, Valdarno Superiore (Italy)	Cuscani Politi, 1963b; Ambrosetti, 1972; Guérin, 1980; Mazza, 1988; Pandolfi and Petronio, 2011; Pandolfi et al., in press
Dihoplus schleiermacheri	HNHM, MFGI, MfN, MNCN, NHML, NHMW, NMB	Eppelsheim (Germany), Pannonian Basin (Hungary, various localities), Vienna Basin (Austria, various localities), Venta del Moro (Spain)	Guérin, 1980; Cerdeño, 1989, 1992
Dihoplus pikermiensis	NHML, NHMW	Pikermi, Samos, Kerassia (Greece)	Geraads, 1988; Giaourtsakis, 2003, 2009; Giaourtsakis et al., 2006
Ceratotherium neumayri	NHML, NHMW	Pikermi, Samos, Kerassia (Greece)	Guérin, 1980; Geraads, 1988, 2005; Giaourtsakis, 2003, 2009; Giaourtsakis et al., 2006
Ceratotherium neumayri	NHMW	Anatolia (Turkey, various localities), Maragha (Iran)	Geraads, 1988, 1994, 2005; Kaya, 1994; Antoine and Saraç, 2005
"*Diceros*" *douariensis*		Douaria (Tunisia), Middle Awash (Ethiopia)	Guérin, 1966; Giaourtsakis et al., 2009

References

Alexejew, A.K., 1916. Fauna pozvonochnykh derevni Novo. Elizabetovki, Odessa, Ukraine, 453 p. (in russian).
Ambrosetti, P., 1972. Lo scheletro di *Dicerorhinus etruscus* (Falc.) di Capitone (Umbria meridionale). Geologica Romana 11, 177–198.
Antoine, P.-O., 2002. Phylogénie et évolution des Elasmotheriina (Mammalia, Rhinocerotidae). Mémoires du Muséum National d'Histoire Naturelle 188, 1–359.
Antoine, P.-O., Saraç, G., 2005. Rhinocerotidae (Mammalia, Perissodactyla) from the late Miocene of Akkaşdaği, Turkey. In: Sen, S. (Ed.), Geology, mammals and environments at Akkaşdaği, late Miocene of Central Anatolia. Geodiversitas 27 (4), 601–632.
Antoine, P.O., Orliac, M.J., Atici, G., Ulusoy, I., Sen, E., Cubukcu, H.E., Albayrak, E., Oyal, N., Aydar, E., Sen, S., 2012. A Rhinocerotid skull cooked-to-death in a 9.2 Ma-old ignimbrite flow of Turkey. PLoS One 7 (11), e49997, doi:10.1371/journal.pone.0049997:1–12.
Arambourg, C., 1959. Vertébrés continentaux da Miocène supérieur de l'Afrique du Nord. Service de la Carte géologique de l'Algérie. Mémoire 4, 5–159.
Azzaroli, A., 1962. Rinoceronti pliocenici del Valdarno inferiore. Palaeontographia Italica 57, 11–20.
Benedek, K., Pécskay, Z., Szabó, C., Jósvai, J., Németh, T., 2004. Paleogene igneous rocks in the Zala Basin (Western Hungary): link to the Paleogene magmatic activity along the Periadriatic lineament. Geologica Carpathica 55 (1), 43–50.
Bonifay, M.F., 1961. Étude des restes de Rhinocéros de Merck provenant de Meyrargues (Bouches-du-Rhone). Annales de Paléontologie 47, 77–89.
Brandt, J.F., 1878. Tentamen synopseos rhinocerotidum viventium, et fossilium. Mémoires des l'Académie Impériale des Sciences de Saint Pétersbourg 26 (5), 1–66.
Breda, M., Collinge, S.E., Parfitt, S.A., Lister, A.M., 2010. Metric analysis of ungulate mammals in the early Middle Pleistocene of Britain, in relation to taxonomy and biostratigraphy: I: Rhinocerotidae and Bovidae. Quaternary International 228 (1–2), 136–156.
Capellini, G., 1894. Rinoceronti fossili del Museo di Bologna. Memorie della Regia Accademia delle Scienze dell'Istituto di Bologna 5 (4), 337–349.
Cerdeño, E., (Colección Tesis Doctorales) 1989. Revisión de la sistemática de los rinocerontes del Neógeno de España. Universidad Complutense de Madrid, Madrid, pp. 1–429.
Cerdeño, E., 1992. Spanish neogene rhinoceroses. Paleontology 35 (2), 297–308.
Cerdeño, E., 1995. Cladistic analysis of the family Rhinocerotidae (Perissodactyla). American Museum Novitates 3143, 1–25.
Codrea, V., 1993. *Dicerorhinus megarhinus* (de Christol) in the Romanian fauna from Măluşteni. Studia Universitatis Babeş-Bolyai. Geologia 38 (2), 67–70.
Cuscani Politi, P., 1963a. Anche il *Rhinoceros megarhinus* nel Pliocene dei dintorni di Siena. Atti dell'Accademia delle Scienze di Siena detta de' Fisiocritici. Siena, s. II 10, 125–149.
Cuscani Politi, P., 1963b. Resti di *Rhinoceros* (*Dicerorhinus*) *etruscus* rinvenuti nel Pliocene del Sense. Atti dell'Accademia delle Scienze di Siena detta de' Fisiocritici. Siena, s. II 10, 25–57.

