

The Evolution of Western Eurasian Neogene Mammal Faunas

*Edited by
Raymond L. Bernor, Volker Fahlbusch, and Hans-Walter Mittmann*

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The Stratigraphical Range of Fossil Rhinoceroses in the Late Neogene of Europe and the Eastern Mediterranean

K. HEISSIG

Fossil rhinoceroses are common faunal elements in Europe and Western Asia during the late Neogene. They are a rather conservative group, not exhibiting many distinctive intrafamily characters, and rather complete skeletal material is needed to make an accurate specific determination. So the considerable later Neogene rhino radiation is largely masked by insufficient materials, making a step-by-step evolutionary reconstruction impossible. Often the most common and completely preserved materials belong to species having a vast chronologic and geographic distribution and providing little valuable information for correlation. However, other rhinoceros lineages are distinctive, and their migration and extinction events are often useful for correlation, albeit a rather coarse one. Only a single multispecific lineage can be tracked across the late Miocene–Pliocene boundary.

Despite the limitations seen for geochronologic correlations (de Bruijn et al. 1992), most rhinoceros species are good ecological indicators. The composition of rhino faunas varies even within the same temporal interval, and over short geographic distances. Unfortunately, rhino paleoecology is not yet well understood, leaving an unrealized treasure of information yet to be developed.

Time-Space Distribution of Middle Miocene–Pliocene European and West Asian Rhinoceroses

The Middle Miocene

During the middle Miocene the Aceratherini and Teleoceratini are the dominant rhinoceroses in both geographic areas considered here. *Brachypotherium brachypus*, *Alicornops simorreensis*, and *Hoploaceratherium*, with its successive species *H. tetradactylum* and *H. bavaricum*, occur throughout the entire region. In Europe the early Miocene holdovers, *Prosantorhinus germanicus*, a small

teleoceratine, and *Plesiaceratherium fahlbuschi*, an Aceratherini, become extinct in MN 6, contracting in their geographic distribution to Central Europe. The single occurrence of *P. mirallesi* in the isolated Central European locality of Georgensgmünd is also its last appearance. Of all these forms, only *Hoploaceratherium* was not already present in the late (MN 5) early Miocene. The successive species of *Hoploaceratherium* can be distinguished only by cranial characters.

The two Rhinocerotini species *Lartetotherium sansaniense* and “*Dicerorhinus*” *steinheimensis* first occurred in Europe during the late early Miocene, and there is no record of them in the Eastern Mediterranean. In the Eastern Mediterranean the influence of Asian faunas is seen by the occurrence of the elasmotherine genus *Begertherium* (Fortelius 1990) with its two successive species, co-occurring with the common genera *Alicornops*, *Hoploaceratherium*, and *Brachypotherium*. The genus *Diceros*, an African immigrant, is found very rarely in Eastern Mediterranean middle Miocene age horizons.

Unfortunately, the middle Miocene is represented by only a few French rhinoceros-bearing localities yielding the most common species. There is no record of rare Western European elasmotherine rhinos after MN 5. Rhinoceroses are not known during this time from Southern Europe, and only from two Southeast European localities, with the only determinable species being *Lartetotherium sansaniense*.

Some of these species have apparently been restricted to very peculiar habitats; their occurrence is not correlated with age or any particular sedimentary environment. Other species occurred over vast geographic areas and for long chronological durations. There is little known about the actual ecology of fossil browsing rhinos. All of the middle Miocene European forms would appear to have been browsers. Thenius (1951) and Heissig (1972) have remarked that *Brachypotherium* did not prefer swampy wood-

