



EVOLUTIONARY HISTORY OF RHINOCEROTINA (MAMMALIA, PERISSODACTYLA)

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BULLET-POINTS ABSTRACT

- The earliest representatives of the group occurred during the Early Miocene.
- The group is well documented during the Late Miocene in Western Eurasia and Africa.
- High species diversity occurred in Eurasia during the Pleistocene.
- The fossil records of *Rhinoceros* and *Dicerorhinus* seems to be confined in the Indian subcontinent and East and South-East Asia.

INTRODUCTION

The tribe Rhinocerotina Gray, 1821 (sensu Antoine, 2002) includes the extant rhinoceroses that are currently distributed in limited areas of SouthAsia and Africa.

The tribe probably originates from Late Oligocene representatives of Teleoceratini, but this hypothesis needs to be better supported by a comprehensive revision of the latter taxon. Rhinocerotina is considered a monophyletic group (Antoine, 2002) supported by several synapomorphies such as the presence of a median frontal horn, enlarged rostral end of the nasals, trend towards the ossification of the nasal septum (Antoine, 2002; Antoine et al., 2003).

MATERIALS AND METHODS

This note is based on specimens, from both original observations and published material, referred to the 5 extant rhinocerotine species and several extinct rhinocerotine taxa (Fig. 1; Tab. 1), that occur in the Neogene and Quaternary fossil record of Eurasia and Africa (Fig. 1). The species list and the list of institutions, where the observed specimens are preserved, are reported in Tab. 1.

Institutional abbreviations

BSPG, Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; **HNHM**, Hungarian Natural History Museum, Budapest, Hungary; **IGF**, Istituto Geo-Paleontologico di Firenze, Florence, Italy; **IRSNB**, Institut royal des Sciences naturelles de Belgique, Bruxelles, Belgium; **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; **MAFI**, Magyar Földtani és Geofizikai Intézet (Geological and Geophysical Institute of Hungary), Budapest, Hungary; **MfN**, Museum für Naturkunde, Berlin, Germany; **MGGC**, Museo di Ge-

ologia Giovanni Capellini, Bologna, Italy; **MGGPD**, 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 Paleontologico Parmense, Parma, Italy; **MPUR**, Museo Paleontologico dell'Università di Roma, Rome, Italy; **MSNAF**, Museo di Storia Naturale, Accademia dei Fisiocritici, Siena, Italy; **MZF**, Museo di Storia Naturale, sezione di Zoologia, Florence, Italy; **NHMUK**, Natural History Museum, London, United Kingdom; **NHMW**, Naturhistorisches Museum, Wien, Austria; **NMB**, Naturhistorisches Museum, Basel, Switzerland; **SMF**, Senckenberg Naturmuseum, Frankfurt, Germany; **ZSM**, Zoologische Staatssammlung, Munich, Germany.

Genus abbreviations

C. = *Ceratotherium*; *Co.* = *Coelodonta*; *D.* = *Dicerorhinus*; *Di.* = *Diceros*; *Dh.* = *Dihoplus*; *G.* = *Gaindatherium*; *L.* = *Lartetotherium*; *P.* = *Paradiceros*; *R.* = *Rhinoceros*; *Ru.* = *Rusingaceros*; *S.* = *Stephanorhinus*.

DISCUSSIONS AND CONCLUSIONS

The earliest European representative of Rhinocerotina is *Lartetotherium sansaniense* (Lartet in Laurillard, 1848), which occurred during the MN4 (early Miocene). *Rusingaceros leakeyi* (Hooijer, 1966) and "*Diceros*" *australis* Guérin, 2000 (both early Miocene in age) are documented in African Continent, whereas the tribe occurred in South Asia as soon as the early Miocene, with *Gaindatherium* cf. *browni* and cf. *Rhinoceros* sp. (Bugti Hills, Pakistan; Antoine et al., 2013) (Fig. 1). The maximum geographic distribution of the tribe occurred in the latest Miocene and the Plio-Pleistocene, when all aceratheriines and teleoceratines went extinct and elasmotheres' diversity drastically reduced. Four latest Miocene Rhinocerotina were certainly identified in Eurasia: *Dihoplus schleiermacheri* (Kaup,



Fig. 1. Distribution of extant and fossil species of subtribe Rhinocerotina. The species are roughly listed according to their occurrences for each epoch and for each considered area.