Cuscani Politi, P., 1973. Resti di *Rhinoceros* (*Dicerorhinus*) *megarhinus* rinvenuti nelle sabbie gialle plioceniche di Val Pugna nei pressi di Siena (Toscana). Atti dell'Accademia delle Scienze di Siena detta de' Fisiocritici. Siena, s. XIV 5, 10–17.
Cuvier, G., 1836. Recherches sur les ossemens fossiles, Atlas. Edmond d'Ocagne édit, Paris, pp. 1–94.
David, A., Eremeico, N., 2003. Findings of *Elasmotherium* cf. *peii* (Chow Minchen, 1958) from sediments of Early Pleistocene (Upper Villafranchian) at Salcia (Republic of Moldova). In: Petculescu, A., Stiuca, E. (Eds.), Advances in Vertebrate Paleontology "Hen to Panta"; A tribute to C. Radulescu and P.M. Samson. Romanian Academy & "E. Racovita" Institute of Speleology, Bucuresti, pp. 41–46.
de Christol, J., 1834. Recherches sur les caractères des grandes espèces de Rhinocéros fossiles. Annales des Sciences Naturelles, Paris, série 2 4, 44–112.
De Giuli, C., 1989. The rodents of the Brisighella Latest Miocene fauna. Bollettino della Società Paleontologica Italiana 28 (2–3), 197–212.
Deng, T., 2006. Neogene rhinoceroses of the Linxia basin (Gansu, China). Courier Forschungsinstitut Senckenberg 256, 43–56.
Deng, T., Wang, X., 2004. New material of the neogene rhinocerotids from the Qaidam basin in Ginghai, China. Vertebrata PalAsiatica 42 (3), 216–229.
Deng, T., Wang, X., Fortelius, M., Li, Q., Wang, Y., Tseng, Z.J., Takeuchi, G.T., Saylor, J.E., Saila, L.K., Xie, G., 2011. Out of Tibet: Pliocene Woolly Rhino suggests high-plateau origin of Ice Age Megaherbivores. Science 333, 1285–1288.
Dolton, G.L., 2006. Pannonian Basin Province, Central Europe (Province 4808)-Petroleum geology, total petroleum systems, and petroleum resource assessment. U.S. Geological Survey Bulletin., pp. 2204-B.
Engesser, B., 1989. The Late Tertiary small mammals of the Maremma region (Tuscany, Italy) 2nd part: Muridae and cricetidae (Rodentia, Mammalia). Bollettino della Società Paleontologica Italiana 28 (2–3), 227–252.
Falconer, H., 1868. On the European Pliocene and Post-Pliocene species of the genus *Rhinoceros*. In: Murchison, C., Hardwicke, R. (Eds.), Palaeontological Memoirs and Notes of the late Hugh Falconer, (2) Mastodon, Elephant, Rhinoceros, Ossiferous Caves. Primeval Man and His Contemporaries, London, pp. 309–403.
Fisher, G., 1814. Zoognosia tabulis synopticis illustrata III : Quadrupedum reliquorum, cerotum et monotrymatum descriptionem continens. Mosquae, Vsevolozsky, 732 p.
Fodor, L., Jelen, B., Márton, E., Skaberne, D., Car, J., Vrabec, M., 1998. Miocene–Pliocene tectonic evolution of the Slovenian Periadriatic fault: implications for Alpine-Carpathian extrusion models. Tectonics 17, 690–709.
Fortelius, M., Mazza, P., Sala, B., 1993. *Stephanorhinus* (Mammalia: Rhinocerotidae) of the Western European Pleistocene, with a revision of *S. etruscus* (Falconer, 1868). Palaeontographia Italica 80, 63–155.
