

Changes in Western European Rhinocerotidae related to climatic variations

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Abstract

The good record of Spanish Neogene Rhinocerotidae is used as the base of the study of their evolutionary patterns and their correlation with climatic changes. The sample has a temporal range from Lower Miocene to Lower Pliocene. From a taxonomical point of view, 15 species (and three indeterminate forms) of five main groups of Rhinocerotidae have been considered. General diversity and first and last records of the species have been signaled for each stage or biozone. Other features here analyzed are relative body size and weight and the gracility index. Rhinocerotid diversity in Spain varies through the Miocene, with a maximum of seven species in the Lower Aragonian falling down to one during the Middle Aragonian. Afterwards three or four species are present until the Upper Turolian and Alfambrian when a new minimal representation is reached. A general trend to size increase is established with an interesting change in the minimal values of each biozone at MN9. This change is supposed to represent the end of the small rhinos that were dominant before. Gracility indexes show a similar trend for all metapodials. There is a slight tendency towards robustness related to size increase, but some changes in gracility within the same sizes are also observed. Turnovers in rhinocerotid associations are here related to changes in environmental conditions. Small and gregarious species disappear in Upper Vallesian, and only large, solitary and more scarce forms remain later on.

1. Introduction

The family Rhinocerotidae was widely spread through Neogene and Quaternary times. The systematics of the European rhinoceroses is fairly well known from Guérin (1980), Heissig (1989), Cerdeño (1989, 1992) but palaeoecological approaches are scarce.

The use of Ungulates is common in palaeoecological studies. These mammals are good indicators as they correlate directly with vegetation and thus with environment (Jarman, 1974; Janis, 1984). Vrba (1985) used the changes in species composition for inferring climatic changes. A number of studies of this kind are based on artiodactyls while rhinos have been rarely studied from this point of view (Cerdeño, 1989; Morales et al., 1993).

Based on the abundant Spanish fossil record we try to point out the close relationship between rhinoceroses and environment, and the effects of climatic variations on the characteristics of this family. Anatomical characters and relative abundance of different species are interpreted in a palaeoenvironmental context.

2. Material and method

This study is based on the Spanish Neogene rhinoceroses which range from Lower Miocene to Lower Pliocene. Villafranchian forms are not included as they are part of the Plio-Pleistocene faunal assemblages. Besides that, evolution and

ecology of this last European rhinos have been studied in more detail by several authors (Loose, 1975; Guérin, 1980, 1984; Fortelius, 1982, 1985, 1990).

The sample includes to the following species:

—Rhinocerotidae indet. I, from the Lower Miocene site of Cetina. One McIII comes from this site; it is distorted and no clear affinities can be established, although it could be close to *Pleuroceros pleuroceros* (Cerdeño, 1992).

—Rhinocerotidae indet. II: another indetermined rhinocerotid is included in Fig. 1 at Puente de Vallecas site; only some unclassifiable enamel fragments have been recovered, but are included in the list as this locality is the only macromammal-bearing site in the MN5 or E biozone.

—Subfamily Menoceratinae Prothero, Manning and Hanson, 1986

Protaceratherium minutum (Cuvier, 1822–1825)

Protaceratherium platyodon (Mermier, 1895)

Protaceratherium mirallesi (Crusafont and Villalta, 1955)

—Subfamily Aceratheriinae Dollo, 1985

Alicornops simorreense (Lartet, 1851)

Alicornops alfambrense Cerdeño and Alcalá, 1989

Hoploaceratherium tetradactylum (Lartet, 1837)

Aceratherium incisivum Kaup, 1832–1834

—Subfamily Rhinocerotinae Owen, 1845

Tribe Teleoceratini Hay, 1902

Diaceratherium aurelianense (Nouel, 1866)

Brachypotherium brachypus (Lartet, 1866)

Prosantorhinus sp.

Tribe Rhinocerotini Owen, 1845

Subtribe Elasmotheriina Bonaparte, 1845

Hispanotherium matritense (Prado, 1864)

Subtribe Dicerorhinina Ringström, 1924

Dicerorhinina indet. cf. *L. montesi*

Lartetotherium montesi (Santafé, Casanovas and Belinchón, 1987)

Lartetotherium sansaniense (Lartet, 1851)

Lartetotherium schleiermachi (Kaup, 1832–1834)

Stephanorhinus miquelcrusafonti (Guérin and Santafé, 1978)

Some comments on this classification are needed. The species *L. montesi* and *L. schleiermachi* have been always determined as genus *Dicerorhinus*. Several papers have made evident the necessity of separating the extant genus *Dicerorhinus* from the other Neogene and Quaternary species included in it (Groves, 1983). Cerdeño (1989, 1992) agrees with him in separating *D. schleiermachi* from *Dicerorhinus*, and states its affinities with *Lartetotherium*, as she does for *D. montesi*. For this reason, we prefer to use provisionally this generic ascription better than *Dicerorhinus* for these two Miocene species, trusting that future findings will provide new data to support this determination.

Concerning *P. platyodon* and *P. mirallesi*, we consider that *Plesiaceratherium* is synonymous of *Protaceratherium* (Cerdeño, 1992) and so we include these species in that latter genus.

The presence of a second rhinoceros species at Córcoles was stated by Alférez et al. (1982), and the species has been recently identified (C. Iñigo, pers. comm.), but this datum has not been published yet, so we have included it as Rhinocerotidae indet. in Fig. 1.

Suprageneric classification follows that of Prothero and Schoch (1989).

General diversity, new records and extinctions have been estimated from the distribution of the species through the Spanish Neogene as shown in Fig. 1. Diversity is expressed by number of species in each stage. New records are appearances of species that were not present in the preceding stage although they were in earlier stages. Extinctions are considered in the same way. In this sense, Vrba (1985) pointed out that changes in faunal composition at tribal level including migration, first and last records could be assumed as caused by climatic changes (Fig. 3).

