THE *HISPANOTHERIUM MATRITENSE* (RHINOCEROTIDAE) FROM CÓRCOLES (GUADALAJARA, SPAIN): ITS CONTRIBUTION TO THE SYSTEMATICS OF THE MIOCENE IRANOTHERIINA

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ABSTRACT - This paper deals with the *Hispanotherium matritense* (Rhinocerotidae) remains from the Miocene site of Córcoles (Guadalajara, Spain), which constitutes the largest sample of this species recovered from a single site. Some skeletal elements are described for the first time for *H. matritense*. This new material allows us to corroborate the synonymy of several genera of Iranotheriina (*Caementodon* and *Begertherium*), previously defended by some authors. This synonymy is also supported at specific level for *Caementodon oettingenae, Begertherium grimmi, Begertherium tekkayai* and *Begertherium borissiaki*.

KEYWORD: SYSTEMATICS, RHINOCEROTIDAE, MIDDLE MIOCENE, SPAIN.

RÉSUMÉ - Les restes de *Hispanotherium matritense* (Rhinocerotidae) du gisement miocène de Córcoles (Guadalajara, Espagne) sont étudiés ici. Ils constituent l'échantillon le plus complet de cette espèce dans un même gisement. Quelques éléments post-crâniens sont décrits pour la première fois pour *H. matritense*. Ce nouveau matériel permet de confirmer la synonymie de certains genres d'*Iranotheriina* (*Caementodon* et *Begertherium*), ainsi que la synonymie au niveau spécifique de *Caementodon oettingenae, Begertherium grimmi, Begertherium tekkayai* et *Begertherium borissiaki*.

MOTS-CLÉS: SYSTÉMATIQUE, RHINOCEROTIDAE, MIOCENE MOYEN, ESPAGNE.

RESUMEN - En este trabajo se estudian los restos de *Hispanotherium matritense* del yacimiento Mioceno de Córcoles (Guadalajara, España), que constituyen la mayor muestra de esta especie en un solo yacimiento. Se describen, por primera vez en *H. matritense*, algunos elementos esqueléticos. Este nuevo material confirma la sinonimia de varios géneros de *Iranotheriina* (*Camentodon* y *Begertherium*) defendida por algunos autores. También se propone la sinonimia a nivel específico para *Caementodon oettingenae, Begertherium grimmi, Begertherium borissiaki* y *Begetherium tekkayai*.

PALABRAS CLAVE: SYSTEMÁTICA, RHINOCEROTIDAE, MIOCENO MEDIO, ESPAÑA.

INTRODUCTION

In 1982, Alférez et al. studied the global context of the Miocene site of Córcoles (Guadalajara, Spain), which is placed within the Lower Aragonian, corresponding to the MN4 of the Mein's (1975) biozonation. From then on the macromammals from Córcoles have been studied in different papers (Alférez et al. 1980; Maldonado et al. 1983; Alférez et al. 1988; Maldonado & Alférez 1988; Moyá & Alférez 1988; Van der Made & Alférez 1988; Iñigo 1993, 1994) obtaining the following faunal list:

Order CARNIVORA
- *Pseudailurus quadridentatus*
- *Pseudailurus* sp.
- *Amphicyon major*
- *Plitocyon armagnacensis*
- *Martes* cf. *pusilla*
- *Martes* sp.

Order ARTIODACTYLA
- *Cainotherium miocaenicum*
- *Cainotherium* sp.
- *Dorcatherium crassum*

Triceromeryx pachecoi
Procervulus dichotomus
Eotragus artenensis
Hydropotopsis sp.
Bunolistriodon lockharti
Bunolistriodon latidens

Order PERISSODACTYLA
Anchitherium corcolense
Hispanotherium matritense
Protaceratherium platyodon
Phyllotillon naricus

Order PROBOSCIDEA
Gomphotherium angustidens

Order PHOLIDOTA
Teutomanis sp.

Order TUBULIDENTATA
Orycteropus sp.

Among this macromammals, the perissodactyls are very abundant (61%), with 654 specimens identified as *Hispanotherium matritense*. A second species of rhinoceros, *Protaceratherium platyodon,* is also present at Córcoles, but only represented by a few elements (Iñigo 1994).

Remains of *H. matritense* so far known from Spanish, Portuguese and French Miocene localities mainly refer to dentition (Prado 1864; Crusafont & Villalta 1947; Zbyzewski 1952; Hernández-Pacheco & Crusafont 1960; Cerdeño & Alberdi 1983; Antunes & Ginsburg 1983; Alberdi et al. 1985; Astibia 1985; Ginsburg et al. 1987; Cerdeño 1989, 1992a, 1992b).

The present study of Córcoles remains provides a better knowledge of the anatomy of *H. matritense*, and a good idea of the morphological and metrical variation within a single population. These new data allow us to discuss anew the controversial synonymy of several Asian "elasmotherines", *Caementodon, Begertherium* and *Beliajevina,* stated by some authors (Antunes & Ginsburg 1983; Ginsburg et al. 1987; Cerdeño 1989, 1995; Prothero et al. 1989), while others support their generic status (Fortelius & Heissig 1989; Fortelius 1990).

The systematic classification of this group of Miocene rhinocerotids follows Cerdeño (1995), considering them as Subtribe Iranotheriina within the Tribe Rhinocerotini.

MATERIAL AND METHOD

The studied material from Córcoles comprises 14 mandibular fragments, 13 dental series, 118 isolated teeth and 519 postcranial elements. The itemized list of these remains is detailed in the Ph. D. of one of us (Iñigo 1993).

They have been directly compared with other European material of *H. matritense,* as well as some Asian "elasmotherines", completed with bibliographic data (Borissiak 1938; Beliajeva 1971; Heissig 1972, 1974, 1976; Antunes & Ginsburg 1983; Ginsburg et al. 1987; Fortelius 1990).

Our methodology follows basically that of Guérin (1980), but scaphoids, unciforms and lateral metapodials have been measured after Cerdeño's (1989) criterion. For the astragalus we have calculated the indexes of depth and asymmetry of the throclea after Alférez & Iñigo (1990).

Statistic parameters for the remains from Córcoles are presented in tables 1-27, and detailed dimensions of each specimen can be checked in Iñigo (1993). Abbreviations used in tables are the following:

Anat: anatomical. Ant: anterior. Art: articular surface. B: breadth. D: diagonal. Dx: deciduous tooth. Dis: distal DL: distance between astragalar lips. DP: depth. F: facet. H: heigth. I: incisor. L: length. M: molar. Max: maximal. Mdl: medial. Min: minimal. P: premolar. Pos: posterior. Prox: proximal. Ran: range. Sust: sustentaculum. Tub: tuberosity.

SYSTEMATIC PALAEONTOLOGY

Order PERISSODACTYLA Owen, 1845
Family RHINOCEROTIDAE Owen, 1845
Subfamily RHINOCEROTINAE Owen, 1845
Tribe RHINOCEROTINI Owen, 1845
Subtribe IRANOTHERIINA Kretzoi, 1943

Genus ***Hispanotherium*** CRUSAFONT & VILLALTA, 1947

Hispanotherium matritense (PRADO, 1864)

Synonyms
1952 *Chilotherium quintanelensis*. Zbyszewsky.
1971 *Begertherium borissiaki*. Beliajeva.
1972 *Caementodon oettingenae*. Heissig.
1974 *Hispanotherium grimmi*. Heissig.
1974 *Beliajevina tekkayai*. Heissig.
1978 *Hispanotherium alpani*. Saraç.
1980 aff. *Aceratherium platyodon*. Boné et al..
1989 *Begertherium grimmi*. Fortelius & Heissig.
1989 *Begertherium tekkayai*. Fortelius & Heissig.

Holotype - Right M^2. Crusafont & Villalta 1947 (Fig. 1). Stored in the Museo Geominero (Madrid, Spain).

Type locality - Puente de Toledo (Madrid, Spain).

Geographical distribution - Western Europe (Iberian Peninsula and France) and Asia (Turkey, Pakistan and Mongolia).

		Córcoles	*H. matritense*	*B. grimmi*[1]	*B. tekkayai*[2]	*B. borissiaki*[3]	*B. caucasica*[4]	*C. oettingenae*[5]
	N	2	1	2		1	2	
	Ran	18.6-21,3		(20)-21			20-22	
L	Mean	19.95	(17.3)	20.5		19	21	
P^1								
	N	2	1	2		1	2	
	Ran	18.5-20.4		23-23			17-19.5	
B	Mean	19.45	16.2	23		25	18.25	
	N	3	7	2	1	1	2	1
	Ran	23.2-25.6	(19.1)-35.7	27-29			28-30	
A	Mean	24.27	24.97	28	23.4	30	29	23
	S	0.71						
P^2								
	N	4	6	2	1	1	2	1
	Ran	28.2-32.9	25.8-32.4	34-38			31-32	
B	Mean	31.05	29.08	36	31.3	29	31.5	28
	S	0.71						
	N	1	7	1		1	2	1
	Ran		(25.4)-31.5				33-34	
L	Mean	32	28.06	26		41	33.5	26
P^3								
	N	4	8	1		1	2	1
	Ran	38.3-40.2	34.2-40.2				35.5-37.5	
A	Mean	39.42	37.52	40		45	36.5	35
	S	0.77						
	N	3	7	2	1	1	2	
	Ran	35.3-37	29.5-32.6	30-36			34-34	
L	Med	35.93	30.08	33	30.2	40	34	
	S							
P^4								
	N	2	9	2	1	1	2	
	Ran	39,7-42.6	(39,5)-48.3	50-52			33-37	
B	Mean	41.15	43.88	51	41.9	45	35	
	N	3	10		2	1	2	1
	Ran	38.2-44.7	33.9-51.8		34.6-39.2		47-57	
L	Mean	41	41.69		36.9	45	47	34
M^1								
	N	3	11		1	1	2	1
	Ran	49.2-54.4	45-52.2				47-51	
B	Mean	52.63	48.91		46.7	53	49	42
	N	3	13	2	1	1	1	1
	Ran	44-47.5	38.7-52.6	42-45				
L	Mean	45.8	47.48	43.5	42	(52)	50	43
M^2								
	N	5	12	1	1	1	2	1
	Ran	46.8-51.4	45.3-60				40-48	
B	Mean	49.22	52.23	53	52	58	44	45
	S	2.09						
	N	3	8				1	1
	Ran	44.7-46	42-52.3	41-56				
L	Mean	45.17	46.36	49.66			53	44
M^3								
	N	3	8					
	Ran	45.8-50	39.4-52.3	47-58				
B	Mean	47.23	45.9	53.33			-	-
	N	3	2					1
	Ran	50.6-54.6	49.1-52.1	53-61				
D	Mean	52.1	50.6	57.66			-	48