Species	Direct Observation	References
<i>"D." steinheimensis</i>	NHFW	Guérin, 1980; Heissig, 1999
<i>"Di." australis</i>	-	Guérin, 2000; Geraads, 2010
<i>"S." miguelsfonti</i>	MNCN	Guérin, 1980; Cerdeño, 1992
<i>C. douariense</i>	MfN, NHMUK	Guérin, 1966; Giaourtsakis et al., 2009; Geraads, 2010;
<i>C. mauritanicum</i>	-	Geraads, 2005, 2010
<i>C. neumayri</i>	NHMUK, NHFW, NMB	Guérin, 1980; Geraads, 1988, 2005; Giaourtsakis, 2009; Antoine & Saraç, 2005; Giaourtsakis et al., 2006
<i>C. simum ssp.</i>	IRSNB, MfN, NHMUK, NMB	Guérin, 1980
<i>C.? primaevum</i>	-	Arambourg, 1959; Geraads, 2010
<i>Co. antiquitatis</i>	HNHM, IGF, MAFI, MfN, MGGC, MPGPD, MPUR, NHMUK, NHFW, NMB	Guérin, 1980
<i>Co. nihowanensis</i>	-	Deng, 2002
<i>Co. thibetana</i>	-	Deng et al., 2011
<i>Co. tologojensis</i>	-	Belyaeva, 1966; Kahlke & Lacomat, 2008
<i>Co. antiquitatis</i>	-	Guérin, 1980
<i>D. cixianensis</i>	-	Chen & Wu, 1976
<i>D. gwebinensis</i>	-	Zin-Maung-Maung-Thein et al., 2008
<i>D. sumatrensis</i>	MNHN, MZF, NHMUK, NMB	Guérin, 1980
<i>Di. bicornis ssp.</i>	MfN, MNHN, NHMUK, NMB, SMF, ZSM	Guérin, 1980
<i>Di. gansuensis</i>	-	Deng & Qiu, 2007
<i>Di. praecox</i>	MfN, NHMUK	Hooijer & Patterson, 1972; Guérin, 1987; Geraads, 2010
<i>Dh. megarhinus</i>	BSPG, IGF, MGGC, MPP, MSNAF, NHMUK, NMB	Guérin, 1980; Pandolfi et al., 2015 and references therein
<i>Dh. pikermiensis</i>	NHMUK, NHFW	Geraads, 1988; Giaourtsakis, 2009; Giaourtsakis et al., 2006
<i>Dh. schleiermachersi</i>	HNHM, MAFI, MfN, MNCN, NHMUK, NHFW, NMB	Guérin, 1980; Cerdeño, 1992
<i>G. browni</i>	-	Colbert, 1934; Khan et al., 2014
<i>G. vidali</i>	-	Heissig, 1972; Khan et al., 2014
<i>L. sansaniense</i>	MfN, MNCN, NMB	Guérin, 1980; Cerdeño, 1996; Heissig, 2012
<i>P. mukirii</i>	NHMUK	Hooijer, 1968; Geraads, 2010; Guérin, 2011
<i>R. platyrhinus</i>	NHMUK,	Falconer & Cautley, 1846; Colbert, 1935; Khan, 1971; Pandolfi & Maiorino, 2016
<i>R. sinensis</i>	-	Matthew & Granger, 1929; Colbert & Hooijer, 1953
<i>R. sivalensis</i>	NHMUK	Falconer & Cautley, 1846; Colbert, 1935; Pandolfi & Maiorino, 2016
<i>R. sondaicus</i>	NHMUK, NMB	Guérin, 1980
<i>R. unicornis</i>	NHMUK, NMB	Guérin, 1980
<i>Ru. leakeyi</i>	NHMUK	Hooijer, 1966; Geraads, 2010
<i>S. etruscus</i>	IGF, MGGC, MNCN, MNHN, MPGPD, MPUR, MSNAF, NHMUK, NMB	Guérin, 1980
<i>S. hemitoechus</i>	IGF, MNCN, MPUR, NHMUK	Guérin, 1980
<i>S. hundsheimensis</i>	MNHN, NHFW, NHMUK	Guérin, 1980
<i>S. jeanvireti</i>	IGF, HNHM, MGGC, NMB	Guérin, 1972, 1980
<i>S. kirchbergensis</i>	MfN, MNHN, MPUR, NHMUK, NMB	Guérin, 1980; Handa & Pandolfi, 2016
<i>S. lantianensis</i>	IVPP	Tong, 2012
<i>S. yunchuchenensis</i>	IVPP	Chow, 1963; Tong, 2012
<i>S.? africanus</i>	-	Arambourg, 1970; Geraads, 2010