We have also used characters related with envi-

Fig. 1. Chronostratigraphical distribution of the main Spanish Neogene localities with rhinocerotids. Temporal range of each stage is not proportionally done. ● = Mein (1975). ●● = Daams and Meulen (1984). 1 = Menoceratinae; 2 = Aceratheriinae; 3 = Teleoceratini; 4 = Elasmotheriini; 5 = Dicerorhini.

STAGE	●	●●	LOCALITY	1	2	3	4	Indet
ALFAMB.	15		LAYNA					o
	14		LA CALERA					o
TUROLIAN	13		VENTA DEL MORO LAS CASIONES EL ARQUILLO LA ALBERCA CENES VEGA EL FARGUE				ooooo	
	12		LOS MANSUETOS CONCLD CREVILLENTE 15		o		o	
	11		PTE. MINERO PIERA CREVILLENTE 2		o		oo	
VALLESIAN	10		CAN TRULLAS CAN GABARRO CAN BARBA CAN JOFRESA CAN PERELLADA MASIA DEL BARBO LA ROMA 2		oo		o	
	9	H I	CAN LLOBATERAS CAN PONSIC SUBS. SABADELL NOMBREVILLA CHLOECHES RELEA LOS VALLES FUENT.	oo	o		? o o o ?	
ARAGONIAN	7/8	G	HOSTALET'S P INF ANDURRIALES BRIHUEGA CERRO DEL OTERO CISTERNA IGA SALDAÑA COCA FUENSALDAÑA CAN ALMIRALL TORIL 3	oo	o		o o o o	
			MORALEJA ARROYO DEL VAL ARMANTES 3 MANCHONES PARACUELLOS 3	oooo		o	o	
	6	F	HENARES 1 PARACUELLOS 5		? cf			
	5	E	PTE. VALLECAS					o
	4	D	ACACIAS PTE. TOLEDO TORRALBA V MUNEBREGA TORRIJCS VALDEMOROS 1A TARAZONA RETAMA				oooooooo	
		B C	BUÑOL CORCOLES ARTESILLA CAN JULIA CAN MAS	o	o	cf	o ? cf	o
RAMBLIAN	3	A	MOLI CALOPA RUBIELOS DE MORA		o o			
		Z	LORANCA	o	cf			
	2	Y	VALQUEMADO CETINA	o				o

	TAJO	EBRO	DUERO	VALLES-PENEDES	DAROCA	TERUEL-CALATAYUD	LEVANTE
15	<i>S. miguelsrusafonti</i>						
14						<i>S. miguelsrusafonti</i>	
13						<i>L. schleiermacheri</i>	<i>L. schleiermacheri</i>
12						<i>L. schleiermacheri</i>	<i>L. schleiermacheri</i>
11				<i>A. incisivum</i> <i>L. schleiermacheri</i>			<i>L. schleiermacheri</i>
10				<i>A. incisivum</i> <i>A. simorreense</i> <i>L. schleiermacheri</i>		<i>A. incisivum</i> <i>A. alfambrense</i> <i>L. schleiermacheri</i>	
9	<i>A. simorreense</i>		<i>A. incisivum</i> <i>A. simorreense</i> <i>L. sansaniense</i>	<i>A. incisivum</i> <i>A. simorreense</i> <i>L. sansaniense</i>			
7/8	<i>L. sansaniense</i>		<i>H. tetradactylum</i> <i>A. simorreense</i> <i>L. sansaniense</i>		<i>A. simorreense</i>		
6	<i>H. tetradactylum</i> ? <i>A. simorreense</i> <i>L. sansaniense</i>				<i>B. brachypus</i> <i>A. simorreense</i>		
5	<i>H. tetradactylum</i> ?						
4b	<i>H. matritense</i>	<i>H. matritense</i>			<i>H. matritense</i>		
4a	<i>P. platyodon</i> <i>H. matritense</i>			<i>P. platyodon</i> <i>L. sansaniense</i> ? <i>P. mirallesi</i>	<i>B. brachypus</i> <i>Prosantorhinus</i> sp. INDET III	<i>D. aurelianense</i>	<i>P. platyodon</i> <i>L. montesi</i> <i>Prosantorhinus</i> sp.
3				<i>D. aurelianense</i>			
2	<i>P. minutum</i> INDET. II						
		INDET. I					

Fig. 2. Geographical distribution of the Spanish Neogene rhinocerotids in different basins.

ronment such as body size and weight and slenderness after data mostly from Cerdeño (1989) and from Santafé (1978) for localities of the Vallés-Penedés basin.

Body weight has been estimated from the M_1 area following Legendre's (1986) formula: $\ln X = \ln Y \times 1.564 + 3.267$, where X = weight, Y = M_1 area.

Skeletal elements we analyzed are the astragalus and metapodials, as they reflect better than other skeletal parts different adaptive trends, as is generally known for the distal segments of the extremities; at the same time, these bones are usually well preserved and provide a wide basis for comparison.

Although many authors have written about body size estimation there is no particular model for rhinoceroses (Damuth and McFadden, 1990).

In relation to perissodactyls, Alberdi et al. (in press) point out the relationship between thickness of distal bones and body size. We have chosen the transversal diameter of the astragalus trochlea (DL) which reflects its whole size and so indicates the relative size of the animal. Measurements in other bones gave the same results.

Gracility has been measured for all complete metapodials in order to evaluate the general pattern followed in rhinocerotid evolution. Gracility index (Guérin, 1980; Cerdeño, 1989) is: $100 \times TD \text{ diaphysis} / L$ (TD = transversal diameter; L = length).

Cranial material is too scarce to use it. Dental characters (hypsodonty, cement, enamel folding) have been frequently considered to deduce preferences in diet, but tooth variability due to different

kind of food is difficult and controversial to interpret (Fortelius, 1990); so we have only referred to dental features in a general way for certain species such *H. matritense*.