TABLE 1 - Comparative dimensions of the upper teeth of *H. matritense* from Córcoles. References: **1,** Heissig 1976. **2,** Fortelius 1990. **3,** Beliajeva 1971. **4,** Borissiak 1938. **5,** Heissig 1972. *Dimensions comparées de la denture supérieure de* H. matritense *de Córcoles.*

		Córcoles	*H. matritense*	*B. grimmi*[1]	*B. tekkayai*[2]	*B. borissiaki*[3]	*B. caucasica*[4]
I_1	N	6					
	Ran	13.2-17.6					
L	Mean	14,58					
	S	1.56					
	N	6					
	Ran	6.8-8.1					
B	Mean	7.35					
	S	0.46					
I_2 (M)	N	2					
	Ran	28.5-30.3					
L	Mean	29,4					
	N	2					
	Ran	17.2-19.5					
B	Mean	18.35					
I_2 (F)	N	4					
	Ran	19.6-25.5					
L	Mean	22.9					
	S	2.87					
	N	4					
	Ran	13-15.8					
B	Mean	14.12					
	S	1.46					
P_2	N	4	7		1	2	2
	Ran	21.5-25.8	18.8-25.5			20-20	24-24
L	Mean	24	21.9		25	20	24
	S	1.91					
	N	5	7			2	2
	Ran	15.9-16.9	14-20		-	16-16	16-17
B	Mean	16.32	15.84			16	16.5
	S	0.46					
P_3	N	12	10			2	1
	Ran	26.7-31	22.3-28.3		28-28.9	26-27	
L	Mean	29.16	24.49		28.4	26.5	26
	S	1.27					
	N	12	10			2	1
	Ran	17,9-21,5	17,4-20		21.4-21.7	18-19	
B	Mean	19.71	18.77		21.5	18.5	19.5
	S	1.12					
P_4	N	4	18	2		1	
	Ran	32.3-33.5	25.6-29.6	27-31			
L	Mean	32.95	27.86	29		30	
	S	0.56					
	N	5	16	2		1	
	Ran	22-23,1	21.4-28.3	(22)-24			
B	Mean	22.56	22.1	23		20	
	S	0.49					
M_1	N	7	13	2		2	2
	Ran	36,1-40	26.6-38.6	33-39	35.8-38.8	35-37	38-39
L	Mean	38.3	33.45	36	37	36	38.5
	S	1.41					
	N	10	13				
	Ran	22.6-25.6	20.6-27.8	22-24	23.5-25.1	2	2
B	Mean	24.26	24.01	22.66	24.3	25-25	22-23
	S	1.09			28.4	25	22.5
M_2	N	6	10	2		1	2
	Ran	42.2-44.6	39.3-42	(40)-48	42.2-46.7		46-46
L	Mean	43.18	41.67	44	44.4	53	46
	S	0.95					
	N	7	10	2	1	1	2
	Ran	22-25.9	24.6-29.7	24-31			24-24
B	Mean	24.29	2.,21	27.5	28.4	23	24
	S	1.33					
M_3	N	5	16	1	1		1
	Ran	45-47,2	36.4-45.9				
L	Mean	46.22	39.71	48	48.9		48
	S	1.26					
	N	5	17	2	1		1
	Ran	24.8-25.5	24.9-28.4	26-29			
B	Mean	25.24	26.7	27.5	27.3		27.3
	S	0.44					

TABLE 2 - Comparative dimensions of the lower teeth of *H. matritense* from Córcoles. References in table 1. *Dimensions comparées de la denture inférieure de* H. matritense *de Córcoles.*

		Córcoles	*H. matritense*	*B. grimmi*[1]	*B. takkayai*[2]
D^1 L	N	13			1
	Ran	19-25,1			
	Mean	22.43			25
	S	1.94			
D^1 B	N	12			1
	Ran	14.4-19.6			
	Mean	17.56			20,5
	S	1.62			
D^2 L	N	2	3		2
	Ran	25.3-27.5	21.7-26.1		29-30
	Mean	26.4	23.77		29.5
D^2 B	N	4	3		2
	Ran	25.3-26.8	13.3-23.8		27.8-31.6
	Mean	25.83	17.1		29.7
	S	0.71			
D^3 L	N	1			
	Ran				31.3-33
	Mean	33.4	-		32.15
D^3 B	N	2	1		
	Ran	30.2-32.7			32.6-38.4
	Mean	31.45	15.8		35.22
D^4 L	N	3	3		
	Ran	38-39.5	34.8-38.6		34.9-40
	Mean	38.9	36.3		36.97
D^4 B	N	2	3		
	Ran	35.6-39	28.3-38.5		38.1
	Mean	37.3	25.7		40.55
D_1 L	N	12			
	Ran	13.9-17.6			11.6-16.5
	Mean	15.35			13.71
	S	1.37			
D_1 B	N	12			
	Ran	8.9-9.2			7.1-9.6
	Mean	8.74			8.41
	S	0.54			
D_2 L	N	8	2	2	
	Ran	21.1-26.6	21.7-23.5	23-24	20.4-24.6
	Mean	22.23	22.6	23.5	23
	S	1.66			
D_2 B	N	8	2	2	
	Ran	11.4-15.7	13.3-14.2	14-15	12.1-15.7
	Mean	12.43	13.75	14.5	14.34
	S	1.35			
D_3 L	N	9	2	1	
	Ran	31.1-34.5	32.4-33.5		28.2-46.3
	Mean	32.24	32.95	34	33.29
	S	1.23			
D_3 B	N	12	3	1	
	Ran	15.2-19.6	15.8-17.5		14.2-18.6
	Mean	16.23	16.37	18	17,29
	S	1.19			
D_4 L	N	5	3	2	
	Ran	34.2-37.4	30-35.6	38-38	30.5-35.6
	Mean	35.8	33.47	38	33.71
	S	1.32			
D_4 B	N	6	3	2	
	Ran	18.1-21.7	18.1-20.3	21-21	16.8-20.8
	Mean	19.3	18.9	21	19.46
	S	1.28			

TABLE 3 - Comparative dimensions of the milk dentition of *H. matritense* from Córcoles. References in table 1. *Dimensions comparées de la denture de lait de* H. matritense *de Córcoles.*

Type stratigraphical level - Middle Miocene, Middle Aragonian, MN4b.

Stratigraphical distribution - Middle Miocene to Upper Miocene, Lower Aragonian to Lower Vallesian.

Diagnosis - Small rhinocerotid with one nasal horn, maybe with sexual dimorphism. Subhipsodont jugal teeth, with very much cement and protocone constricted. Upper premolars with closed median valley. Secondary folds of the enamel developed. I_2 like small tusks, with sexual dimorphism in size. Posteranial skeleton slender, with the McV reduced, not functional.

Description - Anterior teeth (Tab. 2; Fig. 2). It is mainly represented by lower incisors. The I_1 are chisel-shaped and their root is antero-posteriorly flattened. The smallest ones seem to be DI_1. The I_2 are small tusks with two different sizes due to sexual dimorphism. It is surprising the lack of I^1 taking into account the great number of incisors recovered at Córcoles. The presence of this tooth in *H. matritense* is proved by the specimens recovered at Tarazona (Spain) (Astibia 1985).

Deciduous teeth (Tab. 3; Fig. 2) - The upper milk teeth have an ondulated ectoloph. The internal cusp are united on D^3. There is a great variation on the development of the secondary folds. Three specimens (Co-689, Co-3192 and Co-3888) have a small tubercle of enamel at the entrance of the median valley. The protocone of the D^4 is constricted. The lower milk teeth show the posterior valley V-shaped and the D_4 have the anterior one U-shaped. The external groove is well marked only on D_4. The paralophid is bifurcated on D_2 and D_3 (excepting D_2 Co-3186). The D_2 and one D_3 (Co-3159) have a fold on the metalophid. On three D_3 (Co-981, Co-218 and Co-4330) the metaconid projets backwards, and it closes the posterior valley on Co-218.

Permanent teeth (Tab. 1, 2; Fig. 2) - The jugal teeth are subhipsodont with somewhat wrinkled enamel, and they have much cement on the walls and valleys. The upper teeth present an ondulated ectoloph. P1 has developed only the protoloph. The median valley on the premolars (P^2-P^4) is closed, and there is a narrow lingual groove which differenciates the two lingual cusps. The crochet is strongly developed on P and M, bifurcated on P^2 (Co-4949), and one or two cristae are present on the molars. All the molars and one P^3 (Co-5441) have the protocone constricted, as well as the hypocone on the M^1. Only some P^2 and P^3 have a slight lingual cingulum. On the lower teeth, the external wall presents a well marked ridge on the protoconid, and the labial groove is deep. The posterior valley is V-shaped. None has the entoconid well delimited and the metaconid is constricted on three P_3 (Co-3195, Co-3198 and Co-3225). Some specimens present a smooth lateral cingulum at the trigonid.

Postcranial skeleton - In a general sense, the studied bones are medium-sized and slender; they are narrow related to their thickness (antero-posterior diameter).

Atlas - There is only one specimen whose dimensions are: Greatest breadth articular surface=107.6. Greatest height=105.9. Foramen breadth=42.1. Foramen anterior heigth=54.1. Foramen posterior heigth=62.

Scapula - There are three fragmentary specimens with the following mean dimensions: Breadth of the neck=28.95. Depth of the neck=85.9. Depth of the tuber=98. Breadth of the articular surface=53.2. Depth of the articular surface=67.5.

