SPANISH NEOGENE RHINOCEROSES

by ESPERANZA CERDEÑO

ABSTRACT. Nine genera and fourteen species are recognized among the rhinocerotid remains of the Spanish Miocene and Lower Pliocene. *Protaceratherium minutum* and *Prosantorhinus* sp. are reported in Spain for the first time, and the species *Alicornops alfambrense* has been published recently as a final form in the *A. simorrense* evolutionary lineage. The overall diversity of Rhinocerotidae in the Neogene record of Spain is generally much greater than that of the Equidae. Palaeoclimatic curves for the Spanish Neogene show how rhinoceros diversity depended on the relative humidity and the temperature.

THIS paper reviews the rhinocerotids of the Spanish Neogene, with data from the author's Ph.D. (Cerdeño 1989). Up to now, among Spanish Neogene rhinoceroses, only the fossil remains from the Vallés-Penedés basin had been studied in detail (Santafé 1978*a*), and they alone have mainly been used as a point of reference.

The fossil material of rhinoceroses comes from 45 Spanish sites, with more than 2000 identified bones, but including only a few cranial remains. These sites have a wide geographical and temporal distribution. They are located in several sedimentary basins: Ebro, Duero, Calatayud-Teruel, with two main areas (Daroca and Teruel), Tajo, and the Eastern and Betic basins. The chronological distribution of the localities ranges through the Miocene and Lower Pliocene (Ruscinian). As can be seen in Text-figure 1, the fossil record is continuous through that time, and only the base of the middle Aragonian is unknown, which is the case for all macromammal groups, not just rhinocerotids. The biozones I have used are those of Mein (1975) and Daams and Freudenthal (1981). Anatomical abbreviations are: I, incisor; Mc, metacarpal; P, premolar.

SYSTEMATIC PALAEONTOLOGY

Family RHINOCEROTIDAE Owen, 1845

Rhinocerotidae indet. I

The presence of a rhinocerotid in the Lower Miocene of Cetina de Aragón, Zaragoza, is documented only by a distorted McIII whose size and proportions are close to those of the McIII from Paulhiac and Laugnac, France, that Bonis (1973) identified as *Diceratherium pleuroceros*. This name corresponds to *Pleuroceros pleuroceros* as used by Antunes and Ginsburg (1983), Prothero *et al.* (1986) and Guérin (1989). At the moment, it is not possible to assert that the bone from Cetina corresponds to that species, and it is advisable to classify it as Rhinocerotidae indet. I.

Subfamily MENOCERATINAE Prothero, Manning and Hanson, 1986

Protaceratherium minutum (Cuvier, 1822–1825)

The genus *Protaceratherium* has recently been included in the tribe Menoceratini (Heissig 1989) within the subfamily Aceratheriinae, but Prothero and Schoch (1989) consider it as a member of the subfamily Menoceratinae. *Protaceratherium minutum* is the oldest rhinocerotid recorded in the Spanish Neogene. It is known from only two Lower Miocene sites of the Cuenca province, Valquemado and Loranca del Campo. The former corresponds to the MN 2*b* or Y zone in age and the latter to the MN 3*a* or Z (Ginsburg *et al.* 1987*b*). The species is very abundant, with more than 400 remains in Loranca. Among them, there is a cranial fragment

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TABLE 1. Biostratigraphical distribution of the European localities with *Protaceratherium minutum*, after Ginsburg *et al.* (1987), Antunes and Ginsburg (1983), Bonis (1973). 1, Mein (1975); 2, Daams and Meulen (1984).

(1)	(2)	Spain	France	Others
4*a*			Artenay	
3*b*	A			Lisboa I
			Beilleaux	Chitenay
3*a*				
	Z	Loranca		
2*b*			Laugnac	La Chaux
	Y	Valquemado	Selles/Cher	Ulm
2*a*			Moissac	Budenheim
1	X		Paulhiac	
			Pechbonieu	

which coincides basically with the cranium from Budenheim, Germany, figured by Roman (1924), our specimen being wider in the middle of the occipital face.

The small and slender *P. minutum* shows the upper premolars with a strong lingual cingulum, and there is a bridge of union between protoloph and metaloph whose development is variable. This variation can be observed in the sample from Loranca del Campo, as well as in the French remains from Selles-sur-Cher. Both cases also show the different development of the crochet and crista of the upper premolars. Lower teeth from Valquemado show labial and lingual cingula only on P_2, while at Loranca cingula are present on all the premolars and some molars. The differences among the teeth and the postcranial skeleton of the studied samples of *P. minutum* are mainly referred to size. This is greater in Loranca, where a slightly greater thickness can also be observed.