3. Results

3.1. Diversity, new and last records (Fig. 3).

There are strong changes in specific composition and diversity through the considered time span. This led Cerdeño (1992) to distinguish several phases according to rhinos which are here reviewed and slightly modified.

During the Lower Miocene (MN2-3; Y-Z-A) a low diversity is observed, with a clear predominance of *P. minutum* in the MN2 (Y-Z). This species disappears in the next stage (MN3) where only the brachypothere species, *D. aurelianense*, continues (Fig. 1).

The first and more spectacular turnover happens in the MN4a (C) biozone (Fig. 3) with the appearance of 6 new species and an increase of diversity from one species to 7 (with the arrival of *Hispanotherium* at the end of the stage). These species correspond to four groups: menaceratheres, brachypotheres, elasmotheres and dicerorhines, the latter two being new records. This supposes the highest diversity of the Spanish rhinocerotids, although no more than four species have been found at the same site (e.g. Buñol). The greatest specific variation is observed among basins (Fig. 2), which implies high environmental differences among geographic areas.

MN4b or D biozone: is characterized by a minimal diversity represented by the elasmotherine *Hispanotherium matritense*. This is a peculiar rhino which shows a quite interesting geographical distribution (Iberian Peninsula, France, Turkey and other Asian areas) which has suggested a trans-Mediterranean way of migration from the East

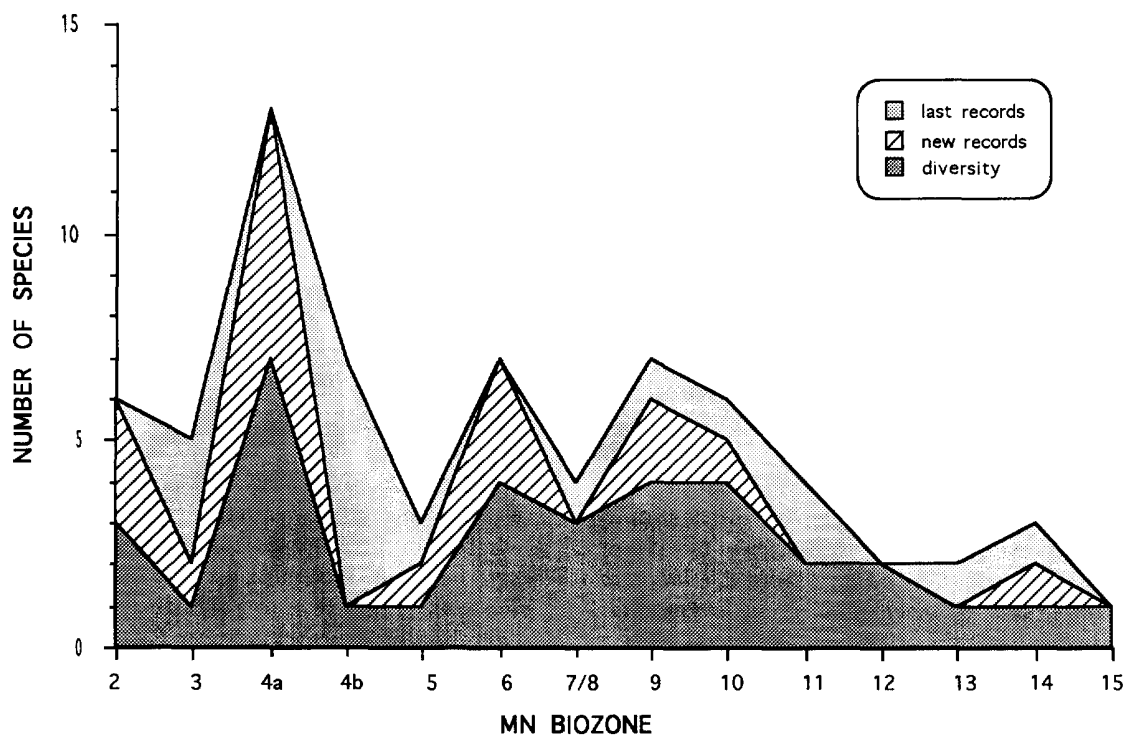


Fig. 3. Last records, new records and general diversity of the family Rhinocerotidae through Spanish Neogene. Temporal range following the Mein's (1975) biozones.

(Antunes, 1979); this seems possible since French remains appears to be more recent (MN5) than the Spanish ones (Ginsburg et al., 1987). While *Hispanotherium*-faunas develop in Spain with this unique rhinoceros, in Portugal (Tagus basin) this species appears together with other species much more scarcely represented, and different rhinocerotids are present in France.

MN5–MN9 biozones: The end of the Middle Aragonian (MN5 or E) and the beginning of the Upper Aragonian (part of MN6 or F) are poorly represented in Spain. This period is marked by the extinction of *H. matritense* and the appearance of an acerathere form, at least in the F zone (the rhinocerotid remains from the E biozone are indeterminate; Fig. 1). Later, in the MN6-7/8 or G biozones a new rapid diversification took place with four new species corresponding to three main groups: aceratheres, brachypotheres and dicero-rhines. At this time another species, the small acerathere *Alicornops simorreense*, becomes clearly predominant. This species is also present in many other European areas, but it is in Spain where it has the best representation, which has allowed establishing its evolutionary pattern through Upper Aragonian and Vallesian (Cerdeño, 1989). All these species appear as immigrants in Western Europe and phylogenetic connections with previous forms are not well established at all. For instance, *Lartetotherium sansaniense* could have some relationship with *L. montesi*, and *Brachypotherium brachypus* with older similar forms as that from La Artesilla (Fig. 1; Cerdeño, 1993). The presence of this brachypothere form is reported only at the MN6 biozone which is supposed to be the last record of the brachypothere group in Spain, while it survives in other Western European localities until Lower Vallesian.