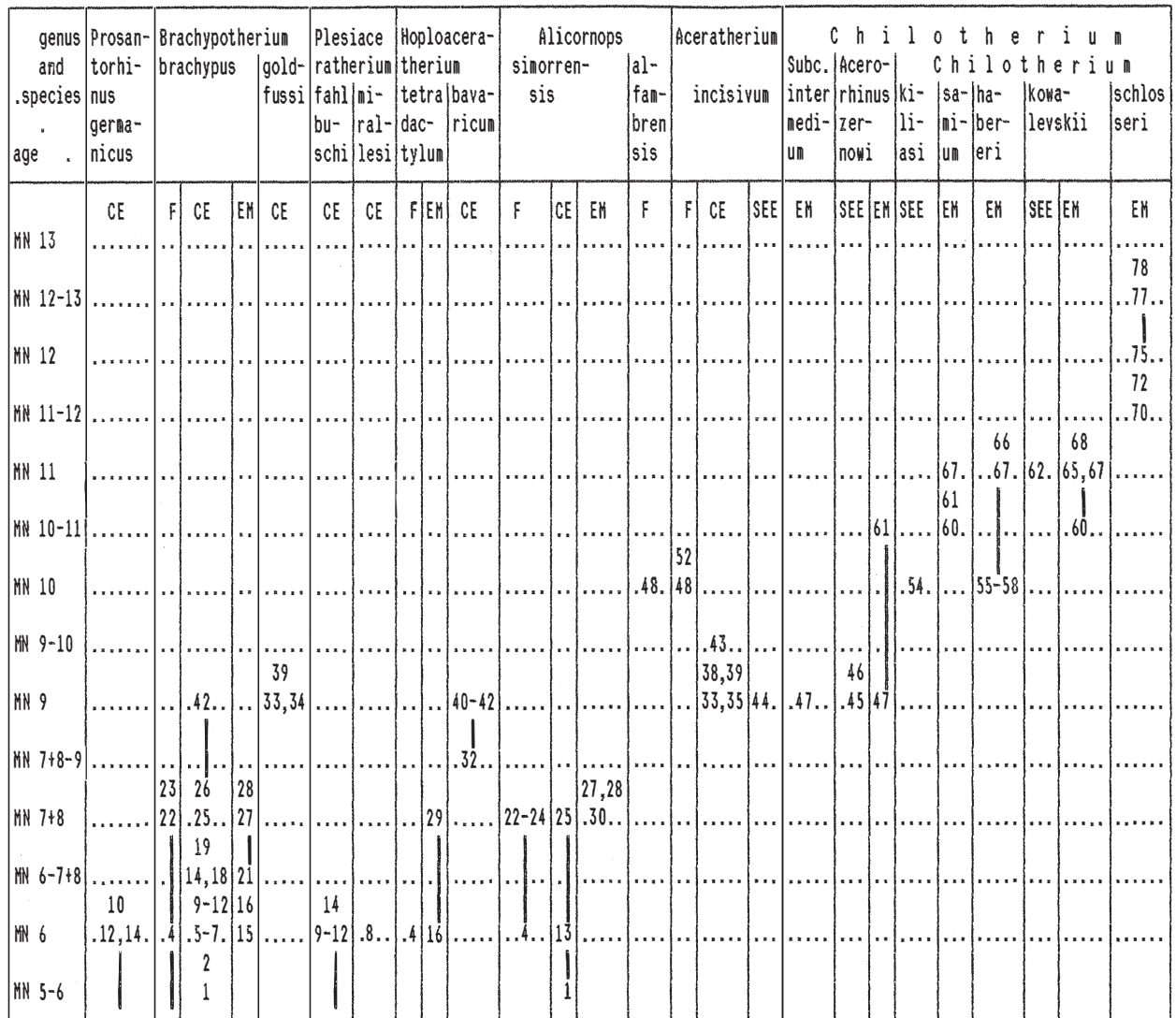


FIGURE 27.1 Stratigraphic range and localities bearing Aceratheriinae species in France (F), Central Europe (CE), Southeastern Europe (SEE), and the Eastern Mediterranean (EM).

lands. The content of the shrub's wooden parts in the diet of the Aceratherini was probably higher than that preferred by *Lartetotherium sansaniense*. In contrast to the European woodlands, the Eastern Mediterranean semi-hypsodont Elasmotherini clearly inhabited dry areas and were adapted to abrasive food that had relatively poor nutritive quality. The presence of some European browsing species is indicative of the occurrence of restricted bush or woodland environments. The lack of Rhinocerotini corresponds with their preference for very soft plants.

The Late Miocene

Rhinoceros geographic distribution and ecological preferences change dramatically in the late Miocene, most probably because of regional climatic change. Sedimentary environments probably were also affected, because rhino-

bearing localities were now numerous in the Eastern Mediterranean, whereas Central European localities younger than the earliest late Miocene (MN 9) are rare.

The change is more radical in the Eastern Mediterranean than in Europe, and the dissimilarities in both regions increase considerably. Whereas no rhino lineage continues across the middle/late Miocene boundary in the Eastern Mediterranean region, the appearance of new elements in Central and Western Europe is followed by a gradual decline in the occurrence of survivors during MN 9 and MN 10. During this time we find the following surviving species: *Brachypotherium goldfussi*, which differs in no essential details from the earlier species *B. brachypus*; *Lartetotherium sansaniense*; *Hoploaceratherium bavaricum*; and *Alicornops simorrensis*. In Western Europe the short-limbed species *Alicornops alfambrensis* Cerdeño 1989 occurs, apparently derived from *A. simorrensis*. There are

genus and species age	Begertherium		Diceros		Ceratotherium			"Dicerorhinus"			Lartetotherium			"Dicerorhinus" schleiermacheri				"D." megarhinus			"D." jeanvireti			"D." guelcru-sa-fonti		Stephanorhinus		
	tek-grai-mi	grai-mi	sp. pri-mae-vus	sp. pri-mae-vus	neu-mayri	neu-mayri	neu-mayri	stein-heim-ensis	stein-heim-ensis	stein-heim-ensis	sansani-ensis	sansani-ensis	sansani-ensis	F	CE	SEE	F	CE	SE	SEE	F	CE	SE	F	SEE	EM	F	SE
MN 17																												
MN 16-17																												
MN 16																												
MN 15																												
MN 14-15																												
MN 14																												
MN 13																												
MN 12-13																												
MN 12																												
MN 11-12																												
MN 11																												
MN 10-11																												
MN 10																												
MN 9-10																												
MN 9																												
MN 7+8-9																												
MN 7+8																												
MN 6-7+8																												
MN 6																												
MN 5-6																												

FIGURE 27.2 Stratigraphic range and localities bearing Rhinocerotinae species in France (F), Central Europe (CE), Southern Europe (SE), Southeastern Europe (SEE), and the Eastern Mediterranean (EM).

only two immigrants: *Aceratherium incisivum* and "Dicerorhinus" *schleiermacheri*, which continue together with the latest survivor, *Brachypotherium*, into MN 10 and later. The last appearance of these forms is masked by their sparse fossil record. Only "Dicerorhinus" *schleiermacheri*

transgresses the late Miocene/early Pliocene boundary, continuing in the early Pliocene as "D." *megarhinus*. The Elasmotheriini and other middle Miocene lineages became extinct in the Eastern Mediterranean at this time and were replaced by an Asian-African rhinoceros fauna.