When the Spanish material is compared with the European data on *P. minutum*, the closest identity is found with the Selles-sur-Cher sample. The French molars are relatively smaller than the premolars and the same also occurs in the Beilleaux sample. The size of the Selles-sur-Cher specimens is closer to those from Valquemado than those from Loranca. This is expected since Selles-sur-Cher is supposed to be almost equivalent in age to the former and older than the latter (Table 1). The trend observed between the two Spanish sites (size increase and slenderness decrease through time) cannot be generalized because younger sites like Beilleaux, France, or Lisbon, Portugal, have smaller-sized specimens than Loranca. The maxillary fragment from Lisbon (Roman and Torres 1907) has been considered as a distinct species, *Protaceratherium tagicum*, because of its smaller size, shorter upper P^4, and the disappearance of the lingual cingulum at the protocone level (Antunes and Ginsburg 1983). As already stated (Cerdeño 1989), these characters show great variation in the different studied samples. So, the size of the Lisbon teeth exceeds those from Beilleaux. On the other hand, the real length of the P^4 cannot be measured because the specimen lacks the ectoloph. The discontinuity of the lingual cingulum at the protocone as well as at the hypocone level has been observed in several specimens from Loranca, Selles-sur-Cher, Beilleaux, and Faluns (Touraine, Anjou). This all suggests that the remains from Lisbon do not constitute a distinct species, at least with the present data, and so they are best included in *P. minutum*.

Concerning the postcranial skeleton, the similarity is retained between Valquemado and Selles-sur-Cher and there is also a clear resemblance with the German remains from Budenheim (Roman 1924), whose dimensions are also smaller than in Loranca.

In Western Europe, *Protaceratherium minutum* ranges from the earliest Lower Miocene (Pechbonieu and Cintegabelle, France; Antunes and Ginsburg 1983) to the early middle Aragonian (Artenay, France) (Table 1). Its best representation corresponds to the MN 2–3 or Y-Z-A biozones, with a variation in size that possibly reflects different habitats among the distinct areas where the species has been found.

Later in the middle Aragonian another genus, *Plesiaceratherium*, whose generic characteristics (Yan and Heissig 1986) are basically those of *Protaceratherium*, has been reported in Spain as well as in other Western European countries. I think both genera must be synonymous because it is just the larger size of *Plesiaceratherium* that marks the difference between them. So, *Protaceratherium* has priority over *Plesiaceratherium*. *Plesiaceratherium platyodon* has been found in several middle Aragonian sites of Western

Europe, such as the Spanish sites of Buñol, Valencia (Belinchón 1987), and Can Más, Barcelona (Santafé 1978*a*). It might be thought that this species is a descendant of *Protaceratherium minutum*.

Subfamily ACERATHERIINAE Dollo, 1885

Alicornops simorrense (Lartet, 1851)
Alicornops alfambrense Cerdeño and Alcalá, 1989

Yan and Heissig (1986) and, more recently, Guérin (1989) and Heissig (1989) have already considered the species *A. simorrense* as the genus *Alicornops*. The definition of this genus would correspond basically with the subgeneric diagnosis (Ginsburg and Guérin 1979) which has been partly reviewed (Cerdeño 1989). One of the characteristics established by Ginsburg and Guérin (1979), the lack of McV, can be clearly refuted by the existence of several well-developed McV in the Spanish sites of Toril-3, Arroyo del Val, and Los Valles de Fuentidueña. At the moment, what really characterizes *Alicornops* is the shortening of the limbs. This genus includes two species, *A. simorrense* and a second one, *A. alfambrense*, recently described from the upper Vallesian of Spain (Cerdeño and Alcalá 1989).

A. simorrense is well known from the upper Aragonian and Vallesian in Western Europe, but it is in Spain that it is best represented with more than 800 remains, among which are three cranial fragments, almost the only ones known for this species. It is widely distributed in the Vallés-Penedés (Santafé 1978*a*, 1978*b*), Duero, Tajo, and Calatayud-Daroca basins. Most of the sites are upper Aragonian and Los Valles de Fuentidueña, Nombrevilla, and Relea are lower Vallesian. Only in the Vallés-Penedés basin has *A. simorrense* been reported in the upper Vallesian at Can Jofresa (Santafé and Casanovas 1978).