Lower Vallesian (MN9): implies the continuity of the two most characteristic species of this phase, and the first record of the acerathere *Aceratherium incisivum*, and the dicerorhine *L. schleiermacheri*. The upper part of Lower Vallesian seems to be a period of transition as these two new appearances will be the characteristic rhinos in the next phase.

Upper Vallesian (MN10) to Middle Turolian (MN12): Besides *A. incisivum* and *L. schleiermacheri* *A. simorreense* still persists in the Upper

Vallesian of the Vallés-Penedés basin (Santafé and Casanovas, 1978), while in central basins *Alicornops alfambrense* appears as a final stage in the *A. simorreense* evolutionary line (Cerdeño and Alcalá, 1989).

General diversity in this phase decreases from the beginning (MN10), with four species, to the end (MN12), with only two.

Upper Turolian (MN13)–Alfambrian (MN14–15): This phase shows a new minimal diversity for no new appearances and the extinction of the last acerathere occur. In the Alfambrian stage, *L. schleiermacheri* disappears and a new immigrant of the same dicerorhine group, *Stephanorhinus miguelcrusafonti*, arrives.

3.2. Body size and weight (Figs. 4 and 5).

The results are interpreted at three different levels:

(a) General pattern: we can state a general trend of increasing size and weight, both estimates following the same pattern. Those differences between the two graphs of Figs. 4 and 5 are due to: sample or taphonomical bias—sites without teeth (Buñol, MN4a), lack of the analyzed elements for a species in a stage (neither astragalus nor M_1 of *L. schleiermacheri* have been recovered from the Lower Vallesian sites)—and the higher dispersion for tooth measures than for the astragalus ones.

Both graphs start with low values corresponding to *P. minutum* in the MN2 going on with *P. platyodon* in the MN4a. These small sized rhinos occur together with a large form of brachypothere.

Within the MN4a a strong increase of values and total range of size happens. They vary from the small size of *P. platyodon* and *H. matritense* to the large sized *L. montesi*.

In MN4b there is a clear decrease in size, which corresponds to the only species of this epoch *H. matritense*. From then to Vallesian stage there is a slight but progressive increase for the maximal values. In the lower Vallesian (MN9), as in the MN4a, the values reach a maximum range. In MN10 biozone the small rhinos have disappeared and the following stages show only large species. In the Upper Turolian all these great values corre-

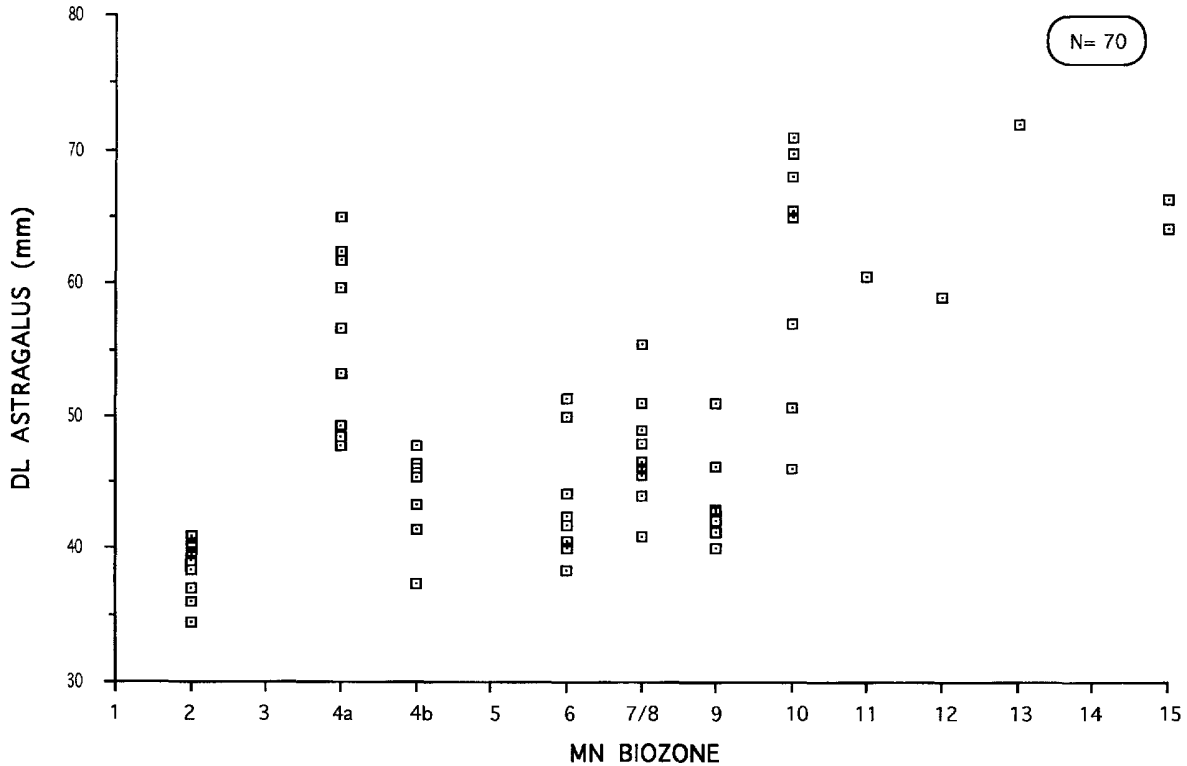


Fig. 4. Size distribution of the Spanish rhinoceros species through Neogene times.

spond to *L. schleiermacheri* (the Spanish remains of this species are specially large compared with other European remains; Cerdeño, 1992) while medium sizes are represented by *A. incisivum*.

The great variation observed between MN10 (for astragalus) or MN11 (for teeth) and MN13 is conditioned by the scarcity of the sample. However, the change is not so great if considering the mean values.