Humerus - Only one proximal fragment and several distal ones, which don't allow further comments.

Radius (Tab. 4) - It presents a deep and wide concavity for the insertion of the biceps braquial. The humeral articular surface forms a marked crest. On the posterior face, the proximal ulnar facets are fused.

	Prox			Diaphysis		Dis		Dis art	
RADIUS	L	B	DP	B	DP	B	D	B	DP
Córcoles									
N	1	9	5	4	4	4	2	4	4
Min		69.7	54	38.7	31	71.3	52	64	33.9
Max		84.1	59.3	47.2	37.1	77.2	57.2	68.9	38.3
Mean	298.1	78.61	56.46	43.78	33.63	74.75	54.6	66.45	36.7
S		6.08	4.18	8.75	9.25	3.5		3.35	5.61
H. matritense									
N=1	(316)	75.8	57.2	47.3	34.5	70.4	49.3	60.4	34.7
B. grimmi[1]									
N	2	6	5	4	4	2	3		3
Min	305	79	57	46	(30)	83	52		36
Max	330	96	63	59	38	93	(58)		(45)
Mean	317.5	86	59.4	51.4	34.5	88	54	-	41
B. caucasica[4]									
N	2	2		2	2	2	2	2	
Min	320	80		44	32	68	41	76	
Max	330	81		46	37	68.5	41	78	
Mean	325	80.5		45	34.5	69	41	80	
C. nettingenae[5]									
N=1	-	-	-	-	-	-	-	80	78

TABLE 4 - Comparative dimensions of the radius of *H. matritense* from Córcoles. References in table 1. *Dimensions comparées du radius de* H. matritense *de Córcoles.*

SCAPHOID		H	B	DP	Prox art B	Prox art DP	Dis art B	Dis art DP
Córcoles								
	N	10	5	7	6	9	4	4
	Min	46.8	39.7	51.3	38.8	33.5	28.7	44.1
	Max	57	43.8	58.3	43.3	46.3	38	45.4
	Mean	51.93	42.02	56	40.66	39.9	34.82	44.63
	S	3.54	1.58	2.66	1.7	3.54	4.33	0.56
H. matritense								
	N	3	2	3	1	2	1	2
	Min	39.1	35.4	56.4		32.2	(23)	40.9
	Max	52.9	40	58.1	29.5	39.7	33.9	48.4
	Mean	48.1	37.7	57.33		35.95	28.45	44.65
B. grimmi[1]	N=1	67	50	71	51	45	30	-
B. caucasica[4]	N=1	54	-	63	-	-	-	-
C. oettingenae[5]	N=1	44	36	57	-	-	-	-

TABLE 5 - Comparative dimensions of the scaphoid of *H. matritense* from Córcoles. References in table 1. *Dimensions comparées du scaphoïde de* H. matritense *de Córcoles.*

Ulna - There is a unique proximal fragment united to the radius. Several distal fragments show that the radius- facet is separated from the pyramidal-facet for a narrow surface which articulates with the semilunar.

Scaphoid (Tab. 5; Fig. 1) - The proximal facet is sub-triangular, with a very pointed medial apex, and quite raised posterior border, giving a great concavity to the facet. There are two medial facets for the semilunar, the upper one runs along the proximal border.

Semilunar (Tab. 6; Fig. 3) - The radius-facet is very convex and stretches backwards over the dorsal face, slightly concave. There is not a clear limit between this one and the ulnar-facet. On the lateral face, the inferior facet for the pyramidal is long and projects backwards beyond the level of the distal unciform-facet. Both distal facets form a strong ridge between them, and that for the magnum is long, reaching the posterior border of the face.

Pyramidal (Tab. 7) - The proximal facet for the ulna is trapezoidal in outline. The antero-external face is higher than wide. On the medial face, the upper facet for the semilunar is a narrow band, hardly developed on some specimens, and the lower facet is long.

Pisiform - The two articular facets are triangular in shape and concave-convex, similar in size, and united at a right angle. The external face of the bone is quite flattened.

Trapezoid (Tab. 8) - Anterior face clearly higher than wide, except on Co-1568, roughly squared. The scaphoid-facet is trapezoidal, and that for the McII is pear-shaped.

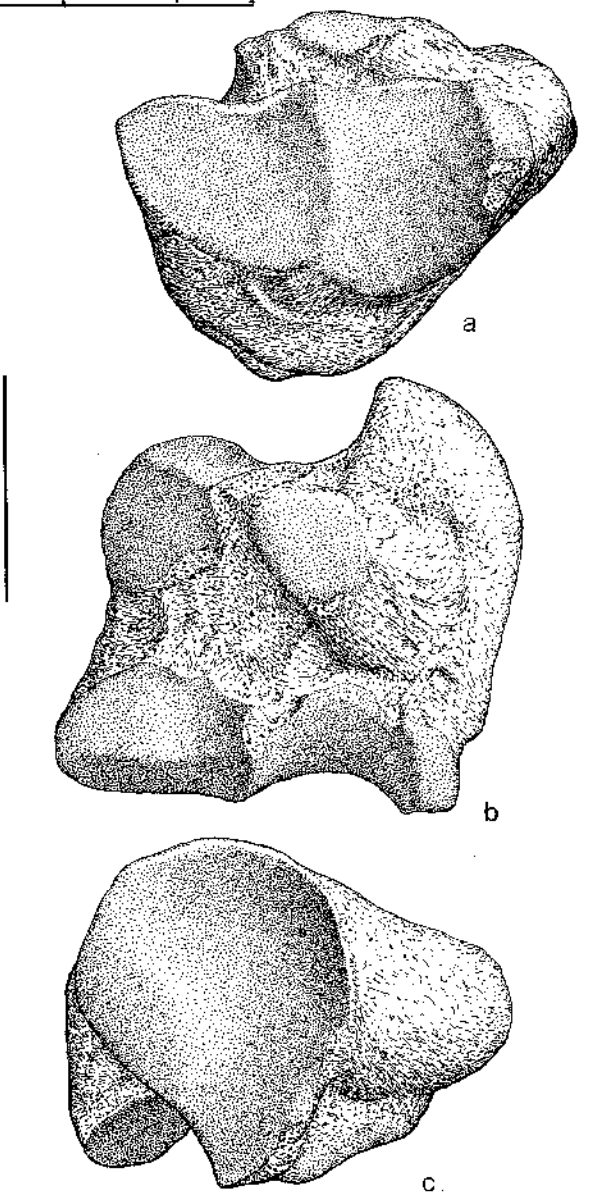


FIGURE 1 - Scaphoid (L) of *H. matritense* from Córcoles (Co-104). **a.** Distal view. **b.** External view. **c.** Proximal view. ***a.*** *Vue distale.* ***b.*** *Vue externe.* ***c.*** *Vue proximale.*

SEMILUNAR	H	B	DP	H ant
Córcoles				
N	8	10	10	17
Min	35.1	33.1	52.8	35
Max	41.7	40.6	58.3	46
Mean	39.3	37.19	56.4	41.08
S	2.13	2.69	1.72	3.07
H. matritense				
N	4	5	4	4
Min	35.4	(31.3)	50.7	37.3
Max	38.9	41	55.8	44
Mean	36.65	37.04	52.85	39.9
B. caucasica[4]				
N=1	-	43	60	43
C. oettingenae[5]				
N	2	2	2	
Min	38	(30)	48	
Max	38	(35)	49	
Mean	38	32,5	48,5	-

TABLE 6 - Comparative dimensions of the semilunar of *H. matritense* from Córcoles. References in table 1. *Dimensions comparées du semi-lunaire de* H. matritense *de Córcoles.*

PYRAMIDAL	H	B	DP
Córcoles			
N	11	10	15
Min	38.4	33.1	32.1
Max	45.8	38.7	39.3
Mean	41.88	35.54	35.55
S	2.79	1.8	1.98
H. matritense			
N	8	9	9
Min	35.5	29	27
Max	46.3	38	39
Mean	40.65	34.41	30.21
B. grimmi[1]			
N=1	39	34	37
B. caucasica[4]			
N=1	45	42	37
C. oettingenae[5]			
N	2	2	2
Min	37	32	24
Max	39	36	27
Mean	38	34	25.5

TABLE 7 - Comparative dimensions of the pyramidal of *H. matritense* from Córcoles. references in table 1. *Dimensions comparées du pyramidal de* H. matritense *de Córcoles.*

Magnum (Tab. 9; Fig. 4) - It also has the anterior face higher than wide. Medially, the trapezoid facet is triangular and usually shows a deep rentrant at its anterior union with the McII-facet.

Unciform (Tab. 10; Fig. 5) - The two proximal facets are united at an obtuse angle. That for the pyramidal is very convex, and it can be projected postero-laterally, without reaching the lateral border. The disto-lateral facets do not show clear limits between them.

McII (Tab. 11; Fig. 6) - The proximal facet is very convex antero-posteriorly and somewhat concave transversely. On the medial face, there is a trapezium-facet whose development is varied. Laterally, the magnum-facet is long and distally projected at its posterior part, while the McIII-facet is only developed anteriorly. The diaphysis is triangular in section. The distal articulation for the first phalanx has a subrectangular outline in distal view, and the median keel is slightly marked.

McIII (Tab. 12; Fig. 6) - Both proximal facets forms a high crest between them. Laterally, both facets for the McIV are well separated, the posterior one being or not united to the magnum facet. The diaphysis is trapezoidal in section. The distal articulation has its proximal border very convex.

McIV (Tab. 13; Fig. 6) - The proximal facet, for the unciform, is triangular in shape, and it forms a continuous articular surface with that for the McV, very convex. The diaphysis is rather bended, and has a triangular section. The distal facet is triangular outlined in distal view, and posteriorly the unevenness between both halves is greater than on the McII.