The cranial fragments of *A. simorrense* come from El Lugarejo, Avila, and belong to an immature individual; Cerro del Otero, Palencia, classified as *Rhinoceros sansaniensis* by Hernández Pacheco and Dantín (1915); and Toril-3, Daroca-Zaragoza, the most complete fragment. As far as can be observed in these fragments, the nasal notch and the anterior orbital edge reach the same level as in *H. tetradactylum* (Guérin 1980) and the processus postglenoideus and posttympanicus are also in contact. The ratio between head and limbs is similar in *A. simorrense* and in the extant species *Rhinoceros unicornis*, *Dicerorhinus sumatrensis*, and *Diceros bicornis* (according to the mean values of Guérin 1980).

The mandible is wide at the symphysis, even for female individuals, as is observed in the two specimens from Toril-3, Daroca, one with small incisors (I_2) (female), and the other one with a much greater I_2 (male).

The upper dentition is larger than in the type specimen from Simorre, France, mainly in P^3 and P^4. There is an increase in size from the upper Aragonian populations to the lower Vallesian, Los Valles de Fuentidueña, Nombrevilla. The same is observed in the postcranial skeleton. The bones are strong and short, mainly the metapodials, but without being massive bones. There are individual morphological variations in the articular facets and, as in the dentition, size is greater in the lower Vallesian, but this increase is not always very obvious, such as in the astragalus.

By contrast, there is a great deal of postcranial material from the upper Vallesian site of La Roma-2, Teruel, whose morphology is comparable to that of *A. simorrense* but with a significantly different size and robustness (Cerdeño and Alcalá 1989). At the moment, *A. alfambrense* has only been identified from La Roma-2, but some of the French remains from Montredon, classified as cf. *Prosantorhinus* (Guérin 1980, 1988), could be ascribed to *A. alfambrense*. This species would constitute a final stage in the evolution of *A. simorrense*, the species from which it would have been derived, from populations like that of Los Valles de Fuentidueña, where the trend of increase in size and strength can already be noticed. At the same time, other populations of *A. simorrense* seem to increase in size, but retain their proportions, such as the upper Vallesian samples from Vallés-Penedés and the French sites.

Hoploaceratherium tetradactylum (Lartet, 1837)

H. tetradactylum has been reported in upper Aragonian sites of the Vallés-Penedés basin (Santafé 1978*a*). Moreover, it is present at three other sites in the Madrid area; Paracuellos-5, where it has been recognized previously by Alberdi *et al.* (1985), but on the basis of some bones that really do not belong to this species. With some doubt, because of the scarcity of remains, *H. tetradactylum* is thought also to be present at Cerro de la Plata and Henares-1 (Cerdeño 1989). On the other hand, its presence cannot be confirmed in the Vallesian site of Nombrevilla (Santafé *et al.* 1982) based on the studied sample (mainly dentary remains) which is comparable to that of *A. simorrense* from Los Valles de Fuentidueña.

H. tetradactylum has recently been removed from the genus *Aceratherium* by Ginsburg and Heissig (1989). One of the diagnostic characters indicated by the authors, the semilunate outline of the centrale in the tarsus, does not agree with my own observations on the type material of the species from Sansan, France.

Aceratherium incisivum Kaup, 1832–1834

This species is better documented in the Vallés-Penedés basin than in the rest of Spain. Alberdi *et al.* (1981) recognized *Aceratherium* cf. *incisivum* at Los Valles de Fuentidueña. It is also present in the Teruel area, the upper Vallesian sites of La Roma-2 and Masía del Barbo, and the middle Turolian site of Concud. The presence of *A. incisivum* at the upper Turolian site of Venta del Moro, Valencia (Guérin 1980; Morales 1984) cannot be supported. The mandible described by the authors does not show the characteristics of the type material from Eppelsheim, Germany (Kaup 1832–1834). The symphysis is narrower and it is more like *Dicerorhinus schleiermacheri* from the latter site. So, this implies that the last appearance of *A. incisivum*, and thus of the subfamily Aceratheriinae in Spain, corresponds to the middle Turolian.

Subfamily RHINOCEROTINAE Owen, 1845

Tribe TELEOCERATINI Hay, 1902

The teleoceratines are not well represented in Spain. There are some reports of the genus *Brachypotherium*, and the presence of the genus *Prosantorhinus* has been established for the first time (Cerdeño 1989).

Rhinocerotidae indet. II cf. *Brachypotherium* Roger, 1904

The oldest remains in the Spanish Neogene related to this group are a few bones and a fragment of an upper I^1 from the Lower Miocene site of Loranca del Campo, Cuenca. These are scarce elements and not significant enough for an accurate identification.