The Central Asian lineage *Chilotherium* s.l. and the African lineage *Ceratotherium neumayri* invade Southeastern Europe and the eastern margin of Central Europe at this time.

There are several occurrences of *Chilotherium* reported from Italy, France, Greece, and Spain, but currently the evidence can only sufficiently support its occurrence in Greece. The French and Spanish remains have been assigned by Cerdeño (1989) to *Alicornops dfambrensis*. The chronologically long-ranging genus *Stephanorhinus pikeri* first occurs in terminal late Miocene horizons of Southeastern Europe and portions of the Eastern Mediterranean. The single record of a true *Diceros* from Kayadibi suggests some ecological differences within the Eastern Mediterranean. *Ceratotherium neumayri* shows some size increase, together with a slight tendency of progressive hypsodonty during the late Miocene interval.

Three subgenera of *Chilotherium* arise from the second Asian Aceratheriinae radiation. Two subgenera there can be traced back to the middle Miocene. Their arrival in the Eastern Mediterranean region begins with *Chilotherium* (*Subchilotherium*) *intermedium*, recorded from only one Anatolian locality. The few undetermined remains from France and Spain may probably belong to this species. *Chilotherium* (*Acerorhinus*), also known from Eastern Asian middle Miocene age horizons, lacks the specializations typical of *Chilotherium* s.s. It occurs at several Anatolian localities with the species *zernowi*, known also from Eastern Europe. The Anatolian record seems to be confined to MN 9 and MN 10, possibly extending into MN 11. Its Eastern Asian relatives are more advanced.

The evolutionary relationships of species included within *Chilotherium* s.s. are not yet well understood. The most primitive form dentally, *Chilotherium samium*, first occurs in Anatolia possibly as early as late MN 10, but certainly by MN 11. The holotype *Ch. samium* comes from an unknown horizon at Samos. *Chilotherium kiliasi* (Geraads and Koufos 1989) occurs at Pentalophos (MN 10). This species was originally described as being referable to *Aceratherium*, but indeed it is typical of a primitive *Chilotherium* and may be closely related to *Chilotherium samium*, the only species with female mandibles not broadened anteriorly. It has to be added that the larger form of this species, reported in Heissig (1975) from Çorak Yerler, is possibly another species belonging to the same lineage.

Chilotherium kowalevskii is the only species of this time period exhibiting characters diverging from other members of this group. *Chilotherium habereri*, also known from China, first occurs a little earlier in time (MN 10) and is possibly closely related to the Maragheh species *Ch. persiae* (for its stratigraphic and chronologic record at Maragheh, see Bernor et al., this volume). It is replaced in MN 12 by the latest and largest *Chilotherium* species, *Ch. schlosseri*, which may very well be derived from *Ch. habe-*

rerii; however, intermediate forms are known only from Eastern Asia. All of these species have near relatives in Eastern and Central Asia, but the lineages are difficult to disentangle. *Chilotherium habereri* seems to be representative of the central stock, from which at least the larger and more hypsodont middle and late Turolian species *Ch. anderssoni* (the Chinese genotype species) and *Ch. schlosseri* are derived. The Maragheh species *Ch. persiae* is also a close relative.

Despite our poor understanding of European rhinoceros ecology, rhino faunal development is consistent with the evolution of a continuous woodland environment. The extinction of most rhino species during the late Miocene corresponds to progressive cooling and development of more temperate woodlands.

To the south and southeast we find a gradual change in landscape to increasingly open habitats and, at the same time, the extension of this more Mediterranean type of climate to the north. Nevertheless, we may conclude fundamental differences between the late and middle Miocene rhino faunas by the distinct faunal break found in the Eastern Mediterranean region. The dominant form, *Ceratotherium neumayri*, was at least partly a grass eater, whereas the genus *Chilotherium* most likely occupied diverse ecological niches, indicated by the number of species. Certainly there were a number of non-graminean herbs that formed their diet. The most brachyodont *Chilotherium* (*Acerorhinus*) may have been the only widespread browser in this region. Only one locality has yielded the African browsing rhinoceros genus *Diceros*, indicative of more densely vegetated areas.

The Pliocene

The basal Pliocene marks yet another turnover in rhinoceros faunas. Very few late Miocene rhinoceros species persist during the Pliocene in the Eastern Mediterranean. Also, Central and Southeastern Europe have very few rhinoceros-bearing localities. Quite to the contrary, Western and Southern Europe have numerous Pliocene rhinoceros localities.