Fukuchi, A., Nakaya, H., Takai, M., Ogino, S., 2009. A preliminary report on the Pliocene rhinoceros from Udunga, Transbaikalia, Russia. Asian Palaeoprimatology. Kioto University Primate Research Institute 5, 61–98.
Gasparik, M., 2001. Neogene proboscidean remains from Hungary; an overview. Fragmenta Palaeontologica Hungarica 19, 61–77.
Geraads, D., 1988. Révision des Rhinocerotidae (Mammalia) du Turolien de Pikermi : comparaison avec les formes voisines. Annales de Paléontologie 74, 13–41.
Geraads, D., 1994. Les gisements de mammifères du Miocène supérieur de Kemiklitepe, Turquie : 4. Rhinocerotidae. Bulletin du Muséum national d'Histoire naturelle, Paris, série 4, section C 16 (1), 81–95.
Geraads, D., 2005. Pliocene Rhinocerotidae (Mammalia) from Hadar and Dikika (Lower Awash, Ethiopia), and a revision of the origin of modern african rhinos. Journal of Vertebrate Paleontology 25 (2), 451–461.
Geraads, D., Spassov, N., 2009. Rhinocerotidae (Mammalia) from the Late Miocene of Bulgaria. Palaeontographica Abteilung A 287, 99–122.
Gervais, P., 1851. Mémoire sur le Rhinocéros fossile à Montpellier. Mémoires de la Section des Sciences. Académie des Sciences et Lettres de Montpellier 2 (1), 59–79.
Giaourtsakis, I.X., 2003. Late Neogene Rhinocerotidae of Greece: distribution, diversity and stratigraphical range. In: Reumer, J.W.F., Wessels, W. (Eds.), Distribution Migration of Tertiary Mammals in Eurasia, Deinsea Rotterdam, 10, pp. 235–253.
Giaourtsakis, I.X., 2009. The Late Miocene mammal fauna of the Mytilinii Basin, Samos Island, Greece: New Collection 9. Rhinocerotidae. Beitrage zur Palaontologie 31, 157–187.
Giaourtsakis, I.X., Heissig, K., 2004. On the nomenclatural status of *Aceratherium incisivum* (Rhinocerotidae, Mammalia). In: Chatzipetros, A.A., Pavlides, S.B. (Eds.), Proceedings of the 5th International Symposium on Eastern Mediterranean Geology, 1. Thessaloniki, pp. 314–317.
Giaourtsakis, I.X., Theodorou, G., Roussiakis, S., Athanassiou, A., Iliopoulos, G., 2006. Late Miocene horned rhinoceroses (Rhinocerotinae, Mammalia) from Kerassia (Euboea, Greece). Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, Stuttgart 239 (3), 367–398.
Giaourtsakis, I.X., Pehlevan, C., Haile-Selassie, Y., 2009. Rhinocerotidae. In: Haile-Selassie, Y., WoldeGabriel, G. (Eds.), *Ardipithecus kadabba*: Late Miocene Evidence from the Middle Awash, Ethiopia. University California Press, Oakland, pp. 429–468.
Gibbard, P.L., Head, M.J., Walker, M.J.C., 2010. Formal ratification of the Quaternary System/Period and the Pleistocene Series/Epoch with a base at 2.58 Ma. Journal of Quaternary Science 25 (2), 96–102.
Gloger, C.W.L., 1841. Gemeinnuetziges Hand- und Hilfsbuch der Naturgeschichte, 1. August Schulz and Co., Breslau, pp. 1–496.
Groves, C.P., 1983. Phylogeny of the living species of rhinoceros. Zeitschriften für Zoologische Systematik und Evolutionsforschung 21, 293–313.