Brachypotherium aurelianense (Nouel, 1866)

Some remains from Rubielos de Mora, Teruel, classified as *Brachypotherium* sp. (Aguirre and Moissenet 1972) seem to correspond to *B. aurelianense*, like those of Molí Calopa (Santafé 1978*a*). Adding to these reports, *B. aurelianense* has been identified in La Artesilla, Zaragoza, from a few remains that include a wide and short astragalus whose size and proportions indicate its identity.

Rubielos de Mora and Molí Calopa are younger sites than Loranca del Campo within the Lower Miocene, zone A, while La Artesilla is even more recent, corresponding to a lower Aragonian age, the lowest part of zone C, and this indicates the most recent known remains of *B. aurelianense* in Spain. Santafé and Belinchón (1988) noted the presence of *B. aurelianense* at Buñol, Valencia, but these remains are *Prosantorhinus* sp. (see below).

Antunes and Ginsburg (1983) believe that *B. aurelianense* must be included in the genus *Diaceratherium*, keeping the genus *Brachypotherium* just for the youngest species *B. brachypus*. I have in preparation a revision of the French Miocene material of brachypotheres, and I prefer now to maintain *B. aurelianense* in *Brachypotherium*.

Brachypotherium brachypus (Lartet, 1837)

B. brachypus was reported in some upper Aragonian Spanish sites of the Daroca area, Zaragoza (Guérin 1980). The fossil material preserved at Utrecht University indicates the presence of this species at Arroyo del Val-4, Manchones-1, and Manchones-2, despite the general scarcity of remains.

Prosanthorhinus sp.

As noted above, another teleoceratine genus, *Prosantorhinus*, has been recognized for the first time in Spain. Checking the lower Aragonian material from Buñol, I found a McIV which caught my attention because of its great robustness and small size. This bone is not coincident in size or proportions with the French *B. aurelianense*. However, a comparison with two McIV casts of *Prosantorhinus germanicus* from Sandelzhausen, Germany, supports the idea of the presence of *Prosantorhinus* at Buñol. Certain differences do not permit the identification of the McIV from Buñol with the German species but, on the other hand, there is some unpublished French material identified as *Prosantorhinus douvillei* (Antunes and Ginsburg 1983, p. 24) with which the Buñol material should be compared.

The McIV from Buñol also presents similarities with the Lisbon material classified either as *Diaceratherium aurelianensis* or as *Gaindatherium rexmanueli* (Antunes and Ginsburg 1983). The identification of the McIV as *Prosantorhinus* caused doubts about the correct classification of the Portuguese material. Furthermore, *Prosantorhinus* was also indicated at Lisbon from some dental remains. The Lisbon material must be revised in detail because some of the bones classified as *D. aurelianensis* could belong to *Prosantorhinus*. Besides, the presence of the genus *Gaindatherium* in Lisbon seems very doubtful. A brachypodial postcranial skeleton has never been associated with this Asian genus, contrary to what is stated for *Prosantorhinus* (Heissig 1972, 1974), and possibly the Portuguese postcranial bones assigned to *Gaindatherium* belong to *Prosantorhinus*.

Present data show that *Prosantorhinus* was distributed in Western Europe in sites in Portugal (Lisbon), Spain (Buñol), France (Baigneaux, Artenay, Beaugency, Savigné, La Romieu), and Germany (Sandelzhausen, Steiermark, Georgensgmünd), coexisting in some cases with *B. aurelianense* (La Romieu, Savigné). The Middle Miocene age of these sites ranges from unit MN 3 (Savigné or Les Beilleaux) to MN 5/6 (Georgensgmünd).

Tribe RHINOCEROTINI Owen, 1845
Subtribe ELASMOTHERIINA Bonaparte, 1845

The third group of rhinocerotids recorded in the Spanish Neogene corresponds to the elasmotherines. This group has changed its rank from family to subtribe, according to Prothero and Schoch (1989).

Hispanotherium matritense (Prado, 1864)

The elasmotherines evolved mostly in Asia, but in the Middle Miocene the species *Hispanotherium matritense* appears in the Iberian Peninsula and recently it has been found in France (Ginsburg *et al.* 1987*a*). First the species (Prado 1864), and later the genus (Crusafont and Villalta 1947) were recognized from dental remains from Puente de Toledo, Madrid. These teeth were characterized by their tendency toward hypsodonty, undulating enamel, and much cement. *H. matritense* has now been recognized in Spain at Dehesa de los Caballos, Plasencia-Cáceres; Torrijos, Toledo; Córcoles, Guadalajara; the Daroca area, Torralba de Ribota, and Tarazona de Aragón, Zaragoza; and recently at La Retama, Cuenca.