The Mio–Pliocene boundary includes the principal extinction event for European rhinoceroses. All Aceratheriini and Teleoceratini disappear from Europe and the Eastern Mediterranean. From MN 14 onward, *Brachypotherium*, *Diceros*, and *Ceratotherium* are restricted to Africa. In Europe only one major lineage has survived the Mio–Pliocene boundary: “*Dicerorhinus*” *schleiermacheri*. This lineage evolves through the successive Pliocene species: “*D.*” *schleiermacheri*—“*D.*” *megarhinus*—*D. jeanvireti*.

“*Dicerorhinus*” *megarhinus* is the only known basal Pliocene rhinoceros. “*Dicerorhinus*” *miguelcрусafonti*, a species of unknown origin, first appears during MN 15 and has a geographic distribution restricted to the Iberian Peninsula

and southern France. "*Diceros*" *megarhinus* is replaced at the beginning of the late Pliocene by its descendant, "*D.*" *jeanvireti*. "*D.*" *jeanvireti* coexists for a short time with the smaller form *Stephanorhinus etruscus*, which itself is probably derived from the Turolian form *St. pikermiensis*. *Stephanorhinus etruscus* is the only rhinoceros species that survives into the Pleistocene.

We have very little knowledge of the Eastern Mediterranean rhino fauna during this temporal interval. Most specimens are insufficient for determination. Some bones from the Turkish MN 17 locality Gülyazi (Gauss/Matuyama boundary, ca. 2.6 Ma; Bernor and Lipscomb 1991; Steininger et al. this volume) conform in their size to *St. etruscus*, but the morphological characters of this form are atypical for the species. Two lower molars of undetermined age from Kobasi, provisionally referred by Heissig (1973) to *Stephanorhinus ringstroemi*, may actually be referable to either "*D.*" *schleiermachersi* or "*D.*" *megarhinus*.

Nearly all of the European and Western Asian Pliocene rhinos had brachyodont cheek teeth and were browsers. The only rhino with somewhat higher crowns was the Western European species "*Dicrorhinus*" *miguelerusfonti*, suggesting an adaptation to a drier Mediterranean climate in Spain and southern France during MN 15. Knowledge of Eastern Mediterranean Pliocene rhino faunas is insufficient to make meaningful comparisons with the rest of Europe.

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APPENDIX 27.1 *Rhinocerotidae Species Reference List Late Neogene, Starting from MN 6*