Guérin, C., 1966. *Diceros douariensis* nov. sp., un rhinocèros du Mio-Pliocène de Tunisie du Nord. Documents des Laboratoires de Géologie de la Faculté des Sciences de Lyon 16, 1–50.
Guérin, C., 1972. Une nouvelle espèce de Rhinocéros (Mammalia, Perissodactyla) à Vialette (Haute-Loire, France) et dans d'autres gisements du Villafranchien Inférieur Europe. *Dicerorhinus jeanvireti* n. sp. Documents des Laboratoires de Géologie de la Faculté des Sciences de Lyon 49, 53–161.
Guérin, C., 1980. Les rhinocéros (Mammalia, Perissodactyla) du Miocène terminal au Pleistocène supérieur en Europe occidentale : comparaison avec les espèces actuelles. Documents des Laboratoires de Géologie de la Faculté des Sciences de Lyon 79, 1–1182.
Guérin, C., 1982. Les Rhinocerotidae (Mammalia, Perissodactyla) du Miocène terminal au Pleistocéne supérieur d'Europe occidentale comparés aux espèces actuelles : tendences evolutives et relations phylogenetiques. Geobios 15 (4), 599–605.
Guérin, C., 2003. Miocene Rhinocerotidae of the Orange River Valley, Namibia. Memoir of the Geological Survey of Namibia 19, 257–281.
Guérin, C., 2004. Les rhinocéros (Mammalia, Perissodactyla) du gisement Villafranchien moyen de Saint-Vallier (Drôme). Geobios 37, 259–278.
Guérin, C., 2010. *Coelodonta antiquitatis praecursor* (Rhinocerotidae) du Pléistocène moyen final de l'aven de Romain-la-Roche (Doubs, France). Revue de Paléobiologie 29 (2), 697–746.
Guérin, C., Santafé-Llopis, J.V., 1978. *Dicerorhinus miguelcrusafonti* nov. sp., une nouvelle espèce de rhinocéros (Mammalia, Perissodactyla) du gisement Pliocène supérieur de Layna (Soria, Espagne) et de la formation Pliocène de Perpignan (Pyrénées-Orientales, France). Geobios 11 (4), 457–491.
Guérin, C., Sen, S., 1998. Rhinocerotidae. In: Sen, S. (Ed.), Le gisement de vertébrés pliocènes de Çalta, Ankara, Turquie. Geodiversitas 20 (3), 397–407.
Guérin, C., Tsoukala, E., 2013. The Tapiridae, Rhinocerotidae and Suidae (Mammalia) of the Early Villafranchian site of Milia (Grevena, Macedonia, Greece). Geodiversitas 35 (2), 447–489.
Guérin, C., Ballesio, R., Meon-Vilain, H., 1969. Le *Dicerorhinus megarhinus* (Mammalia, Rhinocerotidae) du Pliocène de Saint-Laurent-des-Arbres (Gard). Documents des Laboratories de Géologie de la Faculté des Sciences de Lyon, Notes et Mémoires 31, 55–145.
Haas, J., Mioc, P., Pamić, J., Tomljenovic, B., Árkai, P., Bérczi-Makk, A., Koroknai, B., Kovács, S., Felgenhauer, E.R., 2000. Complex structural pattern of the Alpine-Dinaridic-Pannonian triple junction. International Journal of Earth Science 89, 377–389.
Heissig, K., 1989. The Rhinocerotidae. In: Prothero, D.R., Schoch, R.M. (Eds.), The evolution of Perissodactyls, 15. Oxford Monographs on Geology and Geophysics, New York, pp. 399–417.