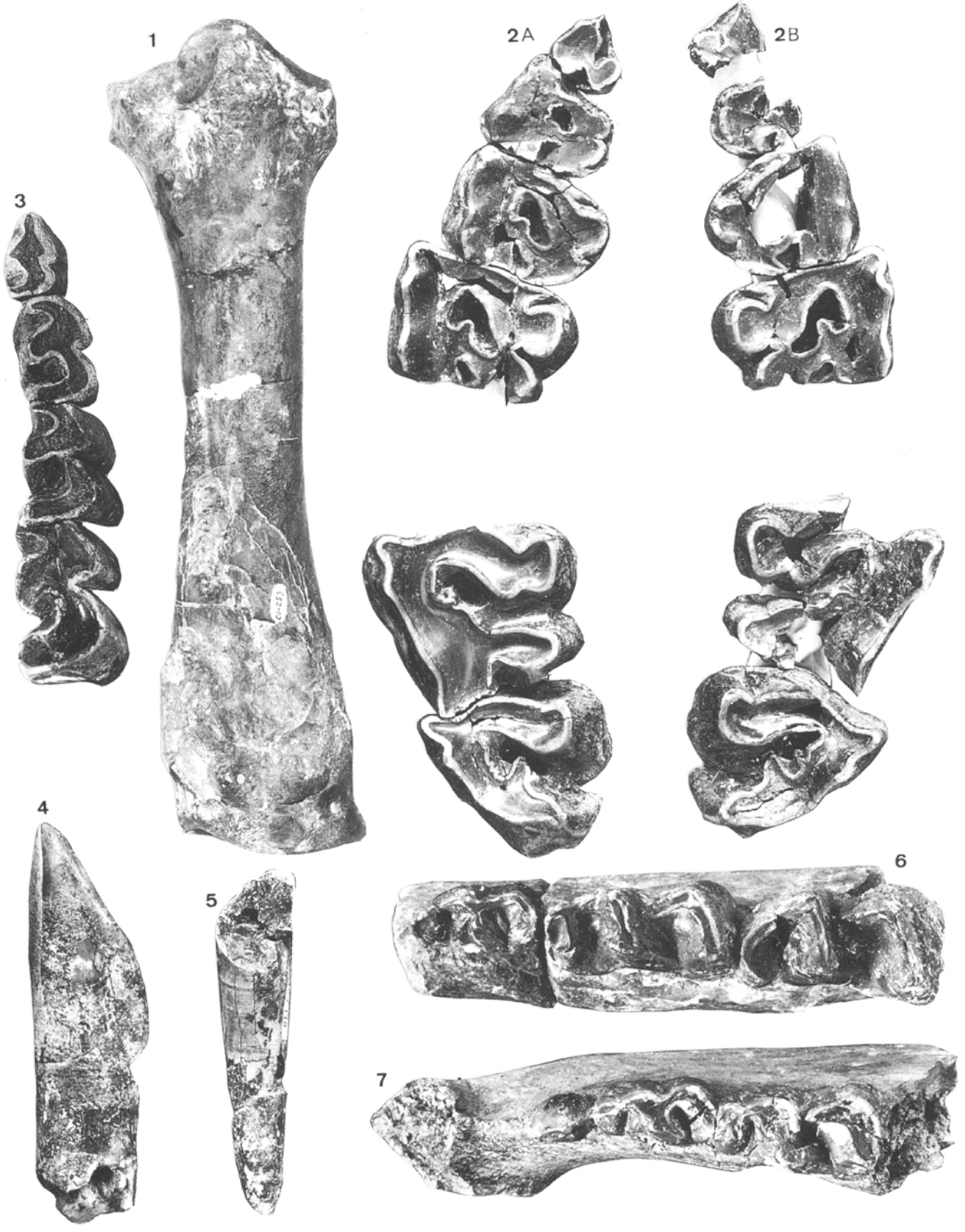
McV (Tab. 14; Fig. 6). It is a small and rounded reduced metapodial, with a large facet for the unciform bended at a right angle. On the medial face, there is a rectangular, concave facet for the McIV.

Patella (Tab. 15) - It is rhomboidal outlined, with a strong proximal apex, and very convex anteriorly.

Tibia (Tab. 16) - The tibial spine is high, with a deep and narrow central groove. An articular surface for the patella runs along the anterior rim of the medial femoral facet. Distally, the astragalus-facet extends posteriorly.

Astragalus (Tab. 17; Fig. 7) - The trochlea is well characterized by its indexes of depth and assimetry (Alférez & Iñigo 1990) whose mean values are 22.57 and 113.5, respectively. The trochlea is separated from the distal articulation by a narrow groove, but the 36.4% of the specimens have the internal lip joined to the navicular-facet. On the

FIGURE 2 - *Hispanotherium matritense*. Córcoles, Guadalajara, Spain. **1.** Co-253, left radius, posterior view. **2.** Upper series of a same individual rhinoceros, occlusal view, (A) right, Co-4943, P^1; Co-4942, P^2; C-4937, P^3; Co-4940, P^4; Co-4935, M^2; Co-4939, M^3. (B) left, Co-4945, P^1; Co-4944, P^2; Co-4941, P^3; Co-4938, P^4; Co-4934, M^2; Co-4936, M^3. **3.** Co-212, right lower series (P_2-M_1), occlusal view. **4.** Co-204, left I_2 of a male individual, occlusal view. **5.** Co-198, right I_2 of a female individual, occlusal view. **6.** Co-1109, right mandibular fragment with D_2-D_4, occlusal view. **7.** Co-3186, right mandibular fragment with D_1-D_4, occlusal view. ***1.*** *Radius gauche, vue postérieure.* ***2.*** *Série supérieure d'un même individu, vue occlusale, (A) droite (B) gauche.* ***3.*** *Série inférieure gauche, vue occlusale.* ***4.*** *I_2 gauche d'un individu mâle, vue occlusale.* ***5.*** *I_2 droite d'un individu femelle, vue occlusale.* ***6.*** *Fragment mandibulaire droit, vue occlusale.* ***7.*** *Fragment mandibulaire droit, vue occlusale. Fig. 1 x 0.5. Fig. 2-5 x 0.75. Fig. 6-7 x 1.*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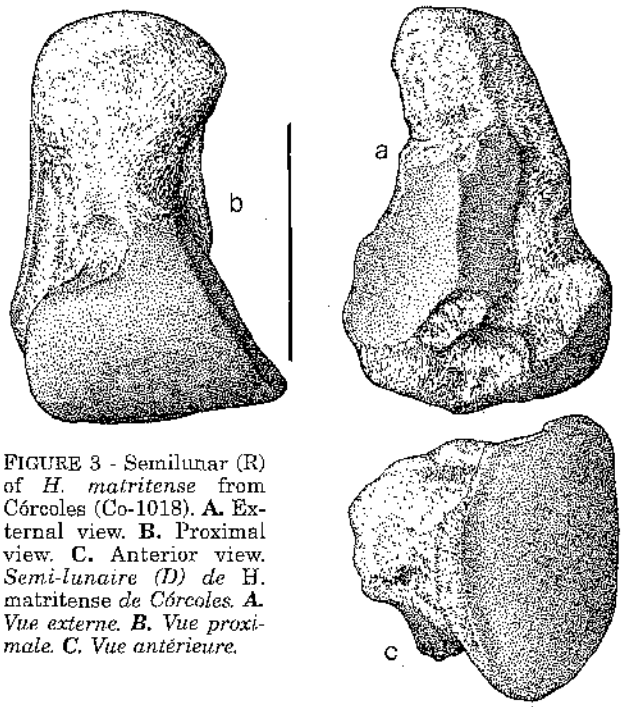

FIGURE 3 - Semilunar (R) of *H. matritense* from Córcoles (Co-1018). **A.** External view. **B.** Proximal view. **C.** Anterior view. *Semi-lunaire (D) de* H. matritense *de Córcoles. **A.** Vue externe. **B.** Vue proximale. **C.** Vue antérieure.*

TRAPEZOID	H	B	DP
Córcoles			
N	14	13	10
Min	21.4	18.5	29.2
Max	29.9	24.4	37.6
Mean	25.45	21.64	33.92
S	2.91	1.82	2.8
H. matritense			
N	4	3	3
Min	23.4	19.2	31.6
Max	27.3	22.1	36,9
Mean	25.02	20.57	34.43
B. caucasica[4]			
N=1	26	22	37
C. oettingenae[5]			
N=1	24	18	26

TABLE 8 - Comparative dimensions of the trapezoid of *H. matritense* from Córcoles. References in table 1. *Dimensions comparées du trapézoïde de* H. matritense *de Córcoles.*

MAGNUM	H	L art	B	DP
Córcoles				
N	5	7	11	4
Min	46.5	44	29.9	67.6
Max	42.8	48.5	39.1	79.7
Mean	47..58	45.71	33.91	72.45
S	0.71	1.58	3.18	5.3
H. matritense				
N	2	1	1	1
Min	40.8			
Max	48.4			
Mean	44.6	30	31.9	70.2
B. grimmi[1]				
N=1	58	37	42	82
B. caucasica[4]				
N=1	42	(25)	28	76
C. oettingenae[5]				
N=1	41	-	28	-

TABLE 9 - Comparative dimensions of the magnum of *H. matritense* from Córcoles. references in table 1. *Dimensions comparées du magnum de* H. matritense *de Córcoles.*

UNCIFORM	H	B	DP max	DP anat
Córcoles				
N	22	17	7	7
Min	33.3	42.8	52.5	43.6
Max	45.2	59.1	78.9	60.4
Mean	39.8	50.48	68.99	54.13
S	2.74	3.52	8.26	5.18
H. matritense				
N	3	2	1	1
Min	32.3	39.7		
Max	35.9	46		
Mean	34.63	43.73	59.5	41.2
B. grimmi[1]				
N=1	43	56	76	60
B. caucasica[4]				
N=1	40	57	63	-
C. oettingenae[5]				
N=1	44	-	-	-

TABLE 10 - Comparative dimensions of the unciform of *H. matritense* from Córcoles. References in table 1. *Dimensions comparées de l'unciforme de* H. matritense *de Córcoles.*

posterior face, the infero-external and internal facets are united. The astragalus Co-534, has the internal facet projected supero-internally. The supero-external facet for the calcaneum projects distally. Both distal articular surfaces form a smooth crest.

