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Diversity and evolutionary trends of the Family Rhinocerotidae (Perissodactyla)

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Abstract

Diversity and evolutionary trends of the Family Rhinocerotidae are presented herein. The sample has a temporal range from the Middle Eocene to recent, including 41 genera and 142 species from Europe, Asia, North America, and Africa. Diversity and the first and last records have been established for each area along a temporal scale. The relative body size and weight and the gracility index of the McIII have been also analysed. The results show that the highest values in diversity and first and last records are reached in Asia. Eurasia and Africa share many taxa, while North America is more independent at generic and specific levels. Very small and very slender taxa are present in Eurasia and North America, absent in Africa. They coexist with brachypodial and generally large forms in Eurasia, whereas in North America they are replaced by large, more robust forms. From the Middle Miocene onward, middle-large sized species with intermediate gracility predominate, often together with the brachypodial ones. The latter type disappears by the Late Miocene, with just one genus remaining in Asia during the Pliocene. At this time a general decline of the Rhinocerotidae occurs, related to a major climatic change, becoming extinct in North America. By the end of the Pleistocene, rhinocerotids disappear from Europe and wide areas of Asia, but they remain in southeast Asia and in Africa, south of the Sahara. © 1998 Elsevier Science B.V. All rights reserved.

Keywords: Rhinocerotidae; Perissodactyla; diversity; body size; weight; gracility; palaeoenvironment

1. Introduction

During the Cenozoic, the Family Rhinocerotidae was widely spread throughout North America, Asia, Europe, and Africa. Their absence in South America seems to be due to the extinction of rhinocerotids in North America before the Panama land bridge was established during the Pliocene, although a tooth fragment indicates that a relict form may have survived into Pliocene times in North America (Madden

and Dalquest, 1990). The hypothesis of an older age for the Great American faunal interchange defended by Campbell and Frailey (1995), based on the presence of mastodont remains in the Late Miocene of Acre (Brazil), is not accepted here since there is likely a mixture of faunas in the Acre Conglomerate (de Paula Couto, 1981, 1982; R. Pascual, pers. commun.). Besides their wide geographical distribution, rhinocerotids constitute a common element within Cenozoic faunas, being in many cases one of the predominant large herbivores in mammal communities. Fossil rhinos have been unequally treated in palaeontological studies. Since last century, several broad

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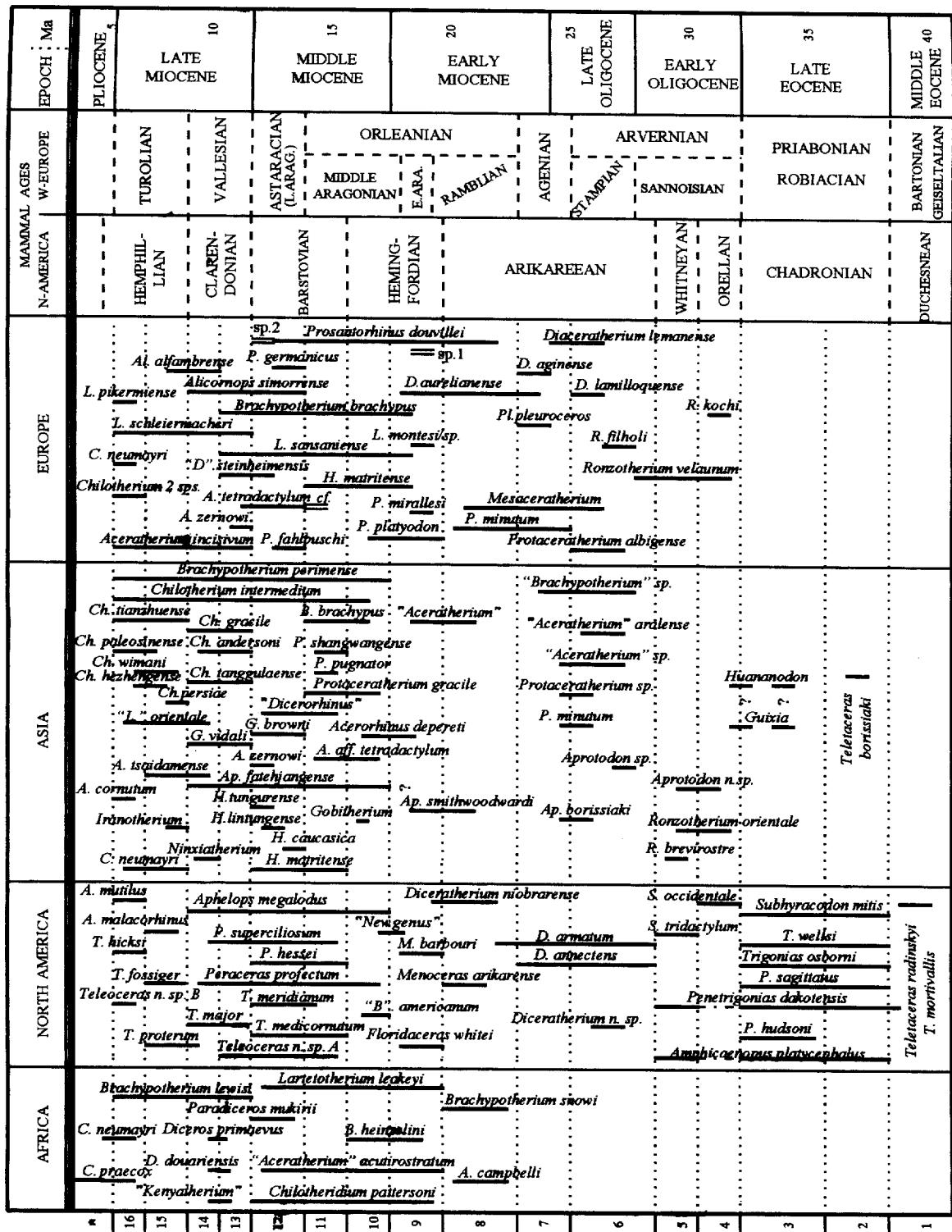


Fig. 1. Biostratigraphic and geographic distribution of the Family Rhinocerotidae. Numbers on the left refer to the conventional time intervals detailed in Fig. 2, but they do not reflect any general established biostratigraphic subdivision.

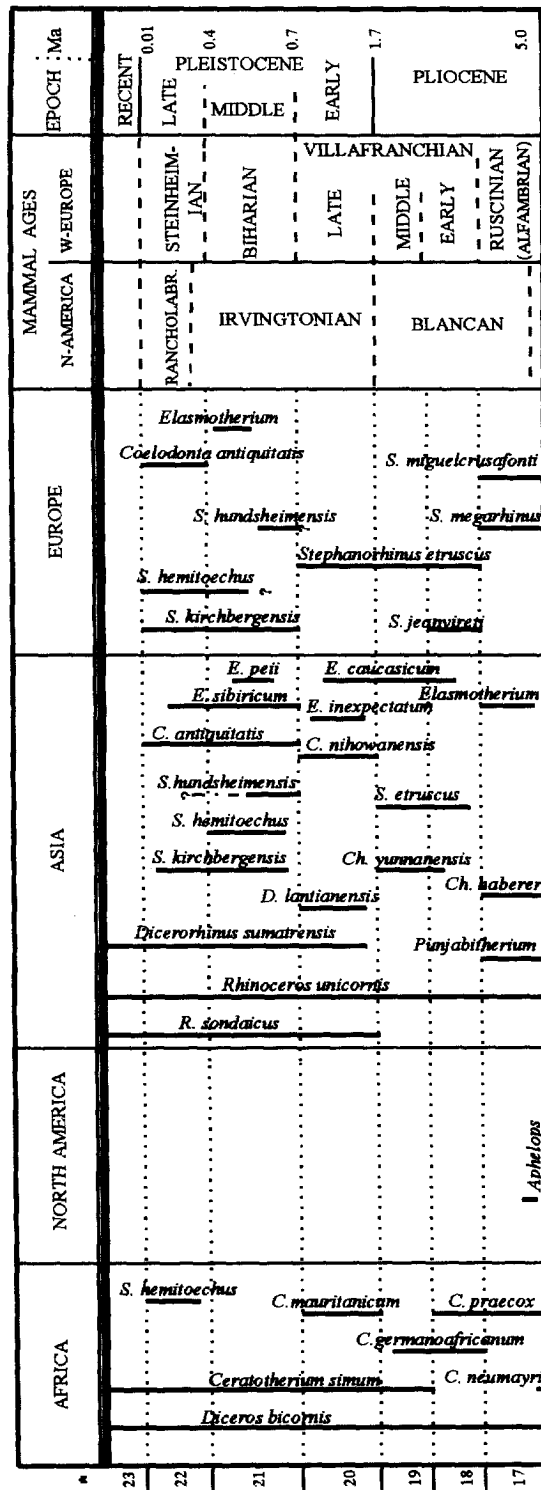


Fig. 1 (continued).

studies and numerous limited papers have been devoted to them (for a summary, see Cerdeño, 1989). During the last decades, a new set of works has provided a great amount of information on systematics, biostratigraphic and palaeoecological aspects of the Family Rhinocerotidae (Hooijer, 1966, 1969, 1976; Heissig, 1972, 1981, 1989; Guérin, 1980a, 1982, 1985, 1994a,b; Fortelius, 1982; Groves, 1983; Prothero et al., 1986, 1989; Fortelius and Heissig, 1989; Cerdeño, 1992, 1995; Fortelius et al., 1993; Cerdeño and Nieto, 1995; among others).

In this paper, a comparative study of the evolutionary trends of Rhinocerotidae, in four main geographical areas, is attempted.

2. Material and methods

Taxa have been considered in four broad geographical areas: Europe, Asia, North America, and Africa. European data are mainly based on data by the author and by Guérin (1980a). Systematics and biostratigraphic distribution of North American rhinos basically follow Prothero (1998). Other own data and many other bibliographic sources have been used for Asian and African taxa.