Finally the Lower Pliocene reflects a slight decrease in size which corresponds to the new species of the Alfambrian stage.

(b) Group level: menaceratheres are all small showing an increasing size trend. Aceratheres present small and medium sizes, beginning with low values and increasing with time. Brachypotheres are scarce but have the biggest sizes of the Aragonian rhinos with an increase within this stage. The only elasmothere form is small and does not show any clear tendency of increasing

size. Finally, dicerorhines firstly appear in the MN4a with medium and large sizes, later only a medium species continues, and from the MN9 onwards only large species are present.

(c) Species level: following comments deal with species with long record or special features.

Protaceratherium minutum is a small, cursorial rhinoceros closely related to *P. platyodon*, and in a lesser degree with *P. mirallesi*. These three species show a clear evolutionary pattern towards increasing size.

A. simorreense tends to increase its size giving place to a clearly larger final form, *A. alfambrense*. The lower values for the former happen within the MN7/8, but it must be noticed that the record from this biozone is broader than that from the MN6.

L. schleiermacheri shows a great variation that could be due to a high ingroup variation but the scarcity of rests does not allow reaching definitive conclusions.

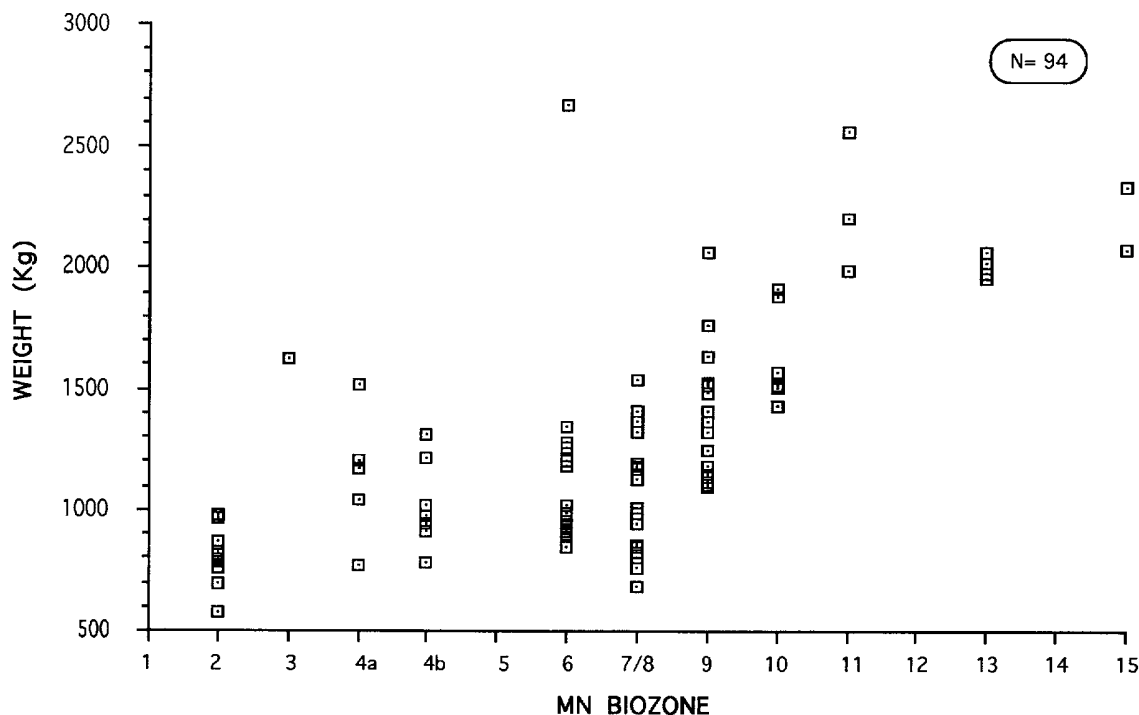


Fig. 5. Weight distribution of the Spanish rhinoceros species through Neogene times.

3.3. Gracility (Fig. 6)

With respect to the slenderness, Fig. 6 represents the values established for all metapodials (McII–McIV and MtII–MtIV). A global view shows the same general trend for all these bones. There is a first decrease of gracility, quite strong due to the great differences between *P. minutum* (very slender; MN2) and the brachypotheres *D. aurelianense* and *Prosantorhinus* (short limbs; MN3–4a). This maximum strongly decreases (increasing gracility) in the MN4b where only the slender *H. matritense* is present. It is followed by a progressive increase in robustness, reaching another maximum in Lower Vallesian (MN9). From then on a new increase in gracility occurs, and it goes into Upper Vallesian, Turolian and Alfambrian stages, and even it will continue in Pleistocene times.

The maximum value of the McIV is clearly detached from the others; it corresponds to *Prosantorhinus* from Buñol which catches the

attention among other species of the genus for its great robustness (Cerdeño, 1989).

Comparing with size evolution, it can be stated that, from Lower Miocene (Ramblian) to Middle Turolian, the larger the size the lesser the gracility. However, Upper Turolian and Alfambrian forms show a large size together with a relatively high slenderness.

4. Discussion and conclusion

The phases previously established with rhinos are compared with the two biozonations currently used for the continental mammal record (Mein, 1975; Daams and Meulen, 1984; De Bruijn et al., 1992).