Calcaneum (Tab. 18; Fig. 8) - The tuber is long and has a strong unevenness. The sustentaculum is at a right angle with the longitudinal axis. On the external face, there are strong rugosities along the distal edge and under the beak. The supero-external facet for the astragalus is bended at an almost right angle, smoother on Co-1042 and Co-4327, and it presents a long distal projection. The internal and infero-external facets for the astragalus are fused. There exist a tibial-facet, but there is no fibular-facet on the lateral side. The distal articulation for the cuboid is triangular and concave-convex.

Cuboid (Tab. 19; Fig. 9) - The anterior face is higher than wide. The calcaneum-facet projects posteriorly and laterally; the astragalus-facet projects posteriorly forming a peak. On the internal face, the anterior facet for the ectocuneiform is separated from the distal articulation by a small, hardly differenciated, surface for the MtIII. The posterior concave part of the navicular-articulation forms a strong crest with the posterior facet for the ectocuneiform, which is large and concave.

Navicular (Tab. 20; Fig. 10) - The proximal facet is subrectangular. On the external face, the ante-

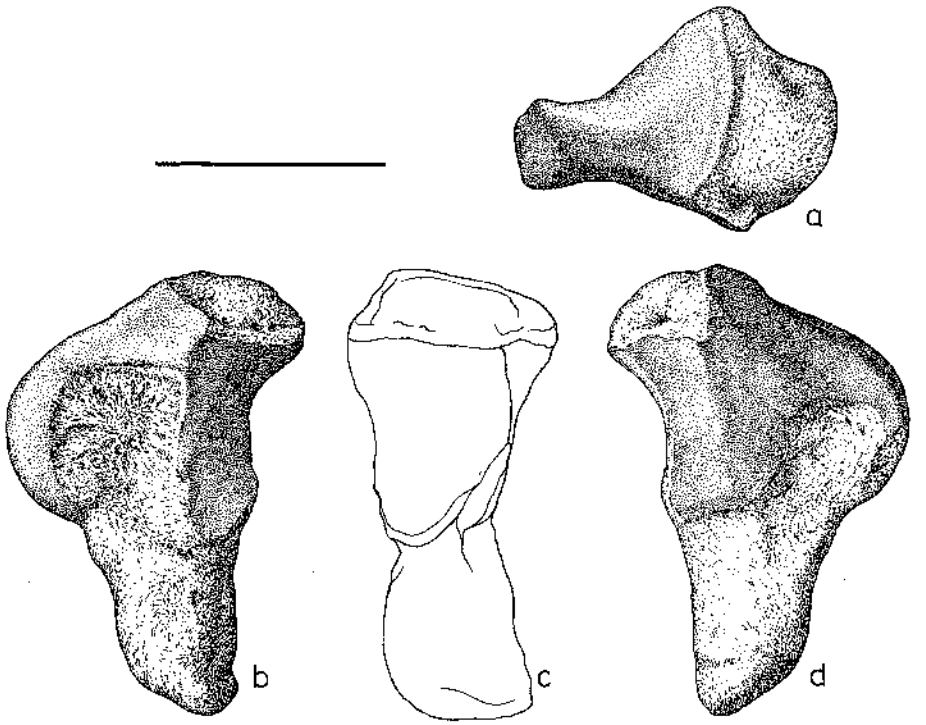

FIGURE 4 - Magnum (R) of *H. matritense* from Córcoles (Co-96). **a.** Proximal view. **b.** External view. **c.** Distal view. d. Internal view. ***a.*** *Vue proximale.* ***b.*** *Vue externe.* ***c.*** *Vue distale.* ***d.*** *Vue interne.*

rior facet for the cuboid is semicircular, and can be united (66% of the specimens) or not to the posterior one. Distally, the ectocuneiform-facet forms an obtuse angle with that for the mesocuneiform, and it is separated from the entocuneiform-facet by a narrow neck.

Ectocuneiform (Tab. 21; Fig. 11) - The proximal and distal facets are triangular in shape, with a deep and wide re-entrant on the external side. The MtIII-facet is concave-convex, and its posterior apex projects distally. On the internal face, the posterior facet for the MtIII is larger than the anterior one.

Mesocuneiform (Tab. 22) - Both proximal and distal facets are triangular outlined. The former is concave, although very slightly on the specimens Co-733 and Co-1183. The facet for the MtII is saddle-shaped. The development of the ectocuneiform-facet varies. There is a large entocuneiform-facet, which is in contact with the distal facet on Co-734 and Co-937.

MtII (Tab. 23; Fig. 6) - The proximal facet is triangular outlined, and it presents a double curvature, transversely concave. The ectocuneiform-facet is large, and may be connected with the proximal facet (54% of the specimens). Laterally, the anterior facet is flat and only articulates with the ectocuneiform; the posterior one differenciates an inferior subfacet for the MtIII. The diaphysis is bended medially, and it is triangular or rounded

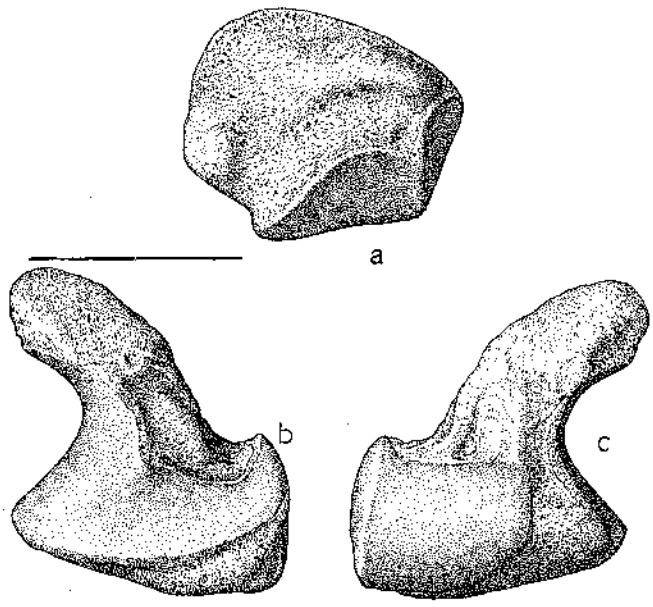

FIGURE 5 - Unciform (L) of *H. matritense* from Córcoles (Co-1022). **A.** Anterior view. **B.** Distal view. **C.** Proximal view. ***A.*** *Vue antérieure.* ***B.*** *Vue distale.* ***C.*** *Vue proximale.*

in section. The distal facet for the first phalanx is anteriorly convex, and subrectangular outlined in distal view.

MtIII (Tab. 24; Fig. 6) - The anterior edge of the ectocuneiform-facet presents a short external

Mc II	L	Prox B	Prox DP	Prox F B	Diaphysis B	Diaphysis DP	Dis B	Dis art B	Dis art DP
Córcoles									
N	1	7	5	11	5	5	2	6	7
Min		25.3	33.9	19.3	23.3	19.1	30.3	28.5	28
Max		31.4	40.3	23.8	27.5	24.1	33	31.6	33
Mean	138.7	27.81	37.82	21.16	25.98	21.62	31.65	30.15	30.13
S		2.26	2.36	1.41	1.63	2.12		1.02	1.72
H. matritense									
N	4	5	4		6	6	5	2	3
Min	122	(26.1)	22,4		16.7	13.6	24	26.4	23
Max	144.5	(29.5)	(27.3)		26.9	22.3	(29.5)	27.7	31.4
Mean	130.5	29.22	24.5	-	22.83	15.8	27.12	27.05	28.26
B. grimmi[1]									
N	3	3	4	3	3	3	3	3	3
Min	144	37	28	28	28	17	32	29	34
Max	162	40	38	33	34	17	43	36	41
Mean	151.3	38.33	33	30.3	30.33	17	36.33	31.66	36.66
B. caucasica[4]									
N=1	148	23	36	-	32	18	-	35	30

TABLE 11 - Comparative dimensions of the McII of *H. matritense* from Córcoles. References in table 1. *Dimensions comparées du McII de* H. matritense *de Córcoles.*

Mc III	L	Prox B	Prox DP	Diaphysis B	Diaphysis DP	Dis B	Dis art B	Dis art DP
Córcoles								
N	1	14	6	6	5	7	8	8
Min		46	32.6	33.4	17.5	44.6	38.1	32
Max		53.2	43	42.1	19.7	54.2	46.6	42.2
Mean	171.5	46.57	38.23	37.02	18.32	49.29	41.86	35.55
S		3.8	3.53	3.63	0.83	3.77	3.29	3.08
F. matritense								
N	2	8	8	7	6	2	2	2
Min	154.1	35.9	26.9	27.1	12.9	37	33	28.5
Max	155.8	45.5	36	43	15.5	39.7	34.1	29
Mean	154.95	39.75	30.75	33.03	14.15	38.35	33.55	28.75
B. grimmi[1]								
N	2	5	5	5	3	2	2	2
Min	168	45	36	(36)	17	50	41	36
Max	170	46	40	37	19	51	42	37
Mean	169	45.6	39	36.6	18	50.5	41.5	36.5
B. caucasica[4]								
N=1	168	46	38	38	21	49	-	38

TABLE 12 - Comparative dimensions of the McIII of *H. matritense* from Córcoles. References in table 1. *Dimensions comparées du McIII de* H. matritense *de Córcoles.*

Mc IV	L	Prox B	Prox DP	Diaphysis B	Diaphysis DP	Dis B	Dis art B	Dis art DP
Córcoles								
N	2	6	8	4	4	8	8	7
Min	129,9	33	31,8	25,3	16,9	33,8	30,3	30
Max	138,4	40	35,7	28	21	40	26,2	35,8
Mean	134,15	37,3	34,01	26,82	18,78	35,7	32,38	32,27
S		2,87	1,68	1,24	2,04	2,16	1,79	2,02
H. matritense								
N	2	5	5	5	5	3	3	3
Min	119,3	30	28,7	25	(27,5)	26,1	23,4	24,7
Max	121,8	32,5	32	(28,5)	(30)	30	28	(26)
Mean	120,55	31,36	30,26	27	28,62	27,97	25,4	25,4
B. grimmi[1]								
N	2	3	3	2	2	2	2	2
Min	140	33	34	27	16	36	30	31
Max	144	36	36	27	17	36	30	31
Mean	142	34,33	35,33	27	16,5	36	30	31
B. caucasica[4]								
N=1	137	33	35	28	20	35	35	35