The postcranial bones are small and slender and they show great similarity with *H. grimmi*, another species described by Heissig (1976) from the Anatolian Peninsula, Turkey, but larger and slightly less slender.

Other forms with clear affinities to *Hispanotherium* have been described from the Miocene of Asia. Antunes and Ginsburg (1983) have considered them as synonyms of *Hispanotherium* at generic level, while Fortelius and Heissig (1989) place them in *Begertherium*.

The geographic distribution of *Hispanotherium* led Antunes (1979) to propose a migration route through the Alpine Arch from the Asian regions to the Iberian Peninsula. This route has also been proposed for the bovids of the tribe Boselaphini (Moyá-Solá and Alférez, in press). Later, *Hispanotherium* may have reached France from Spain.

H. matritense existed briefly in the Iberian Peninsula. In Spain, it is restricted in the middle Aragonian to the zone MN 4*b* or D; Córcoles could be older and seems to be included in zone C (lower Aragonian). In Portugal, *Hispanotherium matritense* appears in younger beds corresponding to the MN 5 unit, as well as in France. On the other hand, the Anatolian species has a greater time span through the whole upper Aragonian.

Fortelius and Heissig (1989) present a cladistic analysis of the elasmotherine group, in which *Caementodon* is very close to *H. matritense*, confirmed by my own observations (Cerdeño 1989). I agree also with these authors when they remove *Shennotherium hipsodontus* (Huang and Yan 1983) from the Elasmotherina because this species does not even show the dental characters of the group.

Tribe RHINOCEROTINI Owen, 1845
Subtribe DICERORHININA Ringström, 1924

The taxonomic rank of this group has varied (Heissig 1989; Prothero *et al.* 1986; Prothero and Schoch 1989), even if the subfamily rank is retained by some authors (Guérin 1989). Within Dicerorhinina, the attribution of species like *L. sansaniense*, *D. schleiermacheri* or *S. miguelcrusafonti* has also been discussed. For the first of these species I use the generic name *Lartetotherium* as defined by Ginsburg (1974), and I agree with Groves (1983) when he considers that the other European species must be separated from the recent genus *Dicerorhinus* (*D. sumatrensis*).

Dicerorhinina indet.

The oldest representative of the dicerorhines in Spain is a rhinoceros from the lower Aragonian of La Artesilla, Zaragoza. The remains are scarce and non-diagnostic. They are identified as Dicerorhinina because of their global similarities with *Dicerorhinus montesi* from Buñol (Santafé *et al.* 1987). This rhinoceros from La Artesilla corresponds to the Rhinocerotidae indet. III of Text-figure 1.

Lartetotherium sansaniense (Lartet, 1851)

Several Spanish sites have provided scarce remains of *Lartetotherium sansaniense*: Paracuellos-3, Madrid; La Cistérniga, Valladolid; Cerro del Otero, Palencia; Coca, Segovia; and Brihuega, Guadalajara, in the upper Aragonian; and Relea, Palencia; Can Ponsic, Barcelona; and perhaps Nombrevilla, Zaragoza, in the lower Vallesian.

Study of the whole complex, and comparison with the type material from Sansan, France, led to the realization that the dentition is basically identical, but the postcranial skeleton is different (Cerdeño 1986). All comparable bones from the named sites are smaller than the bones from Sansan, and only a pyramidal and a cuboid from Paracuellos-5, Madrid, are closer to their French homologues. These latter two bones were first classified as *Aceratherium tetradactylum* (Alberdi *et al.* 1985), but a later revision suggested a *Dicerorhinus* morphology. It is not easy to interpret these *Lartetotherium* remains. Sansan, as well as Paracuellos-5, are older sites than the others and so there could have been a decrease in size with time. Added to this material of *L. sansaniense*, there are some other older remains (lower Aragonian, zone C) whose morphology and size are also closer to Sansan and their relationship is difficult to establish. This is the case for the remains from Can Más (Santafé 1978; Cerdeño 1986) and the *Dicerorhinus montesi* from Buñol (Santafé *et al.* 1987). Following these authors, *D. montesi* is related to *D. schleiermacheri* from the Upper Miocene but it could be more directly related to *Lartetotherium sansaniense*, and even in the same genus. New material of *D. montesi* (the skull and dentition are still unknown) is needed to support this possible relationship.