A total of 41 genera and 142 species, ranging from the Middle Eocene to recent, are included in the study (Fig. 1). The suprageneric classification of these taxa follows the results of the cladistic analysis of the Family Rhinocerotidae (Cerdeño, 1995). The arrangement of taxa in Fig. 1 is not an attempt to reflect phylogenetic lineages; successive species that are directly related are mentioned in the text.

Taxonomic revisions are needed for some taxa such as the Asian and African ‘*Aceratherium*’ or ‘*Dicerorhinus*’ (‘*Dicerorhinus*’ *leakeyi* Hooijer, 1966, is here considered as probable genus *Lartetotherium*), or the North American *Brachypotherium americanum*, which appears closer to *Teleoceras* than to *Brachypotherium* (Prothero, 1998; pers. opinion). After Prothero (1998), *Subhyracodon tridactylum* must be included in *Diceratherium* because of the insinuation of the paired nasal horns. However, after personally observing the former species, I think that the nasal rugosities are hardly developed compared to those of later *Diceratherium*, and I keep the species as *Subhyracodon tridactylum*

(Fig. 1). The Middle Miocene Asian ‘diceratheres’ have been demonstrated to correspond to the aceratherine genus *Acerorhinus* (Heissig, 1975; Qiu et al., 1988), quite different from the North American *Diceratherium*. With respect to the genus *Ronzotherium*, Heissig (1969) considered *Symphysorhachis* as a synonym, while Dashzeveg (1991) stated that the latter must be maintained with its type species *S. brevirostris* Beliajeva. I have followed Heissig’s opinion, since differences established by Dashzeveg (1991) could be considered of specific level. *Beliajevina caucasica* has been definitely considered as a species of *Hispanotherium* (Iñigo and Cerdeño, 1997). The Asian Eocene genera *Huananodon* and *Guixia* are doubtfully included within the Family Rhinocerotidae (Russell and Zhai, 1987), and many Asian taxa need a full revision. In some cases, such as the restriction of the genus *Dicerorhinus* to the present species *D. sumatrensis* or the genus *Stephanorhinus* to the species *S. hundsheimensis*, I have accepted the recent revisions, even when the conclusions are not shared by all the specialists.

Diversity, first records and extinctions are estimated for each geographical area (Figs. 2–4) along a temporal scale. The temporal intervals indicated in Fig. 1 by the numbers 1–23 do not correspond to any established general biozonation (which does not exist), but they combine the North American and European land mammal ages and their subdivisions (Figs. 1 and 2), roughly correlated, in order to obtain a greater detail in comparing different geographical areas. It must be said that the temporal ranges of certain species in Fig. 1 are not precisely delimited in the literature. In this case, for instance, when a species is ascribed to the Vallesian, without further precision, I have placed it in the middle of that age, trying not to favour arbitrarily any of its subdivisions.

Diversity is expressed by the number of taxa in each interval. First records are taxa that are not present in the previous interval; extinctions are evaluated as taxa that are not present in a certain interval but are in the preceding one.

Following Cerdeño and Nieto (1995), body size, weight and slenderness estimates are the characteristics considered to establish differences among rhinos related to environmental changes. Different data sources have often been used to get the mean values for each species. Geographical and temporal differ-

Genus distribution

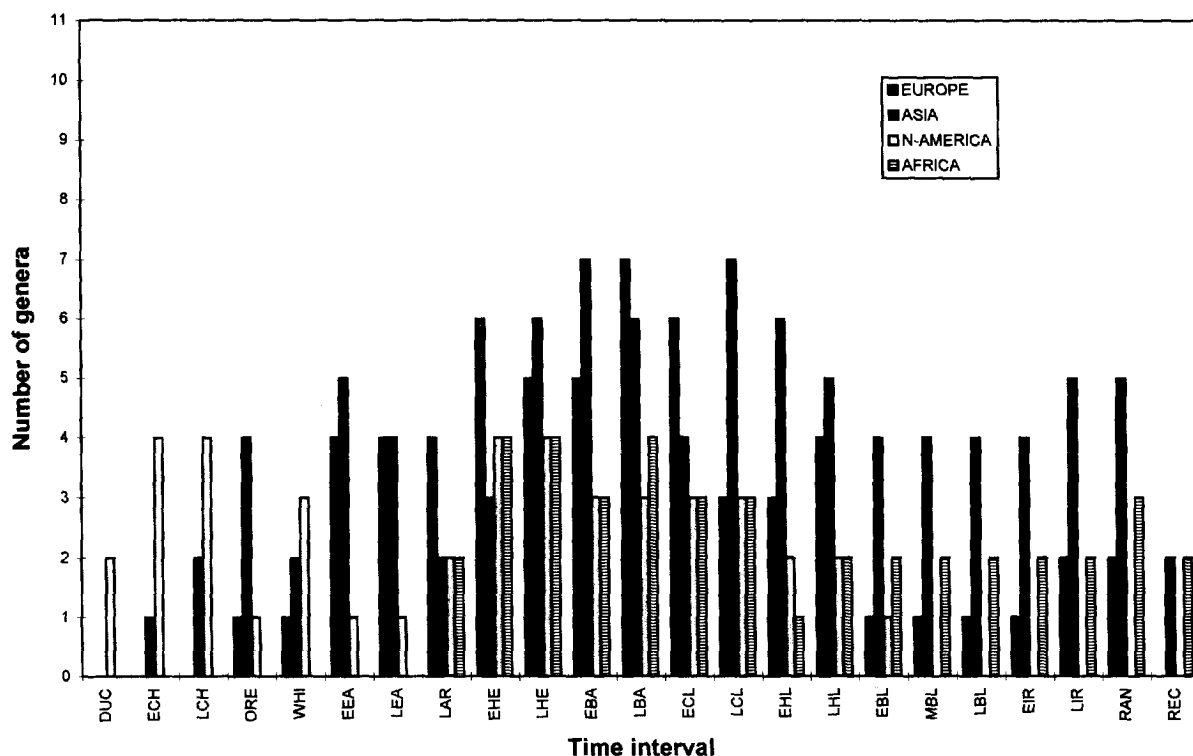


Fig. 2. Temporal distribution of the rhinocerotid genera in different geographic areas. Time intervals: 1, *DUC* = Duchensnean, Bartonian (Middle Eocene); 2, *ECH* = early Chadronian, early Priabonian (early Late Eocene); 3, *LCH* = middle-late Chadronian, late Priabonian (latest Eocene); 4, *ORE* = Orellan, early Sannoisian (earliest Oligocene); 5, *WHI* = Whitneyan, middle-late Sannoisian (middle-late Early Oligocene); 6, *EEA* = earliest Arikareean, Stampian (late Early Oligocene–early Late Oligocene); 7, *LEA* = late early Arikareean, Agenian (Late Oligocene–Early Miocene); 8, *LAR* = late Arikareean, Ramblian (Early Miocene); 9, *EHE* = early Hemingfordian, early Aragonian (late Early Miocene); 10, *LHE* = late Hemingfordian (early Middle Miocene); 11, *EBA* = early Barstovian, late middle Aragonian (Middle Miocene); 12, *LBA* = late Barstovian, late Aragonian (late Middle Miocene); 13, *ECL* = early Clarendonian, early Vallesian (early Late Miocene); 14, *LCL* = late Clarendonian, late Vallesian (early Late Miocene); 15, *EHL* = early Hemphillian, early-middle Turolian (latest Miocene); 16, *LHL* = late Hemphillian, late Turolian (latest Miocene); 17, *EBL* = early Blancan, Alfambrian (Early Pliocene); 18, *MBL* = middle Blancan, early Villafranchian (middle Pliocene); 19, *LBL* = late Blancan, middle Villafranchian (Late Pliocene); 20, *EIR* = early Irvingtonian, late Villafranchian (Early Pleistocene); 21, *LIR* = late Irvingtonian, Biharian (middle Pleistocene); 22, *RAN* = Rancholabrean, Steinheimian (Late Pleistocene); 23, *REC* = recent.

ences among populations of a same species have not been considered, except for *Protaceratherium minutum*; the younger Ramblian Spanish populations of this species are clearly larger than those from other Agenian European sites (author's data detailed in Cerdeño, 1989).

Size is the distance between the lips of the astragalus trochlea (DL). Body weight has been estimated from the M_1 area, following Legendre's (1986) for-

mula:

$$\ln X = a \ln Y + \ln b$$

where X is the weight, Y is the M_1 area, and a and $\ln b$ are constants established for perissodactyls as 1.564 and 3.267, respectively (Legendre, 1986; Alcalá, 1994). Slenderness has been measured for the McIII by means of the gracility index (Guérin, 1980a; Cerdeño, 1989): $100 \times \text{TD diaphysis} / L$ (TD,