Name	Author	Locality	References	Seen	Frequency
Aceratheriinae — Teleoceratini					
<i>Prosantorhinus germanicus</i>	Wang 1929	Georgensgmtind	Heissig 1972	y	c
<i>Prosantorhinus germanicus</i>	Wang 1929	Thannhausen	Heissig 1984	y	c
<i>Prosantorhinus germanicus</i>	Wang 1929	Derching	Heissig 1984	y	c
<i>Prosantorhinus germanicus</i>	Wang 1929	Stätzing	Heissig 1984	y	c
<i>Prosantorhinus germanicus</i>	Wang 1929	Friedberg	Heissig 1984	y	c
<i>Brachypotherium brachypus</i>	Lartet 1837	Simorre	Guérin 1980	y	d
<i>Brachypotherium brachypus</i>	Lartet 1837	Sansan	Guérin 1980	n	s
<i>Brachypotherium brachypus</i>	Lartet 1837	La Grive	Guérin, 1980	n	?
<i>Brachypotherium brachypus</i>	Lartet 1837	Thannhausen	Heissig 1984	y	s
<i>Brachypotherium brachypus</i>	Lartet 1837	Derching	Heissig 1984	y	d
<i>Brachypotherium brachypus</i>	Lartet 1837	Stätzing	Heissig 1984	y	c
<i>Brachypotherium brachypus</i>	Lartet 1837	Friedberg	Heissig 1984	y	c
<i>Brachypotherium brachypus</i>	Lartet 1837	Unterzolling	Heissig 1984	y	c
<i>Brachypotherium brachypus</i>	Lartet 1837	Enghausen	Heissig 1989	y	c
<i>Brachypotherium brachypus</i>	Lartet 1837	Ziemetshausen ib	Heissig 1984	y	c
<i>Brachypotherium brachypus</i>	Lartet 1837	Prambach	Heissig 1984	y	s
<i>Brachypotherium brachypus</i>	Lartet 1837	Langenneufnach	Heissig 1984	y	s
<i>Brachypotherium brachypus</i>	Lartet 1837	Auloh b. Schönbrunn	Heissig 1984	y	s
<i>Brachypotherium brachypus</i>	Lartet 1837	Steinheim a. Albuch	Guérin 1980	y	c
<i>Brachypotherium brachypus</i>	Lartet 1837	Massenhausen	Heissig 1984	y	d
<i>Brachypotherium brachypus</i>	Lartet 1837	Wartenberg	Heissig 1984	y	s
<i>Brachypotherium brachypus</i>	Lartet 1837	Meßkirch	Schlosser 1902	y	c
<i>Brachypotherium brachypus</i>	Lartet 1837	Heudorf	Schlosser 1902	n	s
<i>Brachypotherium brachypus</i>	Lartet 1837	Przeworno	Kowalski 1990	y	s
<i>Brachypotherium brachypus</i>	Lartet 1837	Opole	Kowalski 1990	n	s
<i>Brachypotherium brachypus</i>	Lartet 1837	Pasalar	Alpagut, Andrews & Martin 1990	n	s
<i>Brachypotherium brachypus</i>	Lartet 1837	Candir	Heissig 1976	y	s
<i>Brachypotherium brachypus</i>	Lartet 1837	Tüney	Heissig 1976	y	s
<i>Brachypotherium brachypus</i>	Lartet 1837	Sofca	Heissig 1976	y	s
<i>Brachypotherium brachypus</i>	Lartet 1837	Catakbagyaka	Heissig 1976	y	c
<i>Brachypotherium goldfussi</i>	Kaup 1834	Eppelsheim	Guérin 1980	y	s
<i>Brachypotherium goldfussi</i>	Kaup 1834	Gauweinheim	Guérin 1980	y	c
<i>Brachypotherium goldfussi</i>	Kaup 1834	Melchingen	Schlosser 1902	n	s
Aceratheriinae — Aceratherini					
<i>Plesiaceratherium fahlbuschi</i>	Heissig 1972	Thannhausen	Heissig 1984	y	c
<i>Plesiaceratherium fahlbuschi</i>	Heissig 1972	Stätzing	Heissig 1984	y	c
<i>Plesiaceratherium fahlbuschi</i>	Heissig 1972	Friedberg	Heissig 1984	y	c
<i>Plesiaceratherium fahlbuschi</i>	Heissig 1972	Mainburg	Heissig 1984	y	c
<i>Plesiaceratherium fahlbuschi</i>	Heissig 1972	Unterzolling	Heissig 1984	y	c
<i>Plesiaceratherium mirallesi</i>	Crusafont et al. 1955	Georgensgmtind	Yan & Heissig 1986	y	c
<i>Hoploaceratherium tetradactylum</i>	Lartet 1837	Sansan	Guérin 1980	y	d
<i>Hoploaceratherium aff. tetradactylum</i>	Lartet 1837	Candir	Heissig 1976	y	c
<i>Hoploaceratherium aff. tetradactylum</i>	Lartet 1837	Yeni Eskihisar	Heissig 1976	y	s
<i>Hoploaceratherium bavaricum</i>	Stromer 1902	Niedernkirchen	Heissig 1984	y	s
<i>Hoploaceratherium bavaricum</i>	Stromer 1902	Wartenberg	Heissig 1984	y	s
<i>Hoploaceratherium bavaricum</i>	Stromer 1902	München	Heissig 1984	y	c
<i>Hoploaceratherium bavaricum</i>	Stromer 1902	Oberföhring	Heissig 1984	y	s
<i>Alicornops simorreensis</i>	Lartet 1851	Simorre	Guérin 1980	y	c
<i>Alicornops simorreensis</i>	Lartet 1851	Villefranche d. Astarac	Guérin 1980	y	c
<i>Alicornops simorreensis</i>	Lartet 1851	Sansan	Guérin 1980	y	s
<i>Alicornops simorreensis</i>	Lartet 1851	Tutzing	Heissig 1984	y	s
<i>Alicornops simorreensis</i>	Lartet 1851	Steinheim a. Albuch	Heizmann 1973	y	c
<i>Alicornops simorreensis</i>	Lartet 1851	Meßkirch	Schlosser 1902	n	s
<i>Alicornops simorreensis</i>	Lartet 1851	La Grive	Guérin 1980	y	s
<i>Alicornops simorreensis</i>	Lartet 1851	Sofca	Heissig 1976	y	c
<i>Alicornops simorreensis</i>	Lartet 1851	Catakbagyaka	Heissig 1976	y	c
<i>Alicornops simorreensis</i>	Lartet 1851	Yaylacilar	Heissig 1976	y	c
<i>Alicornops alfambrensis</i>	Cerdeño 1989	Montredon	Cerdeño 1989	n	c
<i>Aceratherium incisivum</i>	Kaup 1832	Eppelsheim	Guérin 1980	y	c
<i>Aceratherium incisivum</i>	Kaup 1832	Hövenegg	Hünemann 1989	y	d
<i>Aceratherium incisivum</i>	Kaup 1832	Wien, Belvedere	Guérin 1980	y	s
<i>Aceratherium incisivum</i>	Kaup 1832	Oppenheim	Guérin 1980	y	c
<i>Aceratherium incisivum</i>	Kaup 1832	Melchingen	Schlosser 1902	n	
<i>Aceratherium incisivum</i>	Kaup 1832	Montredon	Guérin 1980	y	c
<i>Aceratherium incisivum</i>	Kaup 1832	Priay	Guérin 1980	y	c
<i>Aceratherium incisivum</i>	Kaup 1832	Merischleri	Bakalov & Nikolov 1962	n	s
<i>Chilotherium (Subchil.) intermedium</i>	Lydekker 1884	Esme-Akcaköy	Heissig 1975	y	s
<i>Chilotherium (Chil.) samium</i>	Weber 1905	Kayadibi	Heissig 1975	y	c
<i>Chilotherium (Chil.) samium</i>	Weber 1905	Corak Yerler	Heissig 1975	y	