Heissig, K., 1996. The stratigraphical range of fossil rhinoceroses in the Late Neogene of Europe and Eastern Mediterranean. In: Bernor, R.L., Fahlbush, V., Mittman, H.-W. (Eds.), The Evolution of Western Eurasian Neogene Mammal Faunas. Columbia University Press, New York, pp. 339–347.
Heissig, K., 1999. Family Rhinocerotidae. In: Rössner, G.E., Heissig, K. (Eds.), The Miocene Land Mammals of Europe. Pfeil, Munich, pp. 175–188.
Hürzeler, J., Engesser, B., 1976. Les faunes de mammifères néogènes du bassin de Baccinello (Grosseto, Italie). Comptes Rendus de l'Académie des Sciences de Paris 293, 333–336.
ICZN, 1999. International Code of Zoological Nomenclature, 4th ed. The International Trust for Zoological Nomenclature, London.
Kaup, J.-J., 1832. Über *Rhinoceros incisivus* Cuvier und eine neue Art, *Rhinoceros schleiermacheri*. Isis 8, 898–904.
Kahlke, R.D., Lacombat, F., 2008. The earliest immigration of woolly rhinoceros (*Coelodonta tologoijensis*, Rhinocerotidae, Mammalia) into Europe and its adaptive evolution in Palaearctic cold stage mammal faunas. Quaternary Science Reviews 27, 1951–1961.
Kaya, T., 1994. *Ceratotherium neumayri* (Rhinocerotidae, Mammalia) in the Upper Miocene of Western Anatolia. Turkish Journal of Earth Sciences 3, 13–22.
Khomenko, I., 1914. Meoticheskaya Fauna s. Taraklii, Benderskago Uezda. Trudy Bessarabskago Obshchestva Estestvoispytateley i Ljubiteley Estestvoznanya V, 1–55 (in Russian).
Koenigswald, von W., 1988. Paläoklimatische Aussage letztininterglazialer Säugethiere aus der nördlichen Oberrheinebene. In: Koenigswald, von W. (Ed.), Zur Paläoklimatologie des letzten Interglazials im Nordteil der Oberrheinebene. Gustav Fischer, Stuttgart, pp. 205–214.
Koenigswald, von W., 1991. Exoten in der Großsäuger-Fauna des letzten Interglazials von Mitteleuropa. Eiszeitalter und Gegenwart. Hannover 41, 70–84.
Kretzoi, M., 1942. Bemerkungen zum System der nachmiozänen Nashorn-Gattungen. Földani Közlöny 72, 309–318.
Lacombat, F., 2005. Les rhinoceros fossiles des sites prehistoriques de l'Europe Mediterraneenne et du Massif Central – Paleontologie et implications biochronologiques. British Archeological Reports 1419, 1–175.
Lacombat, F., 2006. Morphological and biometrical differentiation of the teeth from Pleistocene species of *Stephanorhinus* (Mammalia, Perissodactyla, Rhinocerotidae) in Mediterranean Europe and the Massif Central, France. Palaeontographica Abt. A 274 (3–6), 71–111.
Lacombat, F., 2007. Phylogeny of the genus Stephanorhinus in the Plio-Pleistocene of Europe. Hallesches Jahrbuch fur Geowissenschaften 23, 63–64.
Lacombat, F., Mörs, T., 2008. The northernmost occurrence of the rare Late Pliocene rhinoceros *Stephanorhinus jeanvireti* (Mammalia, Perissodactyla). Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 249 (2), 157–165.
Magyar, I., Geary, D.H., Müller, P., 1999. Paleogeographic evolution of the Late Miocene Lake Pannon in Central Europe. Palaeogeography, Palaeoclimatology, Palaeoecology 147, 151–167.