Species distribution

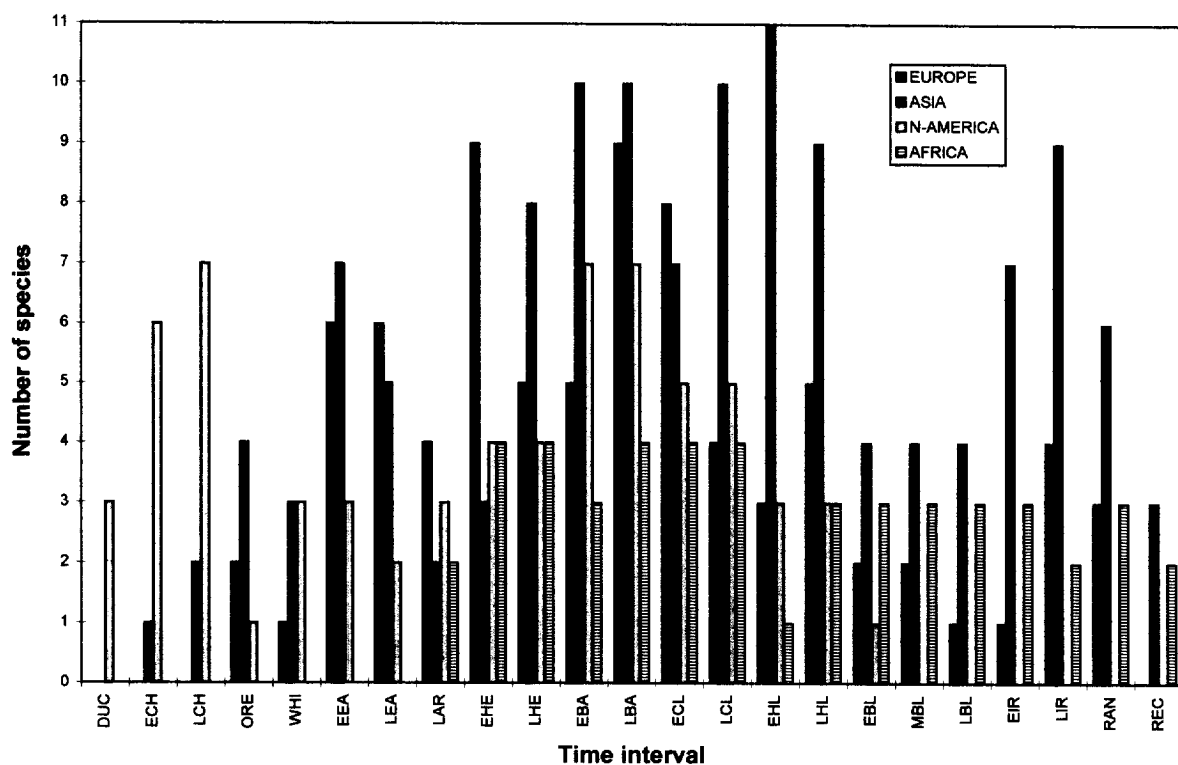


Fig. 3. Temporal distribution of the rhinocerotid species in different geographic areas. Legend as in Fig. 2.

transversal diameter; L, maximal length). I have only used the McIII since data on all metapodials are known to me only for certain taxa; in addition, Cerdeño and Nieto (1995, p. 332) observed that all these bones showed a same general trend.

3. Results

3.1. Diversity (Figs. 1–3)

The oldest known true rhinoceroses (Family Rhinocerotidae; genus *Teletaceras*) occur both in North America and Asia (Hanson, 1989). The North American remains of this genus are Duchesnean (Middle Eocene) in age, and Hanson (1989) proposed a similar age for the Asian species; however, Russell and Zhai (1987) established a Late Eocene age for the locality with *T. borissiaki*.

The Late Eocene (Chadronian) shows the first wide expansion of the family in North America, with seven species of four different genera (Figs. 1–3), most of which cannot be ranked at a subfamilial level (Cerdeño, 1995). In Asia, only two other genera assigned with doubt to the Rhinocerotidae have been recorded in the Late Eocene, *Huananodon* and *Guixia* (You, 1977; Russell and Zhai, 1987). Prothero (1994) considered that many Asian localities included in the Early and middle Oligocene probably correspond to Late Eocene and Early Oligocene, respectively, but this view is not shared by Wang (1992).

From Early Oligocene onward, both Europe and Asia show a relatively high diversity of genera and species, firstly represented by taxa of no clear subfamilial rank (Cerdeño, 1995) and soon by Aceratheriinae and Rhinocerotinae genera. If *Aprotodon* is considered to be a rhinocerotine (Cerdeño, 1995) then

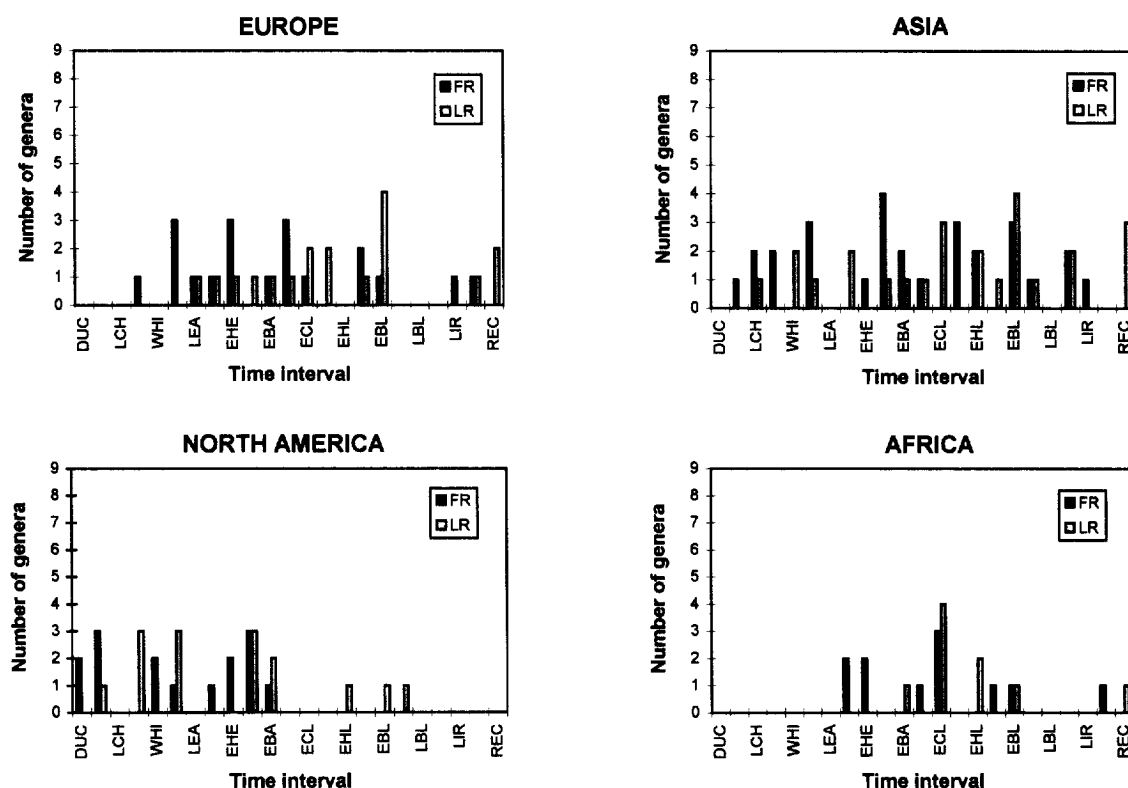


Fig. 4. First and last records of rhinocerotid genera in different geographic areas. Legend as in Fig. 2.

this subfamily appeared in Asia during the Early Oligocene (*Aprotodon* n. sp. Wang, 1992).

Maximal values of diversity are reached in these two areas, especially from late Early Miocene to Late Miocene (middle Orleanian–Aragonian–to Turolian). Since then, maximal diversity is maintained in Asia, with new peaks during the Pleistocene (Figs. 2 and 3). In North America, generic diversity is relatively low, while the number of species is relatively high throughout the Miocene. In Africa, the family does not appear until well into the Early Miocene, with representatives of both subfamilies Aceratheriinae and Rhinocerotinae (Fig. 1). The diversity of African genera and species is low (Figs. 2 and 3).

The strong diversity decline from the latest Miocene onward results from the nearly complete disappearance of the Aceratheriinae, except for the presence of *Chilotherium* in Asia throughout the Pliocene (Fig. 1). The first identification of *Brachypotherium lewisi* in the earliest Pliocene of Sahabi — Libya, Africa — is not confirmed in Bernor

et al. (1987), who identified *Diceros neumayri* in that locality (based on one tooth); the latest locality where *B. lewisi* is certainly present is Mpesida Beds, dated at about 7 Ma (Hooijer, 1963; Pickford and Morales, 1994). During the Pliocene (Blancan; Ruscinian and early-middle Villafranchian), the family became extinct in North America, and during the Late Pleistocene rhinos disappeared from Europe and wide Asian areas, remaining in southeast Asia and Africa until now (Figs. 1–3).

North American genera are different from the Eurasian forms, except the oldest *Teletaceras*, also present in Asia (Fig. 1). Instead, Europe and Asia share many genera and species from the Oligocene to the Pleistocene. These affinities may be greater since the Oligocene Asian ‘*Aceratherium*’ and ‘*Brachypotherium*’ may probably correspond to the European contemporary forms, *Diaceratherium*, *Mesaceratherium*, or *Protaceratherium*. For instance, ‘*Aceratherium*’ *aralense* (Borissiak, 1954) is similar to *Protaceratherium*, a genus which has been rec-

ognized in other Oligocene and Miocene Asian localities (described as genus *Plesiaceratherium* Young; Yan and Heissig, 1986), and is common in the Oligocene and Miocene of Europe (Arvernian to Astaracian). Similarly, some Miocene species from Africa belong to the same Eurasian genera (*Brachypotherium*, *Lartetotherium*, and '*Ac-ratherium*'). Also the Late Miocene *Ceratotherium neumayri* (usually described as *Diceros pachygnathus*) is present in North Africa as well as in some localities of southeastern Europe and western Asia.

3.2. First and last records (Figs. 4–5)

Figs. 4 and 5 present the number of appearances and extinctions of genera and species in each continent.

In Europe, there is a marked peak of first appearances at the end of the Early Miocene, during the early Aragonian (middle Orléanien), with three new genera and seven species. This is followed by an

episode of extinction (two genera and five species) during the middle Aragonian. Later, through Middle and Late Miocene, three genera and five species appear during the Astaracian, followed by the extinction of two genera and four species during the early Vallesian. A new peak of extinction corresponds to the beginning of the Pliocene (Ruscinian), when four genera and six species disappear. During the middle and late Villafranchian there is a period of minimal diversity (*S. etruscus* would be replaced by *S. hundsheimensis* at the end of the late Villafranchian; the latter species is present in localities considered as early-middle Pleistocene; Fortelius et al., 1993, p. 67). Later, four species are present during the Biharian (middle Pleistocene), one of them (*Elasmotherium*) only scarcely recorded in eastern Europe and doubtfully present in western Europe (Guérin, 1980a). *S. hundsheimensis* would not have been coeval with *S. hemitoechus* (Fig. 1), but Fortelius et al. (1993) cite both species at Mauer (just one specimen of the latter).