Name	Author	Locality	References	Seen	Frequency
<i>Chilotherium (Chil.) habereri</i>	Schlosser 1903	Kütkückmece	Heissig 1975	y	s
<i>Chilotherium (Chil.) habereri</i>	Schlosser 1903	Gülpinar	Heissig 1975	y	s
<i>Chilotherium (Chil.) habereri</i>	Schlosser 1903	Basbereket	Heissig 1975	y	s
<i>Chilotherium (Chil.) habereri</i>	Schlosser 1903	Kavakdere	Heissig 1975	y	c
<i>Chilotherium (Chil.) habereri</i>	Schlosser 1903	Selcik	Heissig 1975	y	s
<i>Chilotherium (Chil.) habereri</i>	Schlosser 1903	Samos	Heissig 1975	y	c
<i>Chilotherium (Chil.) kowalevskii</i>	Pavlov 1913	Corak Yerler	Heissig 1975	y	c
<i>Chilotherium (Chil.) kowalevskii</i>	Pavlov 1913	Garkin	Heissig 1975	y	c
<i>Chilotherium (Chil.) kowalevskii</i>	Pavlov 1913	Karacahasan	Heissig 1975	y	s
<i>Chilotherium (Chil.) kowalevskii</i>	Pavlov 1913	Losengrad	Bakalov & Nikolov 1962	n	s
<i>Chilotherium (Chil.) schlosseri</i>	Weber 1905	Mahmutgazi	Heissig 1975	y	s
<i>Chilotherium (Chil.) schlosseri</i>	Weber 1905	Kinik	Heissig 1975	y	c
<i>Chilotherium (Chil.) schlosseri</i>	Weber 1905	Eski Bayirköy	Heissig 1975	y	s
<i>Chilotherium (Chil.) schlosseri</i>	Weber 1905	Amasya	Heissig 1975	y	s
Rhinocerotinae—Elasmotherini					
<i>Begertherium tekkayai</i>	Heissig 1974	Pasalar	Fortelius & Heissig 1989	y	d
<i>Begertherium grimmi</i>	Heissig 1974	Candir	Fortelius & Heissig 1989	y	c
<i>Begertherium grimmi</i>	Heissig 1974	Sofca	Heissig 1976	y	c
<i>Begertherium grimmi</i>	Heissig 1974	Yaylacilar	Heissig 1976	y	d
<i>Begertherium grimmi</i>	Heissig 1974	Catakbagyaka	Heissig 1976	y	c
<i>Begertherium grimmi</i>	Heissig 1974	Zivra	Heissig 1976	y	s
<i>Begertherium grimmi</i>	Heissig 1974	Yeni Eskihisar	Heissig 1976	y	s
Rhinocerotinae—Rhinocerotini					
<i>Diceros primaevus</i>	Arambourg 1959	Kayadibi	Heissig 1976	y	s
<i>Ceratotherium neumayri</i>	Osborn 1900	Hauskirchen	Thenius 1956	y	s
<i>Ceratotherium neumayri</i>	Osborn 1900	Pikermi	Geraads 1989	y	c
<i>Ceratotherium neumayri</i>	Osborn 1900	Samos	Geraads 1989	y	d
<i>Ceratotherium neumayri</i>	Osborn 1900	Thessaloniki	Arambourg & Pivetau 1929	n	c
<i>Ceratotherium neumayri</i>	Osborn 1900	Pentalophos	Geraads & Koufos 1990	n	c
<i>Ceratotherium neumayri</i>	Osborn 1900	Kalimanzi	Bakalov & Nikolov 1962	y	c
<i>Ceratotherium neumayri</i>	Osborn 1900	Esme Akcaköy	Heissig 1976	y	d
<i>Ceratotherium neumayri</i>	Osborn 1900	Kavakdere	Heissig 1976	y	c
<i>Ceratotherium neumayri</i>	Osborn 1900	Gülpinar	Heissig 1976	y	c
<i>Ceratotherium neumayri</i>	Osborn 1900	Basbereket	Heissig 1976	y	s
<i>Ceratotherium neumayri</i>	Osborn 1900	Balciklidere	Heissig 1976	y	s
<i>Ceratotherium neumayri</i>	Osborn 1900	Corak Yerler	Heissig 1976	y	c
<i>Ceratotherium neumayri</i>	Osborn 1900	Garkin	Heissig 1976	y	c
<i>Ceratotherium neumayri</i>	Osborn 1900	Karacahasan	Heissig 1976	y	s