Dicerorhinus schleiermacheri (Kaup, 1832–1834)

Another classical species of *Dicerorhinus*, *D. schleiermacheri*, might also be related to *Lartetotherium*. This large species is well represented in the Upper Miocene of Western Europe. In Spain, it is known in the lower Vallesian of the Vallés-Penedés basin and from several localities in the upper Vallesian of the Teruel area like Masía del Barbo and La Roma-2. The abundant bones from La Roma-2 are very large and some of them surpass the maximum values established by Guérin (1980) for this species. Their robustness is also somewhat greater than at other sites. In the Spanish lower Turolian, *D. schleiermacheri* is present at Piera, Vallés-Penedés; Puente Minero, Teruel; and Crevillente-2, Alicante. At this last site, the species is very well represented by dental remains, but only three bones have been recovered, contrary to what occurs at La Roma-2 where just six teeth have been found. The species is present through the rest of the Turolian, but is much scarcer. It is known from the middle Turolian of Concud, Teruel, and the upper Turolian of Las Casiones and El Arquillo, Teruel; Venta del Moro, Valencia; La Alberca, Murcia; and Los Hornillos and El Fargue, Granada. As already commented, the classification of the mandible from Venta del Moro as *Aceratherium incisivum* (Morales 1984) has been modified (Cerdeño 1989). Together with the mandible, there is a very large cuboid that can be assigned to *Dicerorhinus schleiermacheri*.

Guérin (1980) classified the metapodials from El Fargue as *Diceros pachygnathus* (he identifies this species at Cenes de la Vega, but the described material comes from El Fargue). This taxonomic determination is not

AGE	STAGE	1	2	LOCALITY	i	a	b	c	d	e	f	g	h	j	k	l	m	n	o
PLIOCENE	RUSCINIAN		15	Layna															*
			14	La Calera															*
UPPER MIOCENE	UPPER TUROLIAN			El Fargue														*	
				Cenes de la V.														*	
			13	La Alberca														*	
				Venta del Moro														*	
				Las Casiones														*	
				El Arquillo														*	
	MIDDLE TUROLIAN			Crevillente 15														*	
			12	Los Mansuetos										*				*	
				Concud										*				*	
	LOWER TUROLIAN			Piera										*				*	
			11	Puente Minero														*	
				Crevillente 2														*	
	UPPER VALLESIAN			Can Perellada										*					
			10	Can Jofresa										*					
				Masía del Barbo										*				*	
				La Roma 2								*		*				*	
	LOWER VALLESIAN	I		Can Llobateres							*			*		?			
				Can Ponsic							*					*			
			9	Nombrevilla							*					?			
				Chiloeches							*								
				Los Valles de F.							*			cf					
		H		Relea							*					*			
MIDDLE MIOCENE	UPPER ARAGONIAN			Brihuega												*			
				Coca												*			
			7/8	La Cistérniga							*					*			
		G		Cerro del Otero							*					*			
				Andurriales							*								
				Toril 3							*								
			6	Arroyo del Val		*					*								
				Manchones 1 y 2		*					*								
				Armantes 3							*								
		F		Paracuellos 3							*					*			
				Paracuellos 5									cf			*			
	MIDDLE ARAGONIAN	E	5	Henares 1									?						
				Puente de Toledo											*				
				Tarazona											*				
				Torrijos											*				
		D	4b	Munébrega 1											*				
				Valdemoros 1A											*				
				Torralba V											*				
	LOWER ARAGONIAN			Córcoles											*				
				Buñol			*	*								?	*		
		C	4a	Can Juliá					*										
				Can Más				*								?			
		B		Artesilla	III	*													
LOWER MIOCENE	RAMBLIAN	A		Rubielos de Mora		*													
			3	Molí Calopa		*													
		Z		Loranca	II=cf					*									
		Y	2b	Valquemado						*									
			2a	Cetina de A.	I														

TEXT-FIG. 1. Biostratigraphical distribution of the Rhinocerotidae in the Spanish Neogene localities. 1, Daams and Freudenthal (1981). 2, Mein (1975). *i*, Rhinocerotidae indet.; *a*, *Brachypotherium aurelianense*/*B. brachypus*; *b*, *Prosantorhinus* sp.; *c*, *Plesiaceratherium platyodon*; *d*, *P. mirallesi*; *e*, *Protaceratherium minutum*; *f*, *Alicornops simorrense*; *g*, *A. alfambrense*; *h*, *Hoploaceratherium tetradactylum*; *j*, *Aceratherium incisivum*; *k*, *Hispanotherium matritense*; *l*, *Lartetotherium sansaniense*; *m*, *Dicerorhinus montesi*; *n*, *Dicerorhinus schleiermacheri*; *o*, *Stephanorhinus miguelcrusafonti*.