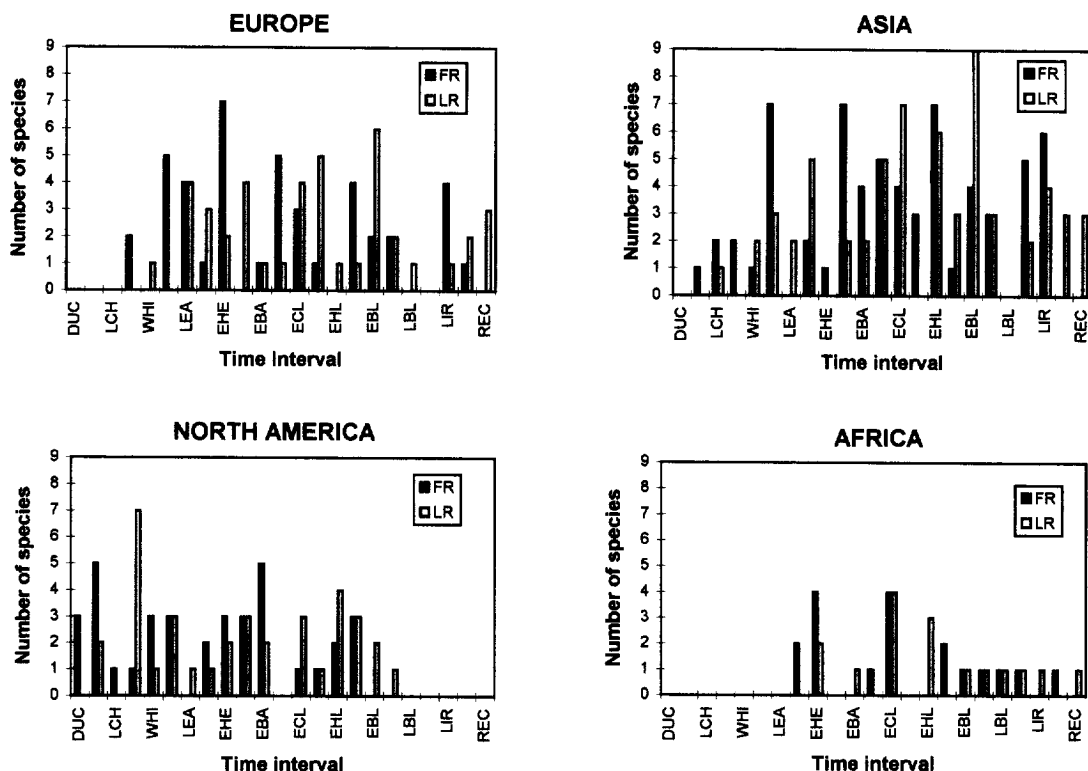


Fig. 5. First and last records of rhinocerotid species in different geographic areas.

In Asia, the rate of first and last records of genera is rather low, with several peaks of 3–4 new genera from the Late Oligocene to Early Pliocene (Fig. 4). Instead, species present high values of FR/LR during the Late Oligocene (late Arvernian; pending a revision of taxa), the Miocene (especially during the middle Aragonian, Astaracian, early Vallesian, and early Turolian; the Early Miocene is poorly recorded), the Early Pliocene (Ruscinian), and the early-middle Pleistocene (late Villafranchian and Biharian). Especially marked is the extinction event (four genera and nine species) during the Ruscinian (Figs. 4 and 5).

In North America, the early Chadronian (Late Eocene) shows the first peak of new records (three genera and five species). The Orellan (earliest Oligocene) is marked by a minimal diversity, implying the extinction of seven species (Fig. 5), although two of them are later recorded again during the Whitneyan (Fig. 1; Prothero, 1998, also considers the species *Subhyracodon kewi*, but he does not indicate its temporal range; after D. Prothero pers. commun., 1997, it is perhaps late Whitneyan, or early Arikareean according to other authors). The rate of turnover is low through the Arikareean and early Hemingfordian. During the late Hemingfordian (early Middle Miocene), three new genera replace those from the early Hemingfordian (Fig. 4), and later during the early Barstovian five new species appear (Fig. 5). From the late Barstovian (late Middle Miocene) to the late Hemphillian (latest Miocene) there is a low rate of replacement, with a final extinction event during the early Blancan (Early Pliocene).

Africa shows a low rate of first and last records, with a maximum of three new genera and four species during the early Late Miocene (early Vallesian) together with the extinction of the four precedent genera and species (Figs. 4 and 5), which implies a total replacement of taxa. One of these new Vallesian genera is *Brachypotherium* which was present before, during the Oleanian (early-Middle Miocene); this suggests a new immigration of this genus from Eurasia.

3.2.1. European taxa

In Europe *Ronzotherium* and *Mesaceratherium* are almost restricted to the Oligocene, although *M. gaimersheimensis* has been recorded in the Early

Miocene of Wintershof-West (Heissig, 1969; De Bruijn et al., 1992). Both genera are close to each other, and seem to be related to the North American *Trigonias* (Heissig, 1989; Cerdeño, 1995). *Ronzotherium* would be an immigrant from Asia, where it is also present during the Early Oligocene. Both appear in Europe after the 'Grande Coupure' (see Section 4).

A short appearance in the late Agenian (Late Oligocene–Early Miocene) corresponds to the rare *P. pleuroceros* (De Bonis, 1973), a form only partially known whose affinities are not clear (Cerdeño, 1995), although formerly related to the North American *Menoceras* (Prothero et al., 1986, 1989).

Two other Oligocene lineages continue into the Early Miocene (Ramblian and early Aragonian; Fig. 1), *Diaceratherium* (Brunet et al., 1987; Cerdeño, 1993), and *Protaceratherium* (Yan and Heissig, 1986; Cerdeño, 1989, 1995). The former is a teleoceratine closely related to the younger *Brachypotherium*, and its origin could be among the '*Brachypotherium*' from the Asian Oligocene. *Protaceratherium* evolves in Europe with three successive species until the middle Oleanian (early-middle Aragonian; a fourth species, *P. mirallesi*, is poorly known from the early Aragonian of Spain), and a fifth species is present in the Astaracian (Fig. 1). The phylogenetic relationships of *Protaceratherium* are not well defined, it may be close to some Oligo–Miocene North American genera (Prothero et al., 1986; Cerdeño, 1995).

Four other lineages appear through the Early Miocene (Ramblian and early Aragonian): *Prosantorhinus* and *Brachypotherium* as teleoceratine representatives (Cerdeño, 1993, 1996a), and the first European rhinocerotines *Lartetotherium* (Ginsburg, 1974; Cerdeño, 1986), and *Hispanotherium* (subtribe Iranotheriina sensu Cerdeño, 1995). The latter has a relatively short duration, and it is only known, in Europe, in the Iberian Peninsula and France, being a characteristic element in the middle Aragonian faunas of Spain and Portugal (Antunes and Ginsburg, 1983; Cerdeño, 1989, 1992; Iñigo and Cerdeño, 1997). *Hispanotherium* and other iranotheriines are better represented in the Miocene of Asia. The other three genera have instead a long duration. Probably originated in Europe and close to *Diaceratherium* and *Brachypotherium*, *Prosantorhinus* reaches the

late Astaracian with four species (two of them very poorly known); *Brachypotherium*, with *B. brachypus*, reaches the early Vallesian; and *Lartetotherium*, with four species, is present until the late Turolian.

During the Astaracian (late Aragonian), two aceratheres appear: *Alicornops* and *Acerorhinus* (= *Hoploaceratherium* in Cerdeño, 1996b), the latter related to the genus *Aceratherium* from the Late Miocene. *Alicornops* is also close to these genera, but ranked in the tribe Alicornopini (Cerdeño, 1995); it is well known by the species *A. simorreense* which evolves in western Europe to *A. alfambrense* from the late Vallesian and early Turolian (Cerdeño and Alcalá, 1989; Cerdeño, 1997).

Two other forms, *Chilotherium* and *Ceratotherium* (first considered as *Diceros*), of Asian and African origin, respectively, briefly appear in south-eastern Europe during the latest Turolian (Solounias, 1981; Geraads, 1988).

The Plio–Pleistocene in Europe is characterized by the genus *Stephanorhinus*, which coexists with *Coelodonta* during the Late Pleistocene (Guérin, 1980a). Both genera widely spread throughout Eurasia, but some species of *Stephanorhinus* are endemic in western Europe. The Asian *Elasmotherium* also appears in eastern Europe in the middle Pleistocene.

3.2.2. Asian taxa

Hanson (1989) recognized the presence of his new genus *Teletaceras* in Asia, with the species *T. borissiakii* Beliajeva from the Late Eocene of Artëm (Maritime Province, Russia). Two possible Rhinocerotidae genera are present in the Late Eocene–Early Oligocene (see comments above). Later, *Ronzotherium* is restricted to the Early Oligocene with two species, *R. orientale* and *R. brevirostre* (Heissig, 1969; Russell and Zhai, 1987). *Aprotodon* also appeared in the Early Oligocene, and evolved in Asia until the early Late Miocene with *A. fatehjangense* (Beliajeva, 1954; Heissig, 1972; Wang, 1992). Firstly considered as a teleoceratine, cladistic analysis of the family made it evident that the relationship of *Aprotodon* with the aceratheres is not well supported (Cerdeño, 1995).