<i>Ceratotherium neumayri</i>	Osborn 1900	Mahmutgazi	Heissig 1976	y	d
<i>Ceratotherium neumayri</i>	Osborn 1900	Kinik	Heissig 1976	y	c
<i>Ceratotherium neumayri</i>	Osborn 1900	Eski Bayirköy	Heissig 1976	y	c
<i>Ceratotherium neumayri</i>	Osborn 1900	Amasya	Heissig 1976	y	s
" <i>Dicerorhinus</i> " <i>steinheimensis</i>	Jäger 1839	Steinheim a. Altbuch	Guérin 1980	y	s
" <i>Dicerorhinus</i> " <i>steinheimensis</i>	Jäger 1839	Thalhausen	Heissig 1984	y	s
" <i>Dicerorhinus</i> " <i>steinheimensis</i>	Jäger 1839	Derndlmühle	Heissig 1984	y	s
" <i>Dicerorhinus</i> " <i>steinheimensis</i>	Jäger 1839	Eibiswald	Thenius 1951	y	c
" <i>Dicerorhinus</i> " <i>steinheimensis</i>	Jäger 1839	Thannhausen	Heissig 1984	y	s
" <i>Dicerorhinus</i> " <i>steinheimensis</i>	Jäger 1839	Derching	Heissig 1984	y	s
" <i>Dicerorhinus</i> " <i>steinheimensis</i>	Jäger 1839	Wartenberg	Heissig 1984	y	s
" <i>Dicerorhinus</i> " <i>steinheimensis</i>	Jäger 1839	Eppelsheim	Osborn 1900	y	s
" <i>Dicerorhinus</i> " <i>steinheimensis</i>	Jäger 1839	La Grive	Guérin 1980	n	s
<i>Lartetotherium sansaniense</i>	Lartet 1851	Sansan	Ginsburg 1974	y	c
<i>Lartetotherium sansaniense</i>	Lartet 1851	La Grive	Guérin 1980	y	s
<i>Lartetotherium sansaniense</i>	Lartet 1851	Stätzling	Heissig 1984	y	s
<i>Lartetotherium sansaniense</i>	Lartet 1851	Massenhausen	Heissig 1984	y	c
<i>Lartetotherium sansaniense</i>	Lartet 1851	Hirblingen	Heissig 1984	y	s
<i>Lartetotherium sansaniense</i>	Lartet 1851	Lurtz	Heissig 1984	y	s
<i>Lartetotherium sansaniense</i>	Lartet 1851	Meßkirch	Schlosser 1902	n	c
<i>Lartetotherium sansaniense</i>	Lartet 1851	Heudorf	Schlosser 1902	n	s
<i>Lartetotherium sansaniense</i>	Lartet 1851	Pozlata	Pavlovic 1963	n	s
" <i>Dicerorhinus</i> " <i>schleiermachi</i>	Kaup 1832	Eppelsheim	Guérin 1980	y	c
" <i>Dicerorhinus</i> " <i>schleiermachi</i>	Kaup 1832	Gauweinheim	Guérin 1980	y	c
" <i>Dicerorhinus</i> " <i>schleiermachi</i>	Kaup 1832	Esselborn	Guérin 1980	y	c
" <i>Dicerorhinus</i> " <i>schleiermachi</i>	Kaup 1832	Dorn Dürkheim	—	y	s
" <i>Dicerorhinus</i> " <i>schleiermachi</i>	Kaup 1832	Melchingen	Schlosser 1902	n	s
" <i>Dicerorhinus</i> " <i>schleiermachi</i>	Kaup 1832	Salmendingen	Schlosser 1902	n	s
" <i>Dicerorhinus</i> " <i>schleiermachi</i>	Kaup 1832	Soblay	Guérin 1980	n	d
" <i>Dicerorhinus</i> " <i>schleiermachi</i>	Kaup 1832	Aubignas	Guérin 1980	n	c
" <i>Dicerorhinus</i> " <i>schleiermachi</i>	Kaup 1832	Charmouille	Guérin 1980	n	c
" <i>Dicerorhinus</i> " <i>schleiermachi</i>	Kaup 1832	Luberon	Guérin 1980	n	c
" <i>Dicerorhinus</i> " <i>schleiermachi</i>	Kaup 1832	Lyon-Croix-Rousse	Guérin 1980	n	s
" <i>Dicerorhinus</i> " <i>schleiermachi</i>	Kaup 1832	Montredon	Guérin 1980	y	c
" <i>Dicerorhinus</i> " <i>schleiermachi</i>	Kaup 1832	Vienne	Guérin 1980	y	c
" <i>Dicerorhinus</i> " <i>schleiermachi</i>	Kaup 1832	Dobrisch	Bakalov & Nikolov 1962	n	c