Magyar, I., Lantos, M., Ujszászi, K., Kordos, L., 2007. Magnetostratigraphic, seismic and biostratigraphic correlations of the Upper Miocene sediments in the northwestern Pannonian Basin System. Geologica Carpathica 58 (3), 277–290.

Maurette, L., 1910. Etude paléontologique du *Rhinoceros leptorhinus* du Pliocène inférieur de Millas (Pyrénées-orientales) et des faunes du Pliocène inférieur en général. Annales de la Société Linnéenne de Lyon 57, 1–26.

Mazza, P., 1988. The Tuscan Early Pleistocene rhinoceros *Dicerorhinus etruscus*. Palaeontographia Italica 75, 1–87.

Osborn, H.F., 1900. Phylogeny of the rhinoceroses of Europe. Bulletin of the American Museum of Natural History 13, 229–267.

Pandolfi, L., 2013. New and revised occurrences of *Dihoplus megarhinus* (Mammalia, Rhinocerotidae) in the Pliocene of Italy. Swiss Journal of Palaeontology 132, 239–255.

Pandolfi, L., 2015. Sistematica e filogenesi dei Rhinocerotini (Mammalia, Rhinocerotidae). [Systematics and phylogeny of Rhinocerotini (Mammalia, Rhinocerotidae)]. Tesi di Dottorato, Università degli Studi di Roma Tre, ciclo XXVII, Roma, pp. 1–319.

Pandolfi, L., Petronio, C., 2011. *Stephanorhinus etruscus* (Falconer, 1868) from Pirro Nord (Apricena, Foggia, Southern Italy) with notes on the late Early Pleistocene rhinoceroses of Italy. Rivista Italiana di Paleontologia e Stratigrafia 117 (1), 173–187.

Pandolfi, L., Tagliacozzo, A., 2015. *Stephanorhinus hemitoechus* (Mammalia, Rhinocerotidae) from the Late Pleistocene of Valle Radice (Sora, Central Italy) and re-evaluation of the morphometric variability of the species in Europe. Geobios 48 (2), 169–191.

Pandolfi, L., Kotsakis, T., Maiorino, L., Petronio, C., Piras, P., 2014. Systematics and Phylogeny of Rhinocerotini (Mammalia, Rhinocerotidae). In: Society of Vertebrate Paleontology, 74th Annual Meeting, Berlin, 5–8 November, Abstract Book, p. 201.

Pandolfi, L., Gasparik, M., Magyar, I., 2015a. Rhinocerotidae from the Upper Miocene deposits of the Western Pannonian Basin (Hungary): implications for migration routes and biogeography. Geologica Carpathica. (in press).

Pandolfi, L., Grossi, F., Frezza, V., in press. New insight into the Pleistocene deposits of Monte delle Piche, Rome, and remarks on the biochronology of *Hippopotamus* (Mammalia, Hippopotamidae) and *Stephanorhinus etruscus* (Mammalia, Rhinocerotidae) in Italy. Estudios Geológicos 71 (1), e026, http://dx.doi.org/10.3989/egeol.41796.337.

Ringström, T., 1924. Nashörner der *Hipparion*-Fauna Nord-Chinas. Palaeontologica Sinica, Series C 1 (4), 1–159.

Rook, L., Ficcarelli, G., Torre, D., 1991. Messianian carnivores from Italy. Bollettino della Società Paleontologica Italiana 30 (17), 7–22.

Rook, L., Abbazzi, L., Engesser, B., 1999. An overview on the Italian Miocene Land Mammal fauna. In: J. Augustì, J., Rook, L., Andrew, P. (Eds.), The evolution of Neogene terrestrial ecosystems in Europe. Cambridge University Press, Cambridge, pp. 191–204.

Rook, L., Oms, O., Benvenuti, M.G., Papini, M., 2011. Magnetostratigraphy of the Late Miocene Baccinello-Cinigiano basin (Tuscany, Italy) and the age of *Oreopithecus bambolii* faunal assemblages. , 286–294.

Sacco, F., 1895. Le rhinocéros de Dusino (*Rhinoceros etruscus* Falc., var. *astensis* Sacc.). Archives du Muséum d'Histoire naturelle de Lyon 6, 1–31.

Schlosser, M., 1921. Die Hipparionenfauna von Veles in Mazedonien. Abhandlungen der Bayerischen Akademie der Wissenschaften 29 (4), 1–55.

Simonelli, V., 1897. I Rinoceronti fossili del museo di Parma. Palaeontographia Italica 3, 89–136.

Symeonidis, N.K., Giaourtsakis, I.X., Seeman, R., Giannopoulos, V.I., 2006. Aivaliki, a new locality with fossil Rhinoceroses near Alistrati (Serres, Greece). Beiträge zur Paläontologie 30, 437–451.

Tong, H., 2012. Evolution of the non-*Coelodonta* dicerorhine lineage in China. Comptes Rendus Palevol 11 (8), 555–562.

Tong, H., Wang, F., Zheng, M., Chen, X., 2014. New fossils of *Stephanorhinus kirchbergensis* and *Elasmotherium peii* from the Nihewan Basin. Acta Anthropologica Sinica 33 (3), 369–388.

Toula, F., 1906. Das Gebiss und Reste der Nasenbeine von *Rhinoceros* (*Ceratorhinus* Osborn) *hundsheimensis*. Abhandlungen der k.k. Geologischen Reichsanstalt, Wien 20 (2), 1–38.

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