Forms ascribed to the genera *Aceratherium* and *Brachypotherium* are present in the Late Oligocene (Fig. 1). *Protaceratherium* is also recorded in the Late Oligocene, represented by the species *P. min-*

utum (Russell and Zhai, 1987), better known in Europe. *Protaceratherium* is present again in the Middle Miocene of Asia with the species *P. gracile* (Young, 1937). This is closer to the European *P. fahlbuschi* than to the older European species of the genus (Yan and Heissig, 1986). *Protaceratherium* would have migrated several times between Asia and Europe: in Oligocene times probably from Asia to Europe; in the opposite way in the early Middle Miocene; and later again to Europe in the late Middle Miocene.

The Early Miocene record of Asian rhinos is not well established. Within the Dera Bugti fauna, Forster-Cooper (1934) recognized two species of 'Aceratherium' and *Chilotherium smith-woodwardi*, the latter later ascribed to the genus *Aprotodon* (Heissig, 1972). 'A. blanfordi' (Lydekker) was also cited in the Middle Miocene levels of the Siwaliks (Colbert, 1935; Heissig, 1972, partially synonymized to *Aprotodon fatehjangense*). Savage (1967) and Savage and Russell (1983) cited some species from Bugti that appear in the more recent levels of Chinji (Heissig, 1972). On the other hand, Sahni and Mitra (1980) state that *Rhinoceros sivalensis* is the only rhino in the Gaj Series (Early Miocene of Pakistan), but this species was defined in the Pliocene and mostly considered to be a synonym of *R. unicornis* (Heissig, 1972; Laurie et al., 1983; Groves, 1983).

During the Middle Miocene, three important lineages are established in Asia, *Chilotherium*, *Brachypotherium*, and *Hispanotherium*. The two first have a wide temporal distribution; the same species of each genus is present in the Siwaliks throughout the Middle and Late Miocene (Heissig, 1972) (Fig. 1). Many other *Chilotherium* species are present during the Late Miocene (Ringström, 1924; Tung et al., 1975; Qiu and Yan, 1982; Zheng, 1982; Li et al., 1984; Tsiskarishvili, 1987). Both are teleoceratine genera, *Chilotherium* appearing closer to the North American *Aphelops*, and *Brachypotherium* to the European *Diaceratherium* (Cerdeño, 1995).

The iranotheriine *Hispanotherium* has four Middle Miocene species, including the one present in Europe as well (Cerdeño, 1996b; Iñigo and Cerdeño, 1997). It is closely related to the Turolian (Late Miocene) *Iranotherium* and probably *Ninxiatherium* (there is further discussion on these genera in Cerdeño, 1995).

Gobitherium mongoliense is a rare species of the early Middle Miocene whose relationships are not well established (see discussion in Cerdeño, 1996b).

Acerorhinus, first considered as a subgenus of *Chilotherium* (Heissig, 1975), is well represented from the late Early Miocene to the Late Miocene of Asia with five species (Fig. 1). *A. zernowi* expanded to eastern Europe (Ukraine), and *A. tetradactylum* reached western Europe. The genus is closer to *Aceratherium* than to *Chilotherium* (Cerdeño, 1995, 1996b).

Gaindatherium has a middle-Late Miocene distribution with two successive species described in the Siwaliks (Heissig, 1972) (Fig. 1). It seems to be more closely related to the genus *Lartetotherium* than to *Rhinoceros* as previously thought (Cerdeño, 1995).

In the Turolian of western Asia, there is a short appearance of the African genus *Ceratotherium*, with *C. neumayri*. Tsiskarishvili (1987) stated the presence of *Diceros gabuniai* in the Vallesian of the Caucasus, related to '*Diceros*' *neumayri*. The generic ascription of that form must be reexamined.

The genus *Rhinoceros* and the related *Punjabitherium* (Kahn, 1971) extend back to the Early Pliocene, while *Dicerorhinus* appears at the beginning of the Pleistocene (*D. lantianensis*; Xu, 1989). *R. sivalensis* from the Early Pliocene has been considered as a subspecies of *R. unicornis* (Groves, 1983; Laurie et al., 1983), as well as the middle Pleistocene *R. kendengindicus* (Guérin, 1980b). Hussain et al. (1992; Fig. 5) identified *Rhinoceros* s.l. in the Late Pliocene of Pakistan. Some forms firstly ascribed to *Dicerorhinus* have been identified as *Stephanorhinus* ('*D.*' *choukoutienensis*, Xu, 1986; and probably '*D.*' *yunchuchenensis*, Chow, 1963).

Stephanorhinus etruscus, *S. hemitoechus*, *S. kirchbergensis*, and *Coelodonta antiquitatis* are present throughout Asia as well as Europe in Plio-Pleistocene times (Guérin, 1980a; Li et al., 1984; Xu, 1986; Qiu, 1990). *S. hundsheimensis* ('*D. etruscus brachycephalus*') seems to be present in the Caucasus in more recent times than in Europe (Guérin and Barychnikov, 1987). Chow (1978) established a second species of *Coelodonta*, *C. nihowanensis*, in the Early Pleistocene of China, although it is not mentioned by later authors such as Xu (1989).

Different species of *Elasmotherium* (including

those of '*Sinootherium*') were described from the Late Pliocene to Late Pleistocene. The systematics of the genus is not clear (Guérin, 1980a), and five species are here considered (Fig. 1): *E. lagrelii*, *E. caucasicum*, *E. sibiricum* (Ringström, 1924; Guérin, 1980a), *E. peii* and *E. inexpectatum* (Chow, 1979). Cladistic analysis (Cerdeño, 1995) showed the affinities of *Elasmotherium* and *Coelodonta* to be closer to one another than to the iranotheriines, which have classically been related to *Elasmotherium*.

3.2.3. North American taxa

Teletaceras radinskyi and *T. mortivallis* are the most primitive representatives of the Family Rhinocerotidae in the Middle Eocene, probably as immigrants from Asia (Hanson, 1989; Prothero, 1998). Slightly younger, at the end of the Duchesnean, Prothero (op. cit.) indicates the presence of *Penetrigonias*. This genus is represented by three species during the Chadronian (Late Eocene). Three other genera are also present throughout the Chadronian: *Trigonias* with *T. osborni* and *T. wellsi*, *Amphicaenopus platycephalus*, and *Subhyracodon mitis*. *A. platycephalus* and *Penetrigonias* are present in the Whitneyan, but they have not been recorded during the Orellan (Prothero, 1998). *A. platycephalus* is a large rhino which seems to be related to the rhinocerotines (Cerdeño, 1995).

Subhyracodon occidentale is the only species known in the Orellan (Early Oligocene), and it is followed by the Whitneyan *S. tridactylum* (see comment above about *S. kewi*). *Subhyracodon* gives rise to the genus *Diceratherium* which appears in the early Arikareean with three species (Fig. 1), *D. armatum* reaching the late Arikareean and being replaced by *D. niobrarense*. Then another genus appears, *Menoceras*, considered as a European immigrant with closer relationships with *Pleuroceros* and *Protaceratherium* (Prothero et al., 1986, 1989; Prothero, 1993; Cerdeño, 1995). *M. arikareense* is followed by *M. barbouri* in the early Hemingfordian (late Early Miocene) (Fig. 1).

Floridaceras whitei is the first North American acerathere in the early Hemingfordian, close to *Aceratherium* (Cerdeño, 1995). Other Aceratherinae are already present by the late Hemingfordian (early Middle Miocene), '*Brachypotherium*'-*Teleoceras*, *Peraceras* and *Aphelops*. *Peraceras* is present un-

til the late Clarendonian, while the other two remain until the end of the Miocene (late Hemphillian) when rhinos became extinct in North America (except for the Pliocene tooth fragment commented above). The genus *Peraceras* appears to be close to the European *Alicornops* (Cerdeño, 1995). *Teleoceras* is the most diversified of these genera with eight recognized species (Fig. 1; Prothero, 1998). This genus and *Aphelops* are close to *Chilotherium* and the other Eurasian teleoceratines (Cerdeño, 1995).

3.2.4. African taxa

The first African rhinoceroses belong to the genera *Brachypotherium* and '*Aceratherium*' (Hooijer, 1963; Hamilton, 1973) of Eurasian origin. The former is represented by three species throughout the Miocene, *B. snowi*, *B. heinzlini*, and *B. lewisi*, although it is not recorded during the Middle Miocene (Fig. 1), and this would imply a second immigration of the genus into Africa. '*Aceratherium*' begins with *A. campbelli* during the Early Miocene, followed by *A. acutirrostratum* during the Middle Miocene. At this time, two other forms are common: the acerathere *Chilotheridium pattersoni* (Hooijer, 1971) and the rhinocerotine *Lartetotherium leakeyi* (Hooijer, 1966), close to the European species of *Lartetotherium*. *Chilotheridium* was firstly related to *Chilotherium* and *Diceratherium*, but cladistic analysis placed it closer to *Alicornops* and *Peraceras* (Cerdeño, 1995).

The lineages leading to the present African forms are established through late Middle and Late Miocene (Fig. 1). *Paradiceros mukirii* is the Middle Miocene representative of the dicerotine group (subtribe Dicerotina), and *Diceros* and *Ceratotherium* appear during the Late Miocene, although *Diceros* has not been recorded during the latest Miocene (Fig. 1), since '*Diceros pachygnathus*' was recognized as *Ceratotherium neumayri* (Geraads, 1988). This supposes a gap in the temporal distribution of *Diceros*, present in the early Late Miocene, and perhaps a generic re-determination should be taken with caution. The early Late Miocene species *Diceros primaevus* was firstly ascribed to the genus *Dicerorhinus*, and later recognized as *Diceros* (Geraads, 1986). The living species *D. bicornis* is identified from Early Pliocene times and *C. simum* from Late Pliocene (Guérin, 1980a). *C. ger-*

manoaffricanum (early-middle Villafranchian) and *C. mauritanicum* (late Villafranchian), first considered as subspecies of *C. simum*, were recently ranked at specific level by Guérin (1994a,b).

A very partially known iranotheriine, *Kenyatherium*, is present in the early Late Miocene of Kenya (Aguirre and Guérin, 1974), and it is probably related to the Asian genus *Iranotherium* from Iran (Mecquenem, 1924).