APPENDIX 27.1 Rhinocerotidae Species Reference List Late Neogene, Starting from MN 6 (Continued)

Name	Author	Locality	References	Seen	Frequency
" <i>Dicerorhinus</i> " <i>megarhinus</i>	de Christol 1834	Montpellier	Guérin 1980	y	d
" <i>Dicerorhinus</i> " <i>megarhinus</i>	de Christol 1834	St. Laurent-des-Arbres	Guérin 1980	n	d
" <i>Dicerorhinus</i> " <i>megarhinus</i>	de Christol 1834	Celleneuve	Guérin 1980	n	s
" <i>Dicerorhinus</i> " <i>megarhinus</i>	de Christol 1834	Ille-sur-Têt	Guérin 1980	n	s
" <i>Dicerorhinus</i> " <i>megarhinus</i>	de Christol 1834	Lens-Lestang	Guérin 1980	n	s
" <i>Dicerorhinus</i> " <i>megarhinus</i>	de Christol 1834	Meyrargues	Guérin 1980	n	c
" <i>Dicerorhinus</i> " <i>megarhinus</i>	de Christol 1834	Millas	Guérin 1980	n	c
" <i>Dicerorhinus</i> " <i>megarhinus</i>	de Christol 1834	Perpignan	Guérin 1980	y	d
" <i>Dicerorhinus</i> " <i>megarhinus</i>	de Christol 1834	Pézenas	Guérin 1980	n	s
" <i>Dicerorhinus</i> " <i>megarhinus</i>	de Christol 1834	Vendargues	Guérin 1980	n	s
" <i>Dicerorhinus</i> " <i>megarhinus</i>	de Christol 1834	Antwerpen	Guérin 1980	n	c
" <i>Dicerorhinus</i> " <i>megarhinus</i>	de Christol 1834	Baccinello	Guérin 1980	n	s
" <i>Dicerorhinus</i> " <i>megarhinus</i>	de Christol 1834	Dusino/San Paolo	Guérin 1980	n	s
" <i>Dicerorhinus</i> " <i>megarhinus</i>	de Christol 1834	Fango Nero	Guérin 1980	n	s
" <i>Dicerorhinus</i> " <i>megarhinus</i>	de Christol 1834	Imola	Guérin 1980	n	s
" <i>Dicerorhinus</i> " <i>megarhinus</i>	de Christol 1834	Monte Bianco	Guérin 1980	n	s
" <i>Dicerorhinus</i> " <i>megarhinus</i>	de Christol 1834	Monte Giogo	Guérin 1980	n	c
" <i>Dicerorhinus</i> " <i>megarhinus</i>	de Christol 1834	Palaia	Guérin 1980	n	s
" <i>Dicerorhinus</i> " <i>megarhinus</i>	de Christol 1834	Wölfersheim	Guérin 1980	n	s
" <i>Dicerorhinus</i> " <i>megarhinus</i>	de Christol 1834	Chrabarsko	Bakalov & Nikolov 1962	y	c
" <i>Dicerorhinus</i> " <i>jeanvireti</i>	Guérin 1972	Vialette	Guérin 1980	y	d
" <i>Dicerorhinus</i> " <i>jeanvireti</i>	Guérin 1972	Desnes	Guérin 1980	n	c
" <i>Dicerorhinus</i> " <i>jeanvireti</i>	Guérin 1972	Capannoli	Guérin 1980	n	s
" <i>Dicerorhinus</i> " <i>jeanvireti</i>	Guérin 1972	Perrier-Etouaires	Guérin 1980	n	c
" <i>Dicerorhinus</i> " <i>jeanvireti</i>	Guérin 1972	Vincent	Guérin 1980	n	s
" <i>Dicerorhinus</i> " <i>jeanvireti</i>	Guérin 1972	Dusino	Guérin 1980	n	c
" <i>Dicerorhinus</i> " <i>jeanvireti</i>	Guérin 1972	Montopoli	Guérin 1980	n	c
" <i>Dicerorhinus</i> " <i>jeanvireti</i>	Guérin 1972	Villafranca d'Asti	Guérin 1980	n	c
" <i>Dicerorhinus</i> " <i>jeanvireti</i>	Guérin 1972	Hajnacka	Fejfar 1964	n	c
" <i>Dicerorhinus</i> " <i>miguelcrusafonti</i>	Guérin & Santafé 1978	Perpignan	Cerdeño 1989	n	c
<i>Stephanorhinus pikermiensis</i>	Toula 1906	Pikermi	Geraads 1988	y	c
<i>Stephanorhinus pikermiensis</i>	Toula 1906	Samos	Geraads 1988	y	s
<i>Stephanorhinus ringstroemi</i>	Arambourg 1959	Köprübasi	Heissig 1975	y	s
<i>Stephanorhinus etruscus</i>	Falconer 1859	Valdarno sup.	Guérin 1980	n	c
<i>Stephanorhinus etruscus</i>	Falconer 1859	Argentario	Bascieri & Segre 1957	n	?
<i>Stephanorhinus etruscus</i>	Falconer 1859	Barberino d.Mugello	Guérin 1980	n	c
<i>Stephanorhinus etruscus</i>	Falconer 1859	Borgo San Lorenzo	Guérin 1980	n	s
<i>Stephanorhinus etruscus</i>	Falconer 1859	Castelnuovo Berardenga	Guérin 1980	n	s
<i>Stephanorhinus etruscus</i>	Falconer 1859	Ferrere d'Asti	Guérin 1980	n	s
<i>Stephanorhinus etruscus</i>	Falconer 1859	Incisa Belbo	Guérin 1980	n	s
<i>Stephanorhinus etruscus</i>	Falconer 1859	Montopoli	Guérin 1980	n	s
<i>Stephanorhinus etruscus</i>	Falconer 1859	Olivola	Guérin 1980	n	d
<i>Stephanorhinus etruscus</i>	Falconer 1859	San Clemente a Signano	Guérin 1980	n	s
<i>Stephanorhinus etruscus</i>	Falconer 1859	Villafranca d'Asti	Guérin 1980	n	s
<i>Stephanorhinus etruscus</i>	Falconer 1859	Chagny	Guérin 1980	n	s
<i>Stephanorhinus etruscus</i>	Falconer 1859	Perrier-Etouaires	Guérin 1980	n	c
<i>Stephanorhinus etruscus</i>	Falconer 1859	Puimoisson	Guérin 1980	n	s
<i>Stephanorhinus etruscus</i>	Falconer 1859	Puy-en-Velay	Guérin 1980	n	c
<i>Stephanorhinus etruscus</i>	Falconer 1859	Saint-Vallier	Guérin 1980	n	d
<i>Stephanorhinus etruscus</i>	Falconer 1859	Saint-Vidal	Guérin 1980	n	s