TABLE 13 - Comparative dimensions of the McIV of *H. matritense* from Córcoles. References in table 1. *Dimensions comparées du McIV de* H. matritense *de Córcoles.*

MC V		H	B	DP
Córcoles				
	N	2	3	3
	Min	28.5	25	18.2
	Max	28.6	26.6	21.1
	Mean	28.55	25.97	20.07

TABLE 14 - Dimensions of the McV of *H. matritense* from Córcoles. *Dimensions du McV de* H. matritense *de Córcoles.*

PATELLA		H	B	DP
Córcoles				
	N	3	4	10
	Min	67,7	71	(31,2)
	Max	70,1	76,5	39,5
	Mean	69,13	73,17	36,9
	S		1.46	2.58

TABLE 15 - Dimensions of the patella of *H. matritense* from Córcoles. *Dimensions de la rotule de* H. matritense *de Córcoles.*

	Prox			Diaphysis		Dis		Dis	art
TIBIA	L	B	DP	B	DP	B	DP	B	DP
Córcoles									
N		1	1	1	1	2	5	2	4
Min						87.5	51.7	70.3	50.4
Max						92.5	64	73.7	61
Mean	-	96	97	49.6	41.4	90	58.76	72	56.4
S							4.67		4.49

TABLE 16 - Comparative dimensions of the tibia of *H. matritense* from Córcoles. References in table 1. *Dimensions comparées du tibia de* H. matritense *de Córcoles.*

ASTRAGALUS	H	B	Med DP	DL	Dis B	Dis B	art DP
Córcoles							
N	11	17	14	19	16	17	16
Min	63.4	63.5	43.3	42.3	58	57.3	37
Max	69	75	58,4	49.6	69.3	66.8	45.1
Mean	66.31	70.39	48.65	46.93	64.21	61.35	40.45
S	2.11	2.11	3.74	2.53	3.25	2.8	2.15
H. matritense							
N	10	8	8	10	8	9	6
Min	(52.3)	61.6	34	(31.5)	(56)	(52)	(30)
Max	69.3	74.8	49.4	47.8	62.3	59.6	42.2
Mean	59.09	65.96	40.52	42.93	58.9	54.82	35.5
B. grimmi[1]							
N	7	8	7			8	7
Min	65	72	51			62	38
Max	77	86	59			76	46
Mean	73	79.5	55.71	-	-	70.75	43.14
B. caucasica[4]							
N=1	58	79	-	-	-	69	43
C. oettingenae[5]							
N	2	2				2	2
Min	54	59				55	30
Max	57	62				56	35
Mean	55.5	60.5	-	-	-	55.5	30.5

TABLE 17 - Comparative dimensions of the astragalus of *H. matritense* from Córcoles. References in table 1. *Dimensions comparées de l'astragale de* H. matritense *de Córcoles.*

zone more convex, well differenciated by an inflexion point. The lateral facets for the MtIV are well separated by a wide depression. The section of the diaphysis is subtrapezoidal. The distal facet is limited anteriorly by a well marked transversal groove. This facet is nearly flat on the anterior face, less convex than on the McIII.

MtIV (Tab. 25; Fig. 6) - The proximal epiphysis has a very developed external tuberosity. The cuboid-facet is roughly rounded or triangular outlined, and it may present a postero-lateral reentrant. Both MtIII-facets have similar size, and they are well separated. The section of the diaphysis is subtriangular. The first phalanx facet has a subtriangular distal outline.

Central phalanx (Tab. 26) - The great number of specimens from Córcoles allow appreciating anatomical differences to separate the anterior phalanges from the posterior ones. Similarly to the extant ungulates, we infer that the most robust specimens correspond to the fore limb, and the most slender ones to the hind limb, modifying what is proposed by Cerdeño (1993) from the material recovered at La Retama site (Cuenca, Spain).

The first phalanges are higher than wide. On the posterior ones, the proximal facet presents a smooth and short central groove, which is not appreciated on the anterior phalanges.

On the third anterior phalanges, the proximal facet occupies almost the whole proximal face, while the posterior phalanges have a relatively smaller facet, laterally bounded by large wrinkled zones. In addition, the posterior face is somewhat

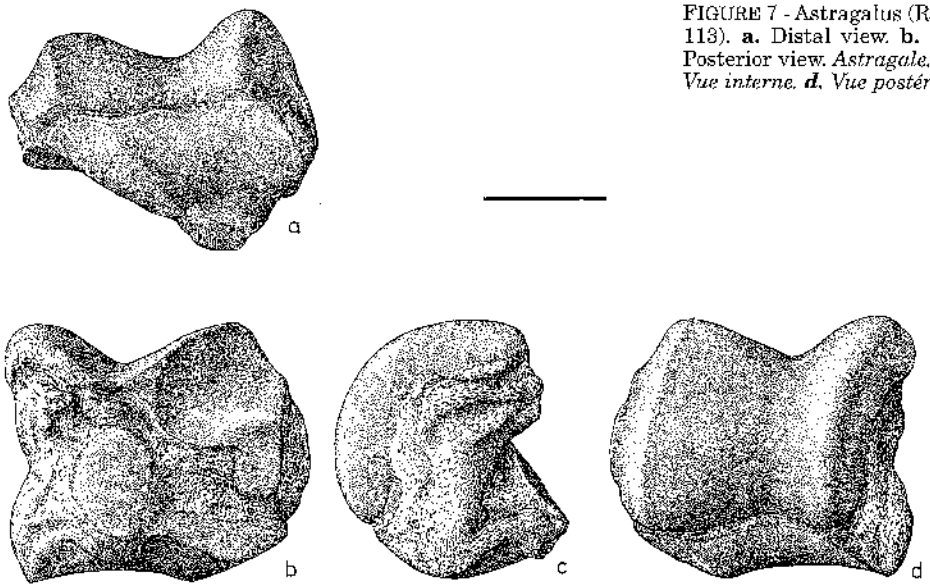

FIGURE 7 - Astragalus (R) of *H. matritense* from Córcoles (Co-113). **a.** Distal view. **b.** Anterior view. **c.** Internal view. **d.** Posterior view. *Astragale. **a.** Vue distale. **b.** Vue antérieure. **c.** Vue interne. **d.** Vue postérieure.*

concave on the anterior phalanges, and flat on the posterior ones.

Lateral phalanges (Tab. 27) - They can be grouped in two samples after their size. We deduce the largest ones can correspond to the fore limb, since the metacarpals are larger than the metatarsals.

Following the distal articulation of the metapodials, we know that the first external phalanges are much turned to the central digit than the first internal phalanges. This characteristic is reflected on the morphology of the distal facet for the second phalanx. On the digit IV, the postero-external apex projects proximally, and the surface is concave-convex following the diagonals. On the contrary, on the internal phalanges, the posterior border of this facet is straight, and the curvature is much smoother.

On the second phalanges, the morphology of the proximal facet correlates with the distal one of the first phalanges, and so with the digit to which they correspond. The specimens of the second digit have a concave facet, while these of the fourth digit have a concave-convexe facet, with a pointed postero-external apex.

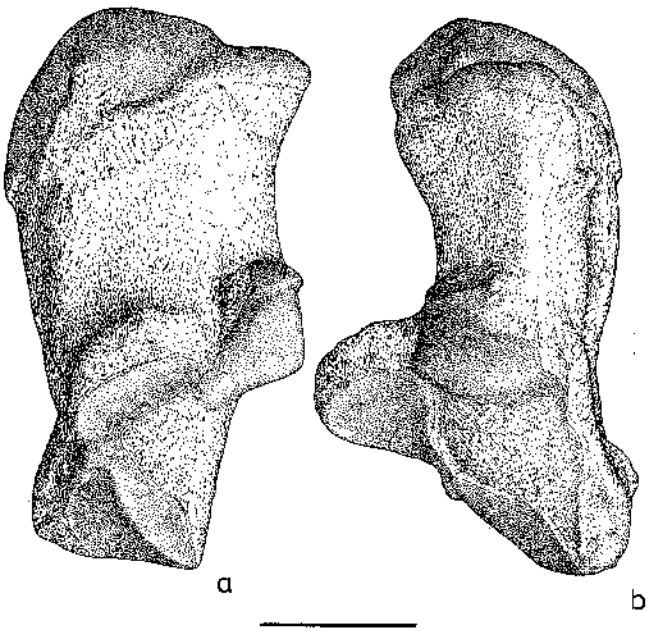

FIGURE 8 - Calcaneum (L) of *H. matritense* from Córcoles (Co-1184). **a.** Internal view. **b.** Anterior view. ***a.** Vue interne. **b.** Vue antérieure.*

FIGURE 6 - *Hispanotherium matritense*. Córcoles, Guadalajara, Spain. **1.** Co-170, right McII, external view. **2.** Co-1050, left McIII, posterior view. **3.** Co-1045, right McIV, medial (A) and posterior (B) views. **4.** Co-4269, right McV, anterior view. **5.** Co-649, right pisiform, external view. **6.** Co-548, left MtIV, medial view. **7.** Co-539, left MtIII, posterior view. **8.** Co-3908, right MtII, anterior view. **9.** Co-1050 and Co-569, left McIII and McIV, proximal view. **10.** Co-3908 and Co-548, left MtIII and MtIV, proximal view. ***1.** McII droit, vue externe. **2.** McIII gauche, vue postérieure. **3.** McIV droit, vues interne (A) et antérieure (B). **4.** McV droit, vue antérieure. **5.** Pisiforme droit, vue externe. **6.** MtIV gauche, vue interne. **7.** MtIII gauche, vue postérieure. **8.** MtII droite, vue antérieure. **9.** McIII et McIV gauches, vue proximale. **10.** MtIII et MtIV gauches, vue proximale.* Fig. 1-3 and 5-10 x 0.75. Fig. 4 x 1.