The Eurasian species *Stephanorhinus hemitoechus* has also been recorded in North Africa in middle-late Pleistocene sites (Guérin, 1980b, 1985).

3.3. Body size and weight (Figs. 6–7)

Data show a parallel general tendency of increasing body size and weight through time (Figs. 6 and 7). This fact is better reflected for Europe and North America where data are more complete. In Asia, the lack of very small forms is due to missing data for some taxa (mainly for the DL astragalus). For instance, *Teletaceras borissiakii* was a very small rhinoceros, but no astragalus nor M₁ data are available to be included in the figures. European data of *P. minutum* have also been used for the Asian representatives. In Africa, body size and weight are rather large and homogeneous, in this case due to the absence of very small species in that area (*Paradiceros mukirii* was relatively small, but close to *L. leakeyi* — Hooijer, 1969, p. 83 — with an estimated weight of 1492.4 kg).

The teleoceratine taxa provide the maximal data in the four areas considered, only surpassed by *Elasmotherium* (few data available) in Europe and Asia.

In general, North American rhinos are smaller in size and weight than those from other continents (most values of DL between 30 and 50, and most weights below 2000 kg; Figs. 6 and 7). On the contrary, Africa shows a general large size with values of DL between 60 and 80, and weights between 1500 and 3000 kg, as well as a huge species. Europe and Asia have a wide range, with DL between 30 and 40 (missing data for some small species) and 80 (with a great number of species of medium-large size: DL between 45 and 75), and weight between 300 and 4000 kg or more.

Most species can be considered medium-large sized, with a body mass between 1000 and 3000 kg,

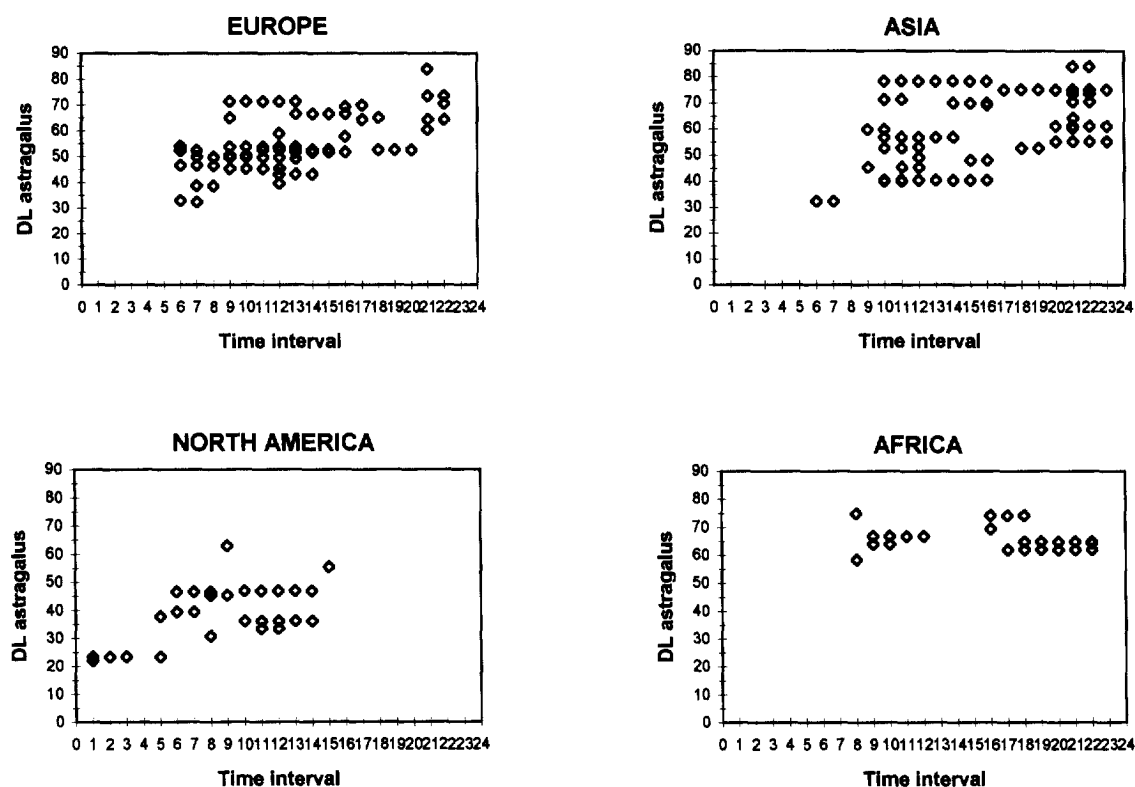


Fig. 6. Size distribution of the rhinocerotid species through time. Legend as in Fig. 2.

and only a few are really huge rhinoceroses such as the *Elasmotherium* species or the large African *Brachypotherium lewisi*; *E. sibiricum* with an estimated weight over 4000 and *E. caucasicum* and *B. lewisi* over 5000 kg (Fig. 7).

The tendency of increasing size (and weight) has been frequently observed within phylogenetic lineages, not only between different species of a genus, but between successive populations of a same species (i.e. *Protaceratherium*, *Diaceratherium*, *Alicornops*, *Hispanotherium*, *Diceratherium*, etc.).

Minimal values correspond to forms such as *Teleaceras*, *Penetrigonas*, *Subhyracodon occidentale*, *Menoceras*, *Protaceratherium albigenae*, *P. minutum*, 'A.' *aralense*, and *Prosantorhinus*, which are far below 1000 kg, most of them being primitive representatives of the Family, placed at the base of the cladogram (Cerdño, 1995), except *Prosantorhinus* which appears as a derived teleoceratine. More derived forms of the Family, both Aceratheriinae and Rhinocerotinae, are in general large sized and

heavy forms, and both have huge representatives among the last species of their own lineages (i.e. *Teleoceras fossiger*, *Brachypotherium lewisi*, *Elasmotherium caucasicum*).

3.4. Gracility (Fig. 8)

Available data on the gracility index of McIII are represented in Fig. 8, and show a general tendency of decreasing gracility through time. The highest gracility (lowest values) corresponds to older small forms. However, the early appearance of robust taxa such as the brachypotheres provides a wide range of values in Europe and Asia during the Oligocene and early-Middle Miocene (Fig. 8).

Except for some small brachypother species, most of the remaining forms show that gracility decreases with increasing size. However, there are large species which are relatively slender (e.g. *S. hemitoechus*, *L. schleiermacheri*) (Cerdño and Nieto, 1995), although the indexes are rather higher

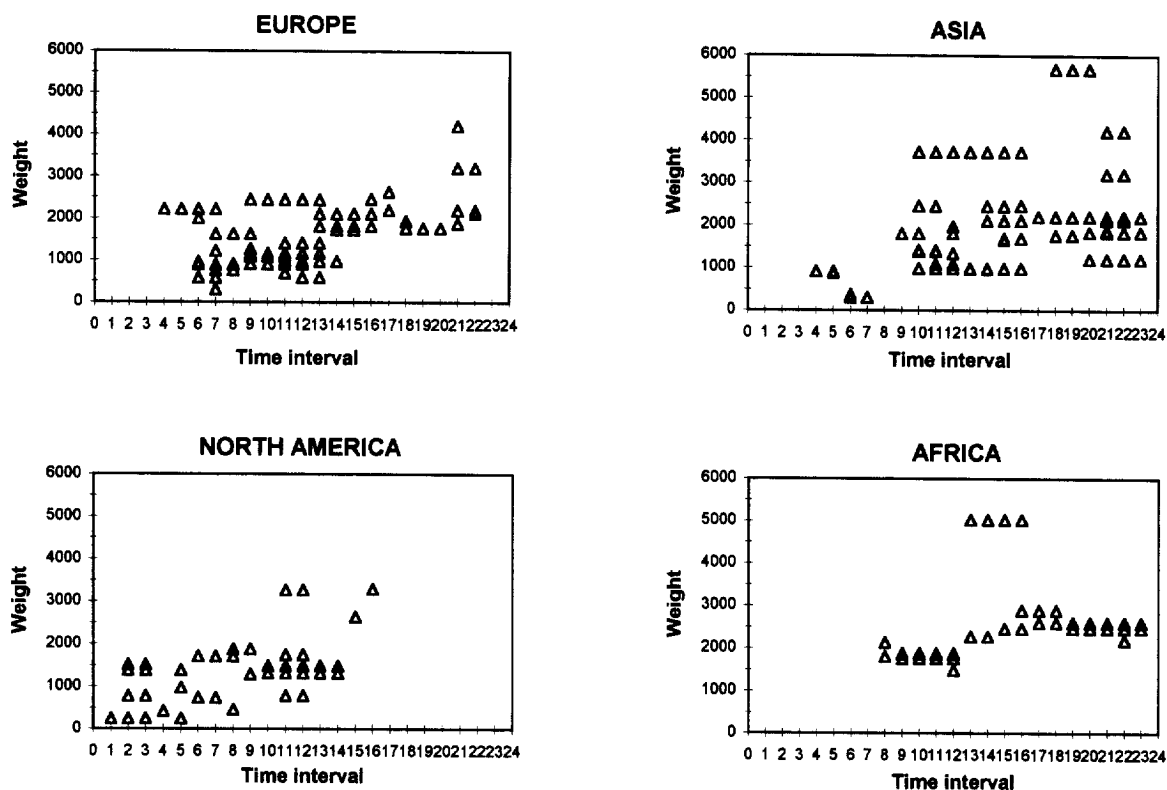


Fig. 7. Weight distribution of the rhinocerotid species through time. Legend as in Fig. 2.

than those of the small cursorial taxa such as *Protaceratherium* or *Hispanotherium*. The lowest gracility corresponds to the Teleoceratini, especially to the North American *Teleoceras fossiger* (43.6). A very robust teleoceratine species is the poorly known *Prosantorhinus* sp. 1 from the Early Miocene of Spain (Fig. 1), whose McIII is unknown, but the McIV has a very high gracility index of 41.4, accompanied by the small size of this rhinoceros (Cerdeño, 1989; Cerdeño and Nieto, 1995). Other small and robust species are among North American rhinos, considered as dwarf species (Prothero and Sereno, 1982).