Tab. 1. List of the species included within the subtribe Rhinocerotina and sources for the considered cranial and dental material. For the genus abbreviation, check the Materials and Methods section.

1832) (which occurred from MN 9 to MN 12 at several central and western European localities), *Dihoplus pikermiensis* (Toula, 1906) (which occurred in the latest Vallesian and Turolian deposits, MN 10-MN 13, of the Balkan Peninsula and Turkey), *Dihoplus megarhinus* (de Christol, 1832) (recently reported from several latest Miocene faunas, MN 12-MN 13, of Hungary, Italy, Ukraine, and China), and *Ceratotherium neumayri* (Osborn, 1900) (reported from several fossiliferous localities, MN 10-MN 13, of the Balkan Peninsula, Caucasus, Anatolia and Iran). Late Miocene African localities which yielded remains of rhinoceros are relatively scarce and often the rhinoceros material was only identified at the generic level (*Ceratotherium* Gray, 1868 or *Diceros* Gray, 1821; Geraads, 2010) or as *Paradicerus* sp., cf. *Ceratotherium* sp. or cf. *Paradicerus mukirii* Hooijer, 1968. According to Guérin (2011) a taxon closely related with the Balkano-Iranian species *C. neumayri* (*Diceros* cf. *pachygnatus* in Guérin, 2011) was present at Aragai and Ngetabkwony (Kenya, around 6 Ma and 5-4.5 Ma respectively). *Ceratotherium douariense* (Guérin, 1966) (= *Diceros douariense*) was established from a partial skull with associated mandible from Douaria (Tunisia, around 7 Ma) but it is doubtfully distinct from *C. neumayri* (Geraads, 2010). The record of *C. douariense* from the Middle Awash (Ethiopia, latest Miocene; Giaourtsakis et al., 2009) was reported as *Diceros?* sp. by Geraads (2010: Tab. 34.I) but without any detailed explanation. *Ceratotherium?* *primaevum* (Arambourg, 1959) (= *Dicerorhinus primaevus* Arambourg, 1959) was named on a partial juvenile skull and associated remains collected at Bou Hanifia (Algeria, around 10 Ma).

During Plio-Pleistocene, the genera *Stephanorhinus* Kretzoi, 1942 and *Coelodonta* Bronn, 1831 were widespread in Eurasia (Fig. 1), but they never occurred in the Indian Subcontinent and in the South-East Asia (e.g., Thailand, Malaysia, Indonesia). *Coelodonta* and *Stephanorhinus* are generally considered sister groups, but Heissig (1981) suggested that any similarities between these two taxa could be related to convergence.

The earliest representatives of the genus *Stephanorhinus* are from the Pliocene of Europe. At least 7 species can be included within this genus: *Stephanorhinus kirchbergensis* (Jäger, 1839) (Early Pleistocene to latest Pleistocene; Eurasia), *Stephanorhinus etruscus* (Falconer, 1868) (late Pliocene to the early Middle Pleistocene; Europe), *Stephanorhinus hemitoechus* (Falconer, 1859) (Middle Pleistocene to the latest Pleistocene; Eurasia and North Africa), *Stephanorhinus hundsheimensis* (Toula, 1902) (latest Early Pleistocene to the Middle Pleistocene; Europe), *Stephanorhinus yunchuchenensis* (Chow, 1963) (latest Early Pleistocene; Eastern China), *Stephanorhinus jeanvireti* (Guérin, 1972) (Late Pliocene to earliest Pleistocene; Europe), and *Stephanorhinus lantianensis* (Hu & Qi, 1978) (latest Early Plei-