justified. *D. pachygnathus* has been defined on material from Pikermi, Greece. Bones from this site (Musée Guimet d'Histoire Naturelle, Lyon) show that differences from *D. schleiermacheri* from La Roma are limited to the greater robustness of the Greek material. On the other hand, Geraads (1988) has revised the rhinocerotids from Pikermi, and has noted the presence of two forms; *Ceratotherium neumayri* (= *Diceros pachygnathus*) and *Dicerorhinus pikermiensis* (= *Dicerorhinus schleiermacheri* var. *orientalis*). This author established cranial differences between these two species, but he could not do the same with the postcranial skeleton (two different morphologies are observed only for some bones). The similarities between the metapodials from El Fargue and *Diceros pachygnathus* are logical since those of *D. pachygnathus* could correspond to the *Dicerorhinus* of Pikermi, a form very close to *Dicerorhinus schleiermacheri*, but less slender. Therefore, the bones from El Fargue must be classified as *Dicerorhinus* cf. *schleiermacheri* (Cerdeño 1989, p. 350). The main difference between these metapodials and the others is the greater relative length of the MtIII.

Stephanorhinus miguelcrusafonti Guérin and Santafé, 1978

S. miguelcrusafonti is the last species studied among the Spanish Neogene dicerorhines. It has also been described as *Dicerorhinus*, but it corresponds to the Plio-Pleistocene group named *Stephanorhinus* (Groves 1983). This species was defined from the Ruscinian Spanish site of Layna, Soria (Guérin and Santafé 1978), and also recognized at Perpignan, France. Furthermore, the species is identified at La Calera, Teruel (Cerdeño 1989). The skull and mandible are still unknown. The anatomical comparative study of *S. miguelcrusafonti* shows the different slenderness of the Spanish metapodials compared to the Perpignan ones, which have the highest indices. Besides this, there are few morphological differences between *S. megarhinus* and the Plio-Pleistocene species. The Spanish rhinoceros can be distinguished from the common Pliocene European species *S. megarhinus*, mainly by its smaller size. The robustness is comparable or slightly less than in *S. megarhinus*, and only the Perpignan bones are stronger than all other Plio-Pleistocene species. The best knowledge of *S. miguelcrusafonti* could lead to two contrary results. Either it is fully confirmed as a different species, or it becomes a variety of *S. megarhinus*, possibly a subspecies. At the end of the Ruscinian, both forms disappear.

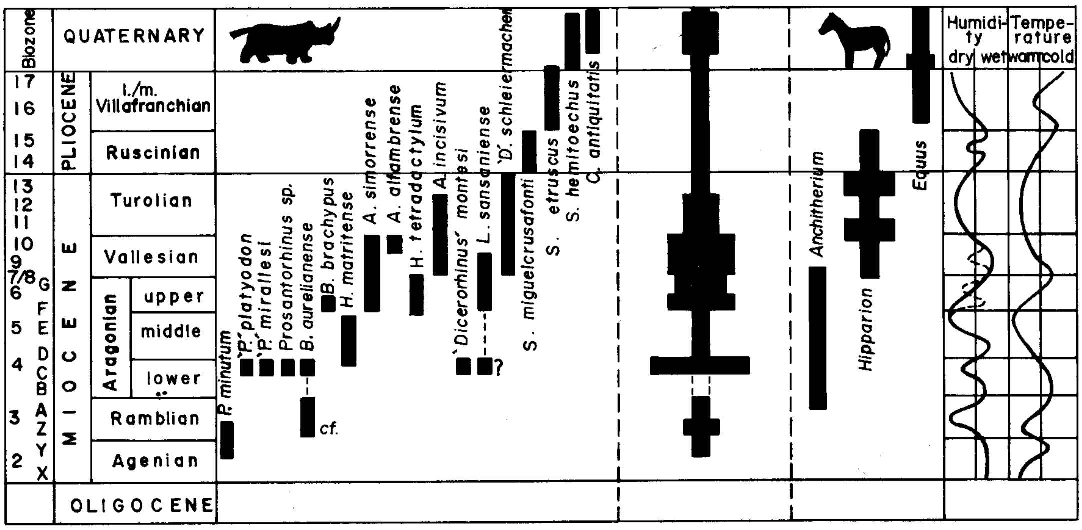
CONCLUSIONS

Nine genera and fourteen species of rhinoceros have been established in the Spanish Neogene. *Protaceratherium minutum* and *Prosantorhinus* sp. are reported in Spain for the first time, and *Alicornops alfambrense* appears in the upper Vallesian as a final stage of the *A. simorrense* evolutionary lineage.