In North America, slender forms disappear by the Middle Miocene, and are replaced by robust forms (since the late Hemingfordian, available data show index values between 30 and 45; Fig. 8). In other areas, the most brachypodial forms disappear during the Late Miocene, while the large species with an intermediate degree of gracility remain (Fig. 8; data of *B. lewisi* lacking in Africa). Very slender forms

are absent in Africa, in accordance with the absence of very small taxa.

As it was for the lesser size and weight, the highest gracility corresponds to the primitive taxa of the Family (*Protaceratherium*, *Ronzotherium*, *Diceratherium*, *Menoceras*; data for others are missing), with the exception of *Hispanotherium*, a derived iranotheriine (Cerdeño, 1995). Except this latter genus (and maybe other iranotheriines whose data are not available), the Rhinocerotinae are of intermediate gracility, even the largest forms. The Aceratheriinae includes a group of intermediate slenderness (more primitive aceratheriines and Alicornopini sensu Cerdeño, 1995) together with the most robust taxa represented by the derived teleoceratines.

3.5. Anatomical types and inferred behaviour

The analysed characters allow the recognition of three main anatomical types of rhinoceroses: (a) small and cursorial; (b) medium-large sized and

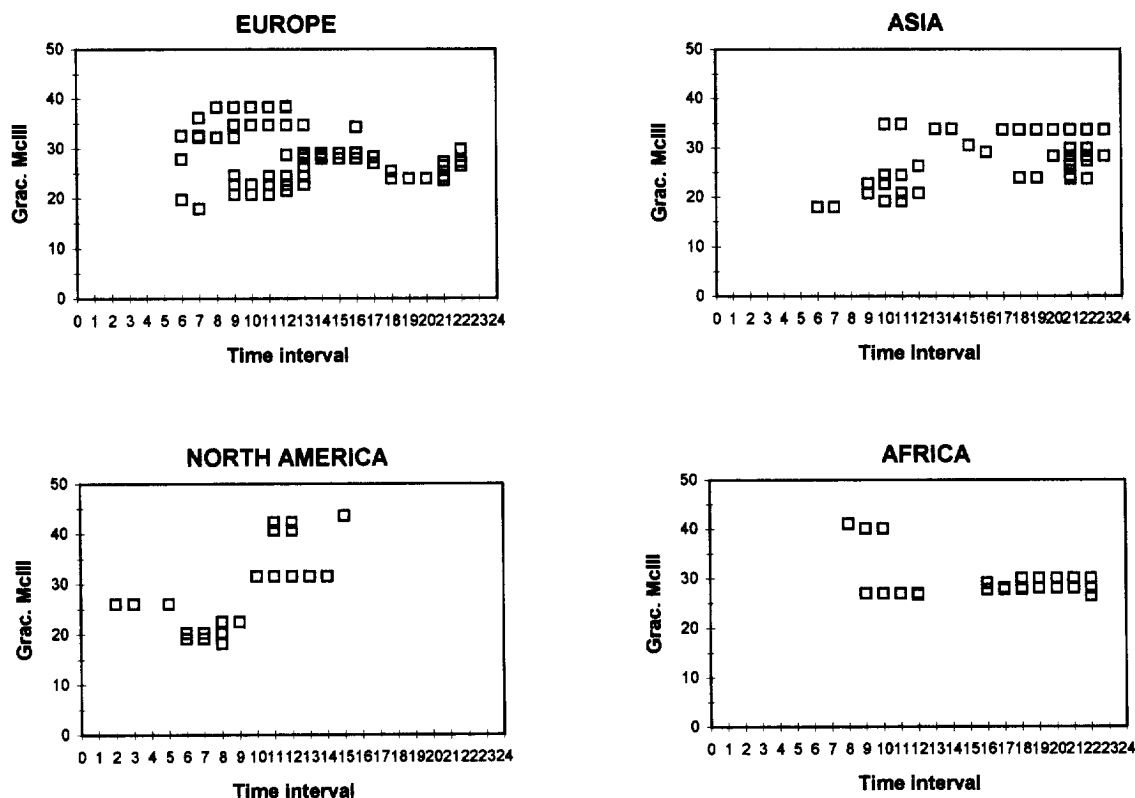


Fig. 8. Gracility distribution of the rhinocerotid species through time. Legend as in Fig. 2.

intermediate gracility; (c) strongly brachypodial, in general correlated with a large size.

For the small species which appear very abundant in certain deposits, a gregarious way of life has been proposed (Prothero, 1987; Cerdéño and Nieto, 1995). This behaviour would provide a way of defense against predators, compensating the small size and the lack of horns (or little developed). This can be applied to forms such as the European *Protaceratherium*, *Hispanotherium matritense*, and *Alicornops simorreense*, or the North American *Menoceras arikareense*, whose female individuals were hornless and males had small paired horns.

Herds of small and cursorial species, mainly browser, would move over large open areas in a temperate climate. For the species *Hispanotherium matritense* an open arid environment has been usually associated, due to its inferred grazer condition (subhypsodont teeth with much cement) and slender extremities. In central Spain, this agrees with the established climatic characteristics (dry and warm

maximum) when the species developed (Cerdéño, 1989; Cerdéño and Nieto, 1995). However, a certain climatic tolerance would be also supported by *H. matritense* since it appears in other areas together with other type of rhinos, and consequently the climatic local conditions are supposed to be less severe (Iñigo and Cerdéño, 1997). This latter is also true for the Asian populations of the species and other congeneric species, which may appear together with aceratheres and other rhinocerotines (Cerdéño, 1996b).

The increasing size in aceratheriines, and together with the development of large horns in rhinocerotines, would be accompanied by a change in behaviour. Rhinos would become a difficult prey for predators, and they probably constituted small groups of individuals as they do today.

The second type of rhinoceros would be mainly a browser with a rather wide range of habitat, from open woodland to grasslands. Differences in hypsodonty have been usually interpreted as a higher or lower degree of grass intake in the diet. For

instance, *Elasmotherium* or *Coelodonta*, very or rather hypsodont, would be grazer herbivores such as the present genus *Ceratotherium*, whereas *Aceratherium*, *Lartetotherium*, and many others would be preferably browsers, as is the present *Diceros*.

Among this anatomical type, differences in leg proportions are observed. So there are forms such as *Alicornops* (*A. simorreense* is relatively small) or *Peraceras* whose limb bones are shortened, but they are not massive as in the brachypotheres; their metapodials have robust epiphyses, but the diaphysis remains relatively narrow. This kind of foot would probably provide a wider supporting area that could be adapted to a softer soil than that of rhinos with straighter and longer metapodials. In a general way, this difference is seen between aceratheres, usually with the fifth metacarpal developed, and rhinocerotines. Among the latter, relatively slender and large forms are common. Eisenmann and Guérin (1984) found that some aceratheres and *L. schleiermacheri* have limb proportions similar to those of tapirs, and consider them as aquaphile forms.

The third type of rhinos have anatomical characteristics comparable to the present hippopotamus, with short and robust legs, with *Teleoceras* as ultimate representative. Swampy habitats or large waterways are associated with them, where they would develop a certain amphibious way of life, probably forming relatively large groups of individuals like extant hippos (Cerdéño and Nieto, 1995; Prothero, 1998). Some species of *Teleoceras* and *Brachypotherium* are rather hypsodont and they would be more grazers than their brachyodont relatives.

Large species are supposed to tolerate a wider range of environmental conditions and to seek out more favourable locations than small species (Brown and Maurer, 1986), and they would be better able to withstand a seasonal decrease in vegetational availability (Janis, 1989). The greater diversity of Miocene rhinos mainly include large forms (types b and c), although some lineages of small species can coexist with them in Eurasia (increasing their size through time). In this area, it is common to find three, even four, species of rhinos at the same site showing these anatomical differences, reflecting a variety of ecological niches in the same area.

Analysed data show that very small and cursorial rhinoceroses are present early in all continents,

except in Africa. Later the three anatomical types were coeval in the Miocene of Eurasia, while in North America the small and cursorial type disappeared during the Early Miocene, before large aceratheres were present. Later small North American species are dwarf forms of *Teleoceras* and *Peraceras* that would be related to a more wooded environment than their larger relatives (Prothero and Sereno, 1982; Prothero, 1987). Large and relatively slender forms, widely represented in other areas by the rhinocerotines, are not present in North America. The replacement of small forms by larger ones in North America can be related to the greater diversity of equids in this continent, whereas in Eurasia rhinos occupied more varied niches. In Africa, the lesser diversity of rhinos may be due to several factors such as the competition with other herbivores (equids, bovids), but also to the restricted immigration of Eurasian species because of geographical barriers. In a general way, the extinction of different groups from the Oligocene onward (hyracodonts and amynodonts among others) would leave available niches to be occupied by rhinos which consequently diversified.