P. minutum correlates well with the whole MN2 biozone, and covers the whole Y but only the lower part of Z zone; however, *P. minutum* is known in Portugal a little more recent as at the site of Horta das Tripas (Antunes and Ginsburg,

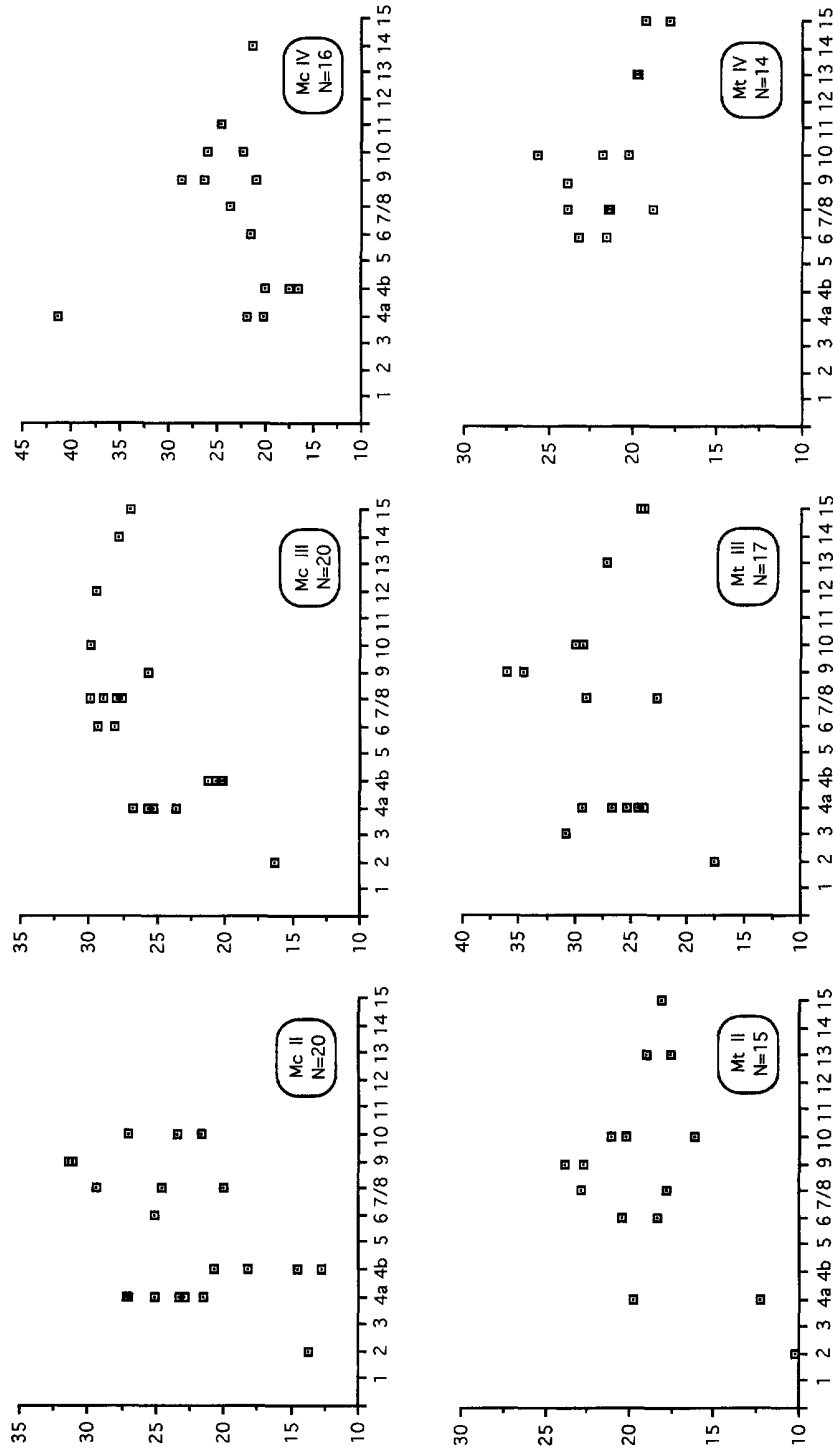


Fig. 6. General evolution of the gracility index in Spanish Neogene rhinocerotids. Temporal range in abscissas after Mein's (1975) biozones.

1983) which is placed at the base of MN3 or the upper part of the Z biozone (Fig. 7), so the Iberian *P. minutum* as a whole better correlates with Y-Z biozones.

In the Middle Aragonian, different rhino phases fit better with C–D zones than with MN4. The presence of *Hispanotherium matritense* as unique representative of the family characterizes the D zone and the upper MN4. The B zone in the lowest part of the Aragonian stage is poorly known from macromammals.

The Upper Aragonian includes two phases regarding rhinos, which correlates better with F–G than with 6–7/8 biozones, since the beginning of that stage shows a poor representation of *Hoploaceratherium tetradactylum* which corresponds to the F biozone (only a part of the MN6); later the G biozone is characterized by *Alicornops simorreense*.

In the Upper Miocene, rhino phases correspond quite well with MN zonation (notice that Daams and Meulen's zones only cover the lower half until the Lower Vallesian). The MN9 (Lower Vallesian) presents more diversity but *A. simorreense* continues as the most abundant species. The MN 10 (Upper Vallesian) marks a change in rhinos composition. *Aceratherium incisivum* becomes abundant, but mainly in the Vallés-Penedés basin. Differences between this one and other Spanish basins have been pointed out for several faunal groups through Neogene, as they belong to different biogeographical areas (Agustí et al., 1984).

Within Turolian stage, MN11 and MN12 show no differences as both are characterized by the coexistence of *A. incisivum* and *L. schleiermacheri*, the former being less frequent than the latter. We must keep in mind that both are less abundant than other older species, showing the general regression of the family. In fact, the Upper Turolian (MN13) witnessed the disappearance of that last aceratherid and the continuity of *L. schleiermacheri* as the only rhinocerotid form. This minimal diversity goes into the Alfambrian stage when another dicerorhine, *S. miguelcrusafonti*, appears.

As concerns paleoenvironmental inferences we have compared our results with the paleoclimatic curves established for the Spanish Neogene (López

et al., 1985; modified in Calvo et al., in press) (Fig. 7).