1
2
3A
3B
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9
10

CALCANEUM	L	Tub B	Tub DP	Sust B	Sust DP	Beak	Pos min B
Córcoles							
N	6	7	8	4	14		12
Min	98.2	36.5	56.4	62	47.5		23.5
Max	109.7	41.6	65	64.1	55		29.8
Mean	104.73	39.62	60.56	63.28	52.42		26.7
S	4.22	1.63	3.34	0.98	2.55		2.06
H. matritense							
N	5	6	5	3	5		6
Min	(96)	(27.8)	(50.5)	(45.3)	51		24.5
Max	106.4	38.4	60	58.6	56.5		31
Mean	102.92	33.62	56.7	51.43	53.68		27.4
B. grimmi[1]							
N	3	2	1	1			3
Min	111	35					27
Max	125	53					38
Mean	118	44	48	66	-		30.67
B. caucasica[4]							
N=1	112	39	63	67	-		27

TABLE 18 - Comparative dimensions of the calcaneum of *H. matritense* from Córcoles. References in table 1. *Dimensions comparées du calcanéum de* H. matritense *de Córcoles.*

CUBOID	H	Ant H	B	DP	Prox art B	Prox art DP
Córcoles						
N	11	20	17	14	15	15
Min	40	31.2	26.1	50.8	28	35.3
Max	52.5	38.8	33.7	65.9	34	46.3
Mean	46.32	34.74	30.68	56.36	30.77	39.09
S	4.08	1.94	2.05	3.39	1.57	3.49
H. matritense						
N	4	7	7	5	5	5
Min	(33.8)	31	23.5	(48.5)	20.4	26.4
Max	41	34.4	(31.4)	52.4	28.6	(37.8)
Mean	36.87	32.66	27.06	50.8	24.52	32.06
B. grimmi[1]						
N=1	52	36	33	65		
B. caucasica[4]						
N		3	3	3		
Min		34	36	57		
Max		35	39	63		
Mean		36	37.33	59.66		
C. oettingenae[5]						
N=1	44		29	47		

TABLE 19 - Comparative dimensions of the cuboid of *H. matritense* from Córcoles. References in table 1. *Dimensions comparées du cuboïde de* H. matritense *de Córcoles.*

NAVICULAR	H	B	DP
Córcoles			
N	26	24	26
Min	20	32.3	41.4
Max	26.6	43	58.2
Mean	24.7	38.14	50.62
S	1.71	2.95	3.83
H. matritense			
N	5	5	5
Min	21.5	35	46
Max	23	37.7	53.2
Mean	22.1	36	49.5
B. grimmi[1]			
N	3	2	2
Min	19	40	46
Max	29	(51)	(55)
Mean	24.66	45.5	50.5
B. caucasica[4]			
N		2	2
Min		38	54
Max		39	57
Mean	-	38.5	55.5

TABLE 20 - Comparative dimensions of the navicular of *H. matritense* from Córcoles. References in table 1. *Dimensions comparées du naviculaire de* H. matritense *de Córcoles.*

ECTOCUNEIFORM	H	B	DP
Córcoles			
N	10	12	7
Min	23.1	37.8	41.9
Max	25.7	43.3	47.6
Mean	24.39	41.28	44.14
S	0.83	1.65	1.75
H. matritense			
N	5	5	2
Min	17.5	31.8	36
Max	22.1	40.6	39.8
Mean	19.76	36.64	37.9
B. caucasica[4]			
N=1	22	44	47

TABLE 21 - Comparative dimensions of the ectocuneiform of *H. matritense* from Córcoles. References in table 1. *Dimensions comparées de l'ectocunéiforme de* H. matritense *de Córcoles.*

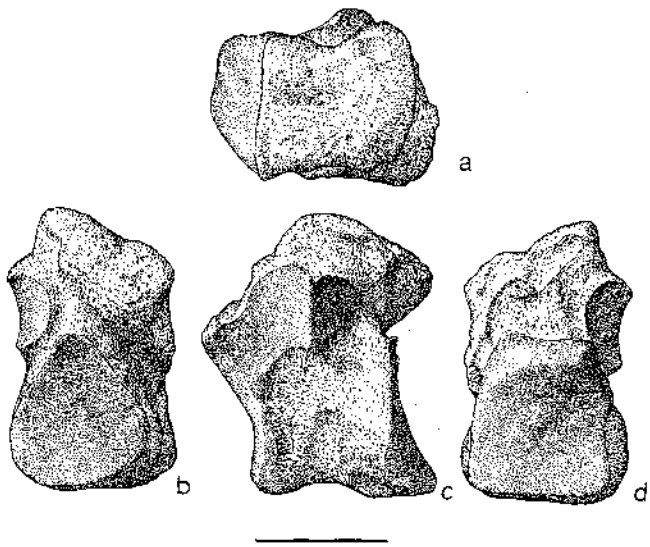


FIGURE 9 - Cuboid (R) of *H. matritense* from Córcoles (Co-1120). **A.** Anterior view. **B.** Distal view. **C.** Internal view. **D.** Proximal view. *Cuboïde (D) de* H. matritense *de Córcoles. **A.** Vue antérieure. **B.** Vue distale. **C.** Vue interne. **D.** Vue proximale.*

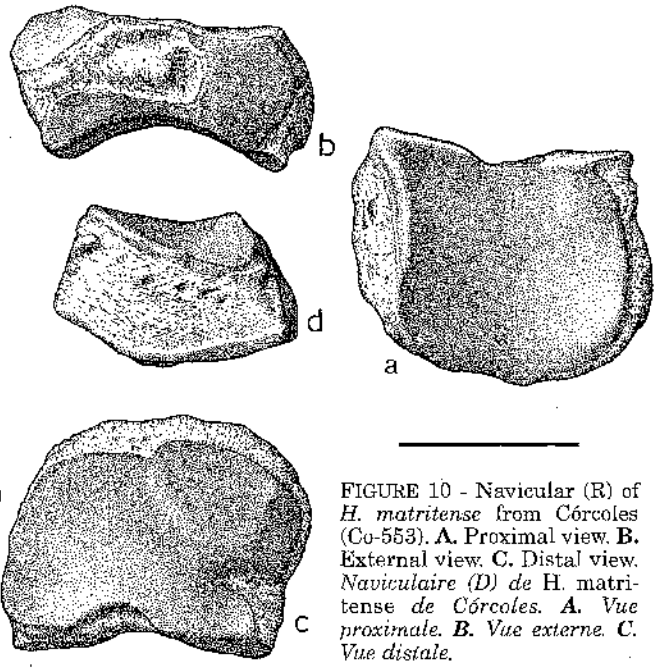


FIGURE 10 - Navicular (R) of *H. matritense* from Córcoles (Co-553). **A.** Proximal view. **B.** External view. **C.** Distal view. *Naviculaire (D) de* H. matritense *de Córcoles. **A.** Vue proximale. **B.** Vue externe. **C.** Vue distale.*

MESOCUNEIFORM	H	B	DP
Córcoles			
N	12	12	10
Min	12.8	14.2	25.1
Max	18.1	18.2	33.1
Med	15.07	16.02	29.05
S	1.72	1.28	2.6

TABLE 22 - Dimensions of the mesocuneiform of *H. matritense* from Córcoles. *Dimensions du mésocunéiforme de* H. matritense *de Córcoles.*

DISCUSSION

The studied material presents the diagnostic characters of *Hispanotherium matritense*, and it is very similar to other described remains of this species, with minor differences (Cerdeño 1989).

Concerning dentition, the greatest variability concerns the enamel folds of the median valley on the upper cheek-teeth, being simpler at Córcoles than on other known specimens. The upper premolars from Torrijos (Toledo, Spain), Puente de Toledo (Madrid, Spain) and Quintanelas (Sabugo, Portugal) present a wider and less deep lingual groove than on the premolars from Córcoles. The M^2 from this site do not present a constricted hypocone, as it is on the M^2 from Quintanelas.

The postcranial elements from Córcoles are similar in size to other known *H. matritense*, only the material from Torrijos being clearly smaller.

The only postcranial bone with an outstanding feature is the semilunar. In Córcoles, it does not present an external groove that limits posteriorly the inferior pyramidal-facet, and this one is pretty longer than on the specimens from Torrijos, Tarazona and La Retama (Cuenca, Spain), where that groove does exist.

		Prox		Prox F	Diaphysis		Dis	Dis art	
MT II	L	B	DP	B	B	DP	B	B	DP
Córcoles									
N	2	13	12	12	6	6	5	10	10
Min	131	(16)	29.3	13.9	19.5	18	26	25.6	25,5
Max	134	23.5	37.7	20.5	22.5	21	28.2	28	30
Mean	132.5	20.63	33.87	16.08	20.87	19.37	27.16	26.65	28.11
S		1,9	2.77	1.86	1.12	1.23	0.96	0.8	1.27
B. grimmi[1]									
N		2	1	2	2	2			
Min		31		28	19	20			
Max		31		31	22	22			
Mean	-	31	33	29.5	20.5	21	-	-	-
B. caucasica[1]									
N=1	-	22	36	-	22	20	-	-	-

TABLE 23 - Comparative dimensions of the MtII of *H. matritense* from Córcoles. References in table 1. *Dimensions comparées du MtII de* H. matritense *de Córcoles.*

Mt III	L	Prox B	Prox DP	Diaphysis B	Diaphysis DP	Dis B	Dis art B	Dis art DP
Córcoles								
N	2	21	8	2	3	5	4	7
Min	145	38.8	33	35	18.3	45.8	39.5	30.8
Max	150.3	49.2	41	36	19.8	52.4	45.8	37.1
Mean	147.65	43.4	36.88	35.5	19.3	48.45	42.23	33.87
S		3.20	3.27			2.82	2.64	2.31
H. matritense								
N	1	2	3	2	2	1	1	
Min		(32.5)	(28)	31.7	16.6			
Max		47	43	41	20			
Mean	147	39.75	34.33	36.35	18.3	(39,5)	(33)	
B. caucasica[4]								
N=1		47	43	41	20			