The diversification of body size and the development of hypsodonty has been related to the development of new food resources, such as the expansion of the savanna–grasslands during the Miocene, particularly with reference to North American horses (Hermanson and MacFadden, 1992). However, recent studies have demonstrated that the savannas as they are defined today (tropical lowland ecosystem dominated by C₄ plants — grasses and sedges — with a clear seasonality of development related to water stress) did not fully develop until the Late Miocene or later (Cerling et al., 1991; Ehleringer et al., 1991; Cerling, 1992), which complicates the explanation of coevolution of hypsodont forms and savannas. Later, MacFadden and Cerling (1994) and Wang et al. (1994) analysed the isotopic composition of tooth enamel from Miocene to Pleistocene horses, and concluded that hypsodont Middle Miocene horses had a diet based on C₃ plants. Consequently, these authors defended a coevolution of hypsodont horses and grasslands dominantly composed of C₃ grasses until the Late Miocene, when a C₄ plant diet became common, associated with a decrease of horse diversity. The record of fossil grasses extends back to the Oligocene and probably to the Eocene, support-

ing the expansion of some kind of grasslands since then (Thomasson and Voorhies, 1990). Cerling et al. (1991) demonstrated the existence of C_4 grasses in Middle Miocene times that “may thus represent a brief, early stage of a succession toward a closed woodland or forest habitat following disturbance.” This could perhaps explain certain short appearances of hypsodont species, but not the generalized tendency. With respect to rhinos, most Miocene species are brachydont and would be browsers, but there are several taxa, such as *Hispanotherium*, *Chilotherium*, or *Teleoceras*, which show a clear tendency to hypsodontology, and a grazing feeding adaptation has usually been attributed to them. Among rhinos, full hypsodontology was only achieved by the Plio–Pleistocene *Elasmotherium*. Isotopic analyses on rhino tooth enamel, similar to those on equid teeth, would provide new data about the type of plants they fed on. The same as horses, hypsodont rhinos would be grazers feeding on C_3 grasslands (even under temperate and subtropical conditions) during early–Middle Miocene, changing to a C_4 -based diet by the Late Miocene–Early Pliocene; this change would coincide with the beginning of the decline of rhinos, as it happened with horses (Wang et al., 1994).

4. Palaeoenvironmental remarks

Changes in faunal composition have been assumed to be due to climatic variation (Vrba, 1985; Opydyke, 1995). Concerning rhinocerotids, Cerdéño and Nieto (1995) related the changes observed in the Spanish record with the variations of temperature and humidity established for the Neogene from other data.

Prothero (1994) indicated that in North America the Chadronian (Late Eocene) is characterized by a high rate of evolutionary turnover, with many new immigrants from Asia. Rhinos at that moment were diversified in North America, whereas they are very poorly recorded in Asia. The genus *Pentetrionias* was already present in the latest Middle Eocene, and evolved in North America through the Chadronian. At the end of the Eocene, a profound climatic change in the Northern Hemisphere has been established, marked by a cooling event, with broad changes in vegetation (Webb, 1989; Vianey-

Liaud, 1991; Prothero, 1994). Evanoff et al. (1994) established a change from a moist subtropical climate, with a predominant woodland habitat, in the latest Eocene of interior North America to a semi-arid warm temperate climate, with open woodlands, in the Early Oligocene. Similar conclusions are reached by Legendre and Hartenberger (1992) for the Eocene–Oligocene of Europe. Rhinos would be affected by this change during the Late Eocene, and their diversity greatly decreased from the Chadronian to the Orellan (earliest Oligocene) in North America (Figs. 1–3), although Prothero (1994) found little decrease in the general diversity between these two ages.

The faunal turnover of the Late Eocene–Early Oligocene is broadly known as the ‘Grande Coupure’, firstly applied to the European record. Global climatic changes would favour migrations, and rhinos would reach Europe from Asia at the beginning of the Oligocene. In Asia, the Eocene faunas have provided only a few rhinos (Russell and Zhai, 1987; Wang, 1992), and it is during the Oligocene when they become more abundant. The faunal turnover of the Eocene–Oligocene especially affected Perissodactyls in these areas. Previously, the group was especially well represented in Asia by hyracodonts and amynodonts, and in Europe by the paleotheres. Since then, rhinos began to greatly diversify. The terminal Eocene event in Asia was not, however, so abrupt as in Europe and North America considering the whole mammalian fauna (Wang, 1992). In Africa, where rhinos are not present at this time, the Eocene–Oligocene transition is not marked by dramatic extinction events or faunal turnovers, and the climate remained relatively stable across that boundary (Rasmussen et al., 1992).

Prothero (1994) compiled evidence that points to another cooling event in the mid-Oligocene together with a major regression of the sea level, but this event was not accompanied by very significant extinctions. Rhinos in North America are represented at that time by the small-medium, cursorial *Diceratherium*, descendant of the Early Oligocene *Subhyracodon*. Europe and Asia also maintain a certain continuity between Early and Late Oligocene genera, sharing several taxa of both types of small and cursorial and larger and brachypodial forms. Diversity is not very high, however, especially con-

sidering that Asian Oligocene rhinos need a detailed taxonomic revision. Wang (1992) signalled an extinction event in the Asian mammal faunas between the Early and mid-Oligocene, which would really correspond to the Early–Late Oligocene boundary. This event is mainly marked by the extinction of archaic mammals. Wang (1992) defended the existence of faunal exchanges between Asia and North America throughout the Oligocene, but with respect to rhinoceroses North America shows a local evolution of the group at that time, without immigrant taxa.

A general increase of temperature seems to have occurred during the Early Miocene, reaching a maximum at the end of this epoch (Janis, 1989). A general increase of rhinocerotid diversity (taxonomic as well as anatomical) happened at the late Early Miocene in all areas considered. Migration waves from Asia occurred through the Early Miocene in different ways. Rhinos reached Africa for the first time, and new taxa appeared in Europe. There was an expansion of aceratheres, and rhinocerotines also reached Europe and Africa during the late Early Miocene. In North America *Menoceras* appeared in the Early Miocene, followed by other immigrants during the late Early Miocene.

Through the Early and Middle Miocene open grasslands developed throughout the world, although they were not strictly equivalent to present grasslands–savannas (see comments above). By the early Middle Miocene, diversity of rhinos increased in Asia, whereas it slightly decreased in Europe, where dry and warm conditions have been established in some areas (Calvo et al., 1993). For Janis (1989, p. 466) “... it appears that Asian faunas were more protected from climatic change than the European forms, regardless of absolute latitude, possibly because of their more continental setting”. In Africa, the rhinoceros diversity hardly changed until the Late Miocene. In North America, the turnover between Early and Middle Miocene (early-late Hemphillian) also implies the extinction of the cursorial anatomical type and the appearance of the brachypodial one (Teleoceratini and Alicornopini sensu Cerdéño, 1995). As stated above, this lesser diversity of rhinos seems to be compensated by the greater diversity of equids with respect to the other areas, where equids are very abundant but less diverse.

As a whole, the Family Rhinocerotidae reaches its maximal diversity through Middle Miocene and earliest Late Miocene.

According to Janis (1989), a temperature drop occurred at the start of the Late Miocene, with an expansion of open and arid habitats, although Webb (1989) indicated a persistence of an optimum savanna mosaic in the Clarendonian (early Late Miocene). In Spain, maxima of warm and wet conditions were established for the Vallesian, but during the Turolian aridity increased (Calvo et al., 1993; Cerdéño and Nieto, 1995). This trend of cooling and drying culminated at the end of the Miocene with a global change, known as the Messinian salinity crisis (Gautier et al., 1994) which caused the desiccation of the Mediterranean, and the establishment of broad land connections between Eurasia and Africa.

Concerning rhinos, the beginning of the Late Miocene in Africa included replacement of the four Middle Miocene taxa by four new taxa, two of which are immigrants from Eurasia, and two of autochthonous origin (*Diceros* species, close to *Paradiceros*). In North America most species continued into the Late Miocene, and diversity slightly decreased. In Europe there was a greater decrease, with several lineages going into the Late Miocene and two new immigrants. A similar trend is shown in Asia, with some new taxa of autochthonous origin.

A greater change is reflected by rhinoceroses in all areas in the middle of the Late Miocene (Vallesian–Turolian and Clarendonian–Hemphillian boundaries), not only by a replacement of taxa, but also by a decrease of diversity. The spread of increasingly open and drier habitats during the Late Miocene is accompanied by faunal turnovers in all continents, and particularly a clear decline of the ungulate fauna is established (Janis, 1989; Webb, 1989; Flynn et al., 1991; Prothero, 1993; Opdyke, 1995), here corroborated by the rhinoceroses. At the same time, the climatic conditions would have favoured the dispersal of equids, which reached a high diversity (Webb, 1989; Janis, 1989; Cerdéño and Nieto, 1995). During the latest Miocene (late Turolian; late Hemphillian) the diversity of rhinos is rather low. Some species from Africa or Asia shortly appeared in southern Europe at that time, their migration favoured by the established land connections across the Mediterranean. Finally, rhinos

disappeared from North America, and so did the aceratheres from all areas, except Pliocene Asian species of *Chilotherium*.

Just before the Pliocene–Pleistocene boundary, isotopic evidences reflect a glacial retreat and a rise of the sea level, initiating the refilling of the Mediterranean (Opdyke, 1995). In general terms, the Pliocene and Pleistocene were characterized by a progressive deterioration of the climate, with increasing cooling and drying in higher latitudes (Janis, 1989), although a relatively warm period has been established in the middle Pliocene, about 4–3.4 Ma, followed by a steady cooling trend (Opdyke, 1995). Rhinos had already disappeared from North America by these times, and their diversity was low in other areas, always greater in Asia. The woolly rhino, *Coelodonta antiquitatis*, better adapted to cold climates, was widely spread throughout Eurasia, associated with the relatively slender *Stephanorhinus* in many areas. The recent Asian genera were present in lower latitudes. In Africa, where glacial events were less severe than in Eurasia, only the two extant species survive from the Early Pliocene (except the sporadic appearance of *S. hemitoechus* in the north during the Late Pleistocene). In Europe and Asia, rhinoceros diversity increased during the middle Pleistocene. This can be related to a major dispersal event at the end of the Villafranchian (Early–middle Pleistocene boundary) coincident with the intensification of the Northern Hemispheric glaciation (Opdyke, 1995).

Late Pleistocene extinctions affected many faunal elements, especially large forms like rhinos and proboscideans in the Old World. Following some authors (see references in Janis, 1989), hindgut fermenters (e.g. perissodactyls) were more vulnerable, among ungulates, to climatic and vegetational variations at the end of the Pleistocene. Since then, rhinos survived only in Africa, south of the Sahara, and in southeastern Asia, where their distribution areas have been drastically reduced through the last two centuries, and the five extant species are now in danger of extinction.

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