The Spanish Miocene and Lower Pliocene (Ruscinian) are quite well documented for rhinoceroses, and only two biozones are poorly known for macromammals (not only for rhinoceroses): zone MN 2*a* or X in the Lower Miocene and zone MN 3/4 or B in the early Middle Miocene (lower Aragonian).

Spanish rhinocerotids document several stages that can be grouped as follows:

1. Lower Miocene, zones MN 2*b*–MN 3*a* or Y–Z. Characterized by the abundant presence of *Protaceratherium minutum*. This species is coeval with cf. *Brachypotherium* at Loranca del Campo.
2. Lower–Middle Miocene, zones MN 3*b*–MN 4*a* or A-(B)-C. Corresponds to a period of highest diversity, but with a rather low numerical representation. There are six species, although no more than four at the same site (e.g. Buñol).
3. Middle Aragonian, zone MN 4*b* or D. *Hispanotherium matritense* is the only rhinoceros known in the sites of this age, very abundant in localities like Córcoles or Torrijos.
4. Middle–upper Aragonian, zones MN 5/6 or E–F. Rather poorly documented, and apparently only recognized in the Madrid area. Rich sites for macromammal fauna such as Paracuellos-5 have provided only a very few remains of rhinocerotids, compared to the abundance of the equid *Anchitherium*.
5. Upper Aragonian–Vallesian, zones MN 6–MN 10. *Alicornops simorrense* is characteristic at this time. It is widely distributed in Spanish basins with its best representation in Western Europe. It can coexist with *Brachypotherium brachypus* or *Lartetotherium sansaniense*, but always as the predominant species. *A. simorrense* does not appear in Spain during the upper Vallesian, except in the one site of Can Jofresa, Vallés-Penedés basin. However, a probable descendant, *A. alfambrense*,



TEXT-FIG. 2. Schematic representation of the global diversity of the Spanish Rhinocerotidae compared with the diversity of Equidae and global palaeoclimatic changes.

is present at La Roma-2, Teruel basin. In the rest of Western Europe, *A. simorrense* has been identified in the upper Vallesian, but it is possible that a part of this material, as well as cf. *Prosantorhinus* sp. D from Montredon, France (Guérin 1980, 1988), could be related to *A. alfambrense*.

6. Turolian–Ruscinian, zones MN 11–MN 15. Characterized by the decline of the family Rhinocerotidae. Rhinoceroses are abundant in macromammal faunas until the upper Vallesian, but after the Turolian they become more and more scarce. Despite this, rhinocerotids persist until the Upper Pleistocene.

The passage between the last two stages is gradual. In fact, the most characteristic Turolian form, *Dicerorhinus schleiermacheri*, is already present in the upper Vallesian, together with *A. incisivum*. This latter species is occasionally found in the lower and middle Turolian. As early as the latest Miocene (MN 13), *D. schleiermacheri* is the only extant rhinoceros which is replaced by *Stephanorhinus miguelcrusafonti* in the Ruscinian. This one, in its turn, is the only representative of the family at that time and is replaced by *S. etruscus* in the Villafranchian.

All these different stages give us a global temporal distribution which is compared with that of the equids (Text-figure 2). The greatest diversity of the Rhinocerotidae coincides with the development of just one equid, *Anchitherium aurelianense*, a species that hardly varies through the Aragonian. The arrival of the equid *Hipparion*, among other immigrants, occurs at the same time that rhinocerotids begin to decline.

The global distribution of the rhinocerotids can be correlated with the palaeoclimatic curves established by López *et al.* (1987) for the Spanish Neogene (Text-fig. 2), mainly based on micromammals. The predominance of *Protaceratherium minutum* coincides with a warm and wet period which becomes gradually drier and colder. Daams and Meulen (1984) have also established from micromammal faunas a humid environment during the transition Agenian–lower Aragonian. The next stage, with higher diversity, corresponds to both cold and wet maxima in the palaeoclimatic curves. *Hispanotherium matritense* occurs when the conditions become drier, the temperature increases, and the humidity reaches a minimum. This species was well adapted to arid conditions, and it seems that the environment was more advantageous for this rhinoceros than for other macromammals like the equid *Anchitherium*. This would explain their different representation in the middle Aragonian sites. Later, palaeoclimatic curves show that *Alicornops simorrense* apparently lived in a moderate climate with a global tendency to cold weather with humidity oscillations. The last period is characterized once again by maximum arid conditions in the Turolian which decrease towards the Ruscinian. Possibly, the Turolian aridity favoured *Hipparion* over rhinoceroses which do not regain their previous diversity.

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