The first stage is wet and warm and becomes wetter and cooler at the upper part of the MN2. The small, cursorial and brachyodont *Protaceratherium minutum*, and the short-legged brachypothere *Diaceratherium aurelianense* are present; the latter is scarce and is assumed to be associated to swampy habitats. A woodland environment with abundant fluvial valleys probably was present. The extreme gracility of *P. minutum* points to a more open habitat.

Two successive drastic changes in humidity and an increase of temperature took place during the upper part of MN3 (A zone) and the MN4a. The resulting warm and moist climate supported the maximum diversity of rhinoceroses in the Spanish Neogene. The environmental changes would lead to a great diversity of ecological niches and to strong differences among basins. Seven species are present during this span of time, but no more than four have been recorded in one site and one basin, and only three are shared by several basins. There are three main types of rhinos following their paleoecological requirements: *Prosantorhinus* and *B. brachypus*, associated with swamps; menaceratheres and *Lartetotherium* with open woodlands; and finally *Hispanotherium matritense* with open and arid areas.

This last species appears at the end of this period, when the climate becomes drier and reaches a maximum of aridity (maximal dry and warm conditions) during the D biozone. *Hispanotherium matritense* is the only representative of the family Rhinocerotidae in Spain all along the MN4b or D. This species is a typical rhino characterized by very slender limbs and sub-hypsodont teeth with much cement; these dental features are linked to feeding on grasses, and its cursorial locomotion also points to an open habitat.

The unique coexistence of *H. matritense* with other rhinocerotid species at Córcoles (Alferez et al., 1982; Iñigo, pers. comm.) as well as at the Lisbon area in Portugal (Antunes and Ginsburg, 1983) can be related to less severe climatic conditions; as we can see in Fig. 1, Córcoles is placed at the end of the C zone when climate was not so dry. The high specialization on a grazing diet of

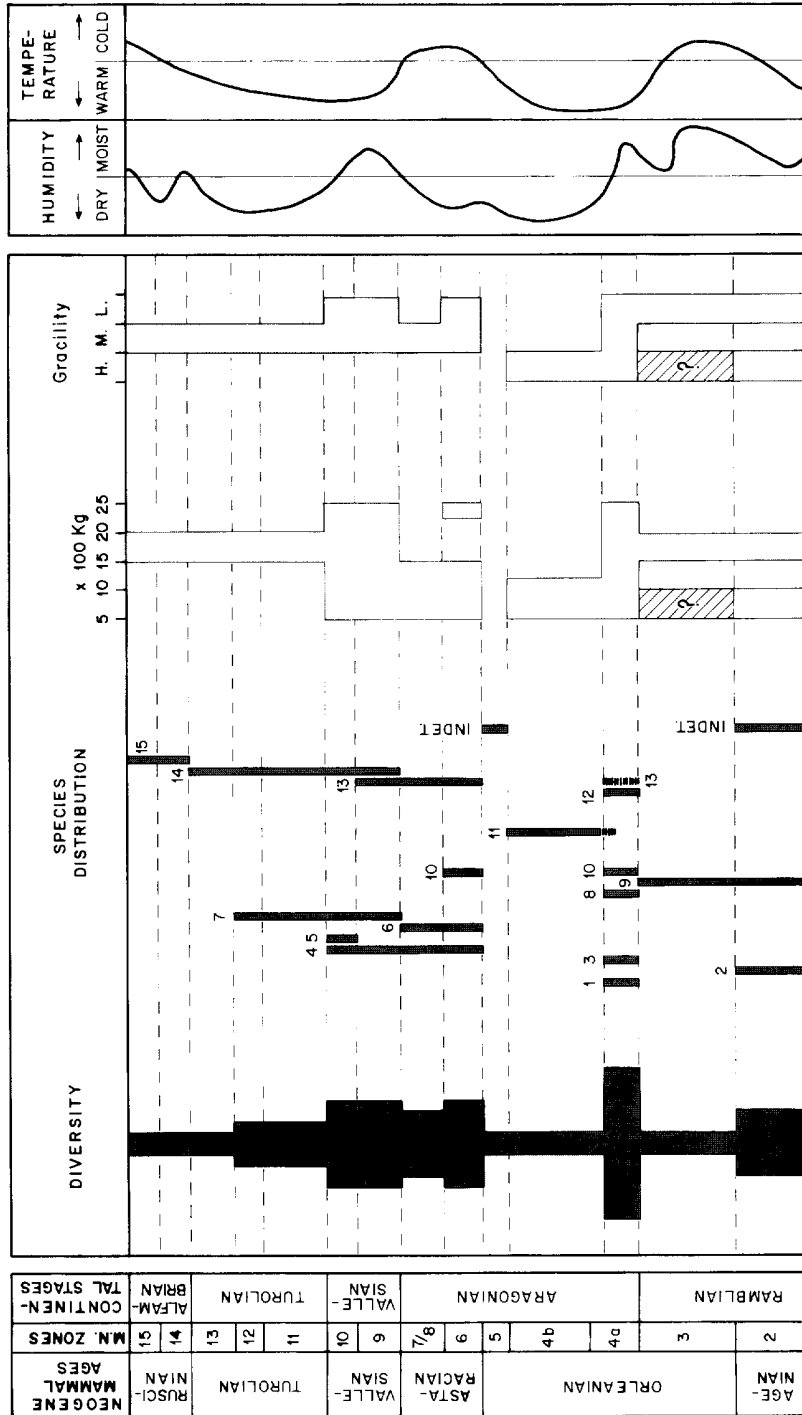


Fig. 7. Chronostratigraphic correlation between Spanish rhinocerotid distribution, diversity and morphological features and the paleoclimatic curves (Calvo et al., in press). The continuity between *P. minutum* and *P. platyodon* during MN 3 is supposed. Weights and gracility indexes not available in certain stages are estimated from the same species of other periods.