stocene; Eastern China). “*Stephanorhinus*” *miguelcrusafonti* (Guérin & Santafé-Llopis, 1978) (Early Pliocene; Western Europe) is provisionally retained within this genus, whereas *Stephanorhinus? africanus* (Arambourg, 1970) (early to middle Pliocene; Tunisia and Chad) has an uncertain taxonomic position. Heissig (1999) suggested a paraphyly of *Stephanorhinus*, considering two evolutionary lineages, one from *Dihoplus schleiermachersi* to *S. jeanvireti* through “*D.*” *megarhinus*, and the other one from *Dihoplus pikermiensis* (= *Stephanorhinus pikermiensis* in Heissig, 1999) to *S. etruscus* and other species. However, the debate on the phylogenetic relationships within this group of rhinoceroses is far from being settled by consensus.

Coelodonta evolved in Central Asia since the middle Pliocene (with the species *Coelodonta thibetana* Deng et al., 2011 from the Tibetan Plateau) and reached Western Europe only during the Middle Pleistocene; within this genus the major apomorphies were acquired by *Coelodonta antiquitatis* (Blumenbach, 1799). During the last glacial maximum, the woolly rhino was present from Iberian Peninsula to Siberia and from Scotland to Greece.

The genera *Ceratotherium* [with *C. mauritanicum* (Pomel, 1888) and *C. simum* (Burchell, 1817)] and *Diceros* (with *D. praecox* (Hooijer & Patterson, 1872) and *D. bicornis* (Linnaeus, 1758)) were widespread throughout Africa during the Plio-Pleistocene. *C. mauritanicum* was present from the Late Pliocene to Late Pleistocene, in particular in North Africa, and it was probably the ancestor of *C. simum* (Geraads, 2010), which occurred for the first time in East Africa during the Early Pleistocene. Contrary to *C. simum*, *D. bicornis* has never been recorded North of the Sahara desert.

The genus *Rhinoceros* Linnaeus, 1758 was mainly limited in the Indian Subcontinent and some areas of Southeastern Asia during the Pleistocene and Holocene (Fig. 1). *Rhinoceros sivalensis* Falconer & Cautley, 1846 and *Rhinoceros platyrhinus* Falconer & Cautley, 1846 co-occurred in Southern Himalayas (Upper Siwaliks). *Rhinoceros unicornis* Linnaeus, 1758, currently is represented by a few populations located in some areas of Nepal and India (Assam and western Bengal), was documented from Early Pleistocene localities of Java, southern China, India and Pakistan and several Middle Pleistocene localities of the South-East Asia. During the Late Pleistocene, *R. unicornis* was present in China, Vietnam, Southern India and Sri Lanka (Antoine, 2012). *Rhinoceros sondaicus* Desmarest, 1822 is currently present in limited areas of Western Java and Southern Vietnam; but in historical times it was widespread in several areas of South-East Asia and India. Subfossil remains of *R. sondaicus* were collected at Sumatra, Borneo, Java and Malaysia, and the species was also present in southern China (Antoine, 2012). *R. sondaicus* occurred during the Pleistocene at Java, Malaysia, Vietnam, and Cambodia.

The genus *Dicerorhinus* Gloger, 1841 only occurred in the Southeastern Asia during the Plio-Pleistocene with extant species *Dicerorhinus sumatrensis* (Fischer, 1814) and the extinct species *Dicerorhinus gwebinensis* Zin-Maung-Maung-Thein et al., 2008.

Some Rhinocerotina species belonging to different lineages and biogeographic areas, i.e. *C. simum* (Africa), *Co. antiquitatis* (Northern Eurasia), *R. platyrhinus* (Indian Subcontinent), acquired similar morphological characters through their evolution, probably under the control of similar selective pressures (Pandolfi & Maiorino, 2016).

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