H. matritense probably caused its extinction with the cooling of the climate, which would imply certain modification of the vegetational cover.

The extinction of *H. matritense* at the late Middle Aragonian supposes the end of the small, slender and cursorial rhinos that dominated the first stages. Later on, the species are clearly more robust, and the relatively cursorial rhinos that appear later are larger and also much more scarce.

A short period which is poorly recorded (F zone; Fig. 1) precedes a cold but still dry epoch (MN6), which becomes wetter at the end of the Middle Miocene. During this phase *Alicornops simorrense* develops and becomes dominant. This rhinoceros is characterized by short and robust limbs, although they are not massive and would allow it a certain cursorial locomotion taking into account its small size (Fig. 4; MN6-7/8). All species present in this period are typically woodland dwellers and one of them, the hippopotamus-like *Brachypotherium brachypus*, associated to swamps. This fact and the abundance of *A. simorrense* would seem to contradict the dry and cold conditions reflected by the paleoclimatic curves; but can point to a coniferous woodland with

local humid places—i.e. river valleys—where *B. brachypus* could develop.

The Vallesian stage experienced a strong climatic change, as a maximum of warm and moist conditions is reached. During the Lower Vallesian *A. simorrense* is still the most abundant species, showing a slight increase in size with respect to the Aragonian populations (Cerdeño, 1992). This trend seems to be somewhat different in the Vallés-Penedés basin, where there is the only record of *A. simorrense* in the Spanish Upper Vallesian at Can Jofresa (Santafé and Casanovas, 1978). Meanwhile, in central basins, *A. simorrense* gives place to *A. alfambrense* as a final form of its evolutionary line, possibly influenced by that climatic change that would be less marked at the Vallés-Penedés and other European areas.

At the end of the Vallesian the climate becomes drier again, and the Turolian is also characterized by arid conditions (dry and warm). At this epoch rhinoceroses have already begun to decline; climatic conditions may have contribute to this decline at the same time as they would have favoured the dispersal of the equid *Hipparion*, which reaches its maximal diversity. After the

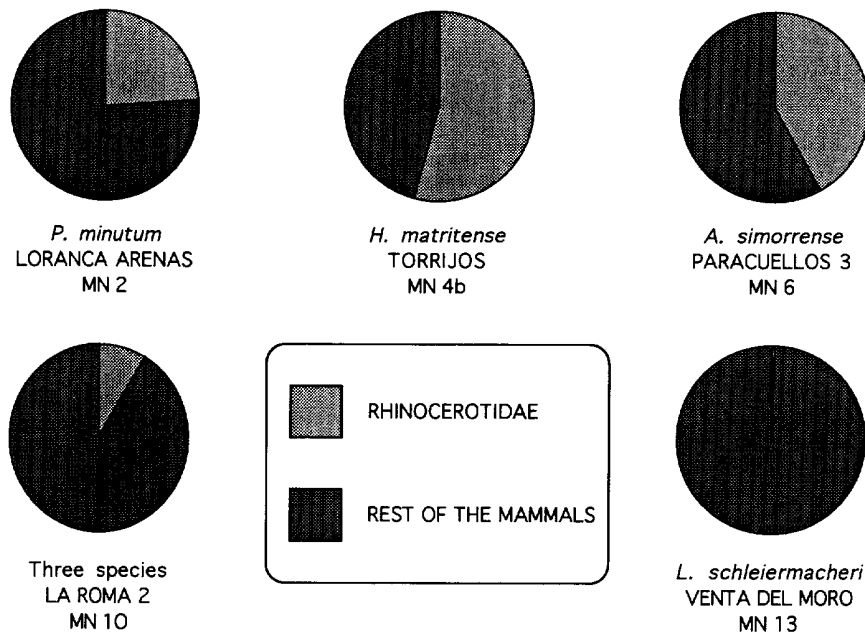


Fig. 8. Relative abundance of rhinocerotid species at different Spanish Neogene localities.

extinction of *A. simorrense* no other small, abundant rhino will be present in the Spanish record.

L. schleiermacheri is a relatively cursorial but large form with somewhat hypsodont teeth. It has been assigned to a forested habitat (Guérin, 1980) although its characteristics seem to point to a more open, savanna-like environment such is supposed for this stage.

Finally the passage Turolian–Alfambrian, when *L. schleiermacheri* is replaced by *S. miguelcrusafonti*, is characterized by an increase in humidity and a decrease of temperatures. The curve of humidity however changes rapidly again reaching a new peak of dryness followed by a progressive tendency to moister conditions until the Alfambrian–Villafranchian limit. The curve of temperature has progressively decreased until this same limit; so the end of Alfambrian stage is cold and relatively humid.

The rhinocerotid distribution commented before shows a quite interesting fact which reflects in a certain way the behaviour of these mammals. This fact refers to the great abundance of species such as *P. minutum*, *H. matritense* and *A. simorrens* (Fig. 8). All of them are small and it can be assumed that they had a gregarious behaviour. They would form large groups of individuals, as herds, which would roam over wide areas, without territoriality. This behaviour would provide a sort of defense against predators that would compensate their defenceless condition due to the small size and the lack of horns. General size increased with time (Fig. 7), and this fact is found together with a much lesser number of individuals of the species (Fig. 8). We interpret this as a general change of behaviour; rhinoceroses would form small groups of several individuals, as occurs in extant species, or even they would be solitary animals (males during non-reproductive season). Predation on this kind of rhinos would be difficult because of their size, and the large horns of some species would have a defensive role.

After the arrival of *Hipparion* only the second type of strategy occurs. This ubiquitous equid may have been better adapted to the new environmental conditions of the Vallesian–Turolian times, and took the gregarious role played earlier by rhinos, becoming the dominant form among Perisso-

dactyls, while rhinocerotids do not reach again their previous success.

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