TABLE 24 - Comparative dimensions of the MtIII of *H. matritense* from Córcoles. References in table 1. *Dimensions comparées du MtIII de* H. matritense *de Córcoles.*

Mt IV	L	Prox B	Prox DP	Diaphysis B	Diaphysis DP	Dis B	Dis art B	Dis art DP
Córcoles								
N	2	10	9	7	7	2	5	5
Min	137	31.5	30.3	21.9	20.6	29.6	27.1	27
Max	143.3	42	41.2	25.2	25	31.9	31.6	29,7
Mean	140.15	37.91	36.13	23.17	21.96	30.75	28.74	28,28
S		2.74	2.97	1.16	1.43		1.69	0.96
H. matritense								
N=1		35	30,3					
B. grimmi[1]								
N	1	5	5	3	2	1	1	1
Min		37	35	23	20			
Max		40	45	27	21			
Mean	147	39.4	40	24.66	20.5	30	28	34
B. caucasica[4]								
N=1	145	34	31	24	20	29	28	32
C. oettingenae[5]								
N=1								

TABLE 25 - Comparative dimensions of the MtIV of *H. matritense* from Córcoles. References in table 1. *Dimensions comparées du MtIV de* H. matritense *de Córcoles.*

CENTRAL PHALANX	H	B	DP	Prox art B	Prox art DP	Dis art B	Dis art DP
First, fore limb							
N	8	6		6	4	2	2
Min	28.7	36.2		34.2	21	33.8	19
Max	36.7	42.8		41	28.9	37.7	21.6
Mean	31.55	38.65		37.33	25.58	35.75	20.3
S	2.67	2.7		2.81	3.35		
First, hind limb							
N	11	11		11	6	9	5
Min	25.3	38.4		34.4	23.8	33.5	19.3
Max	31.8	44.2		40.7	27.9	39.3	33
Mean	29.06	41.46		37.92	25.27	36.47	22.96
S	1.71	2.03		2.02	1.44	1.81	5.78
Second, fore limb							
N	7	7	6	7	6	6	6
Min	20.2	39.6	19	35.5	17.4	36.6	15.8
Max	24.2	46.3	22.3	41.2	20.5	40.7	18.9
Mean	21.94	2.09	20.87	37.56	18.78	38.53	17.33
S	1.54	2.26	1.34	1.81	1.25	1.84	1.3
Second, hind limb							
N	4	6	6	6	5	2	6
Min	22.4	35.7	18.8	31	16.8	31.2	15.3
Max	24.7	41	21.5	38	19.4	35.9	17.2
Mean	23.55	38.75	20.86	33.72	18.28	33.55	16.78
S	0.94	1.98	1.02	2.97	1.03		1.34

TABLE 26 - Comparative dimensions of the central phalanx of *H. matritense* from Córcoles. References in table 1. *Dimensions comparées des phalanges du doigt central de* H. matritense *de Córcoles.*

The *H. matritense* from Córcoles greatly contributes to the knowledge of this species. First of all, the I_1 are described for the first time for *H. matritense*; the sexual dimorphism on the I_2 is stated; and many milk molars are described, quite scarce at other sites. Besides, the constriction of the

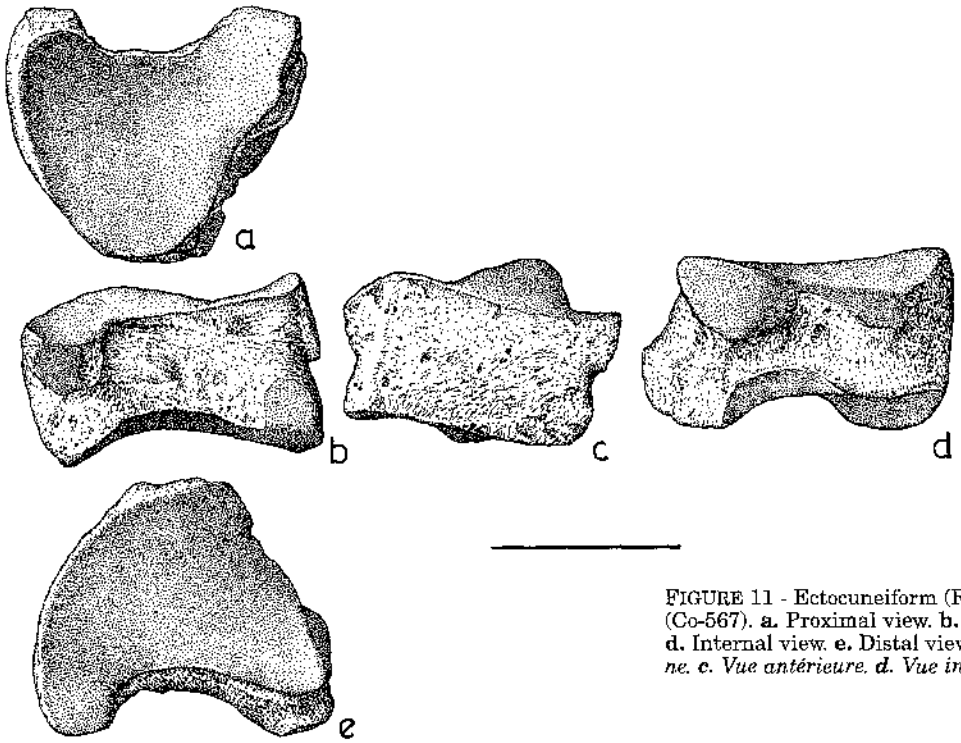


FIGURE 11 - Ectocuneiform (R) of *H. matritense* from Córcoles (Co-567). **a.** Proximal view. **b.** External view. **c.** Anterior view. **d.** Internal view. **e.** Distal view. ***a.*** *Vue proximale.* ***b.*** *Vue externe.* ***c.*** *Vue antérieure.* ***d.*** *Vue interne.* ***e.*** *Vue distale.*

metaconid on the lower teeth has been observed with a low frequency within the sample, and lead us to exclude this character from the diagnosis of the species. Concerning the postcranial skeleton, the remains from Córcoles constitute the best sample of *H. matritense* at a single site.

The whole sample has therefore allowed a more complete comparison with other "elasmotherines", whose synonymy with *Hispanotherium* has been previously proposed (Antunes & Ginsburg 1983; Cerdeño 1989). The first authors stated the synonymy between *Hispanotherium* and the genera *Begertherium, Caementodon* and *Beliajevina*. Cerdeño (1989) supported this opinion, considering two species of *Hispanotherium*: *H. matritense* and *H. grimmi*, even questioning their possible synonymy. She included *Camentodon oettingenae* and *Begertherium borissiaki* into *H. matritense*, and did not justify the separation of *Beliajevina caucasica* from *H. grimmi*. The same author (Cerdeño 1989) observed a trend towards a decrease of slenderness from *H. matritense* to *H. grimmi* and *B. caucasica*. However, among the Córcoles sample, there is a McIII stronger than the Asian specimens (Fig. 12).

The synonymy of *C. oettingenae, B. borissiaki* and *B. tekkayai* with *H. matritense* is confirmed when compared with the remains from Córcoles.

The morphology of *B. grimmi* and *B. caucasica* fits quite well within the observed variation of *H. matritense*, and minor differences concerning the postcranial bones could be due to intraspecific variation.

The tooth size is very similar for these three rhinos (Figs. 13-14). On the contrary, the postcranial skeleton of *B. grimmi* and *B. caucasica* is usually larger than the mean values of *H. matritense*. For some bones, a lesser relative breath (breath/thickness) is verified in *H. matritense* (Tab. 4-25).

In summary, the material from Córcoles closes *H. matritense* to *B. grimmi*, and lead us to state their synonymy at both generic and specific levels. The size of *B. caucasica* separates this taxa as a different species, but it does not seem enough to justify a distinct genus.

In contrast with this viewpoint, Fortelius and Heissig (1989) consider the taxonomical validity of all the "elasmotherine" species. They state that *C. oettingenae* differs from *H. matritense* by its smaller size and the slightly marked folds on the ectoloph on the upper teeth. However, this latter statement is also valid for *H. matritense*, and there are not metrical differences.

The same authors present a cladogram of the "elasmotherine" species using some characters that are debatable. For instance, they establish the lesser development of the I_2 in *Begertherium*, though this statement has been already refuted by Cerdeño (1989) based on the presence of small I_2 of *H. matritense* at Quintanelas, and the variation of the I_2 from Torrijos, also observed now at Córcoles.

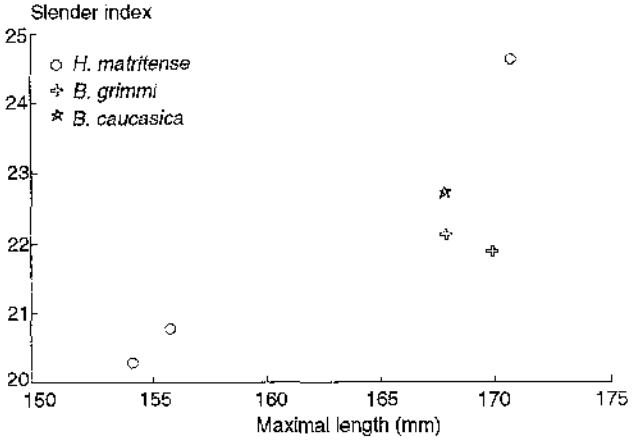
LATERAL PHALANX	H	B	DP	Prox art B	Prox art DP	Dis art B	Dis art DP
First, fore limb Digit II							
N	8	9	8	7	4	7	5
Min	30	27.8	26	25.3	24	23.5	20.7
Max	33.8	34.3	31	28	25.7	28.7	26.3
Mean	31	31.03	28.09	26.42	24.85	26.14	22.24
S	1.19	1.87	1.41	0.97	0.83	1.8	2.34
First, fore limb Digit IV							
N	6	6	5	5	4	7	7
Min	29.6	31.2	25.3	26	23	25.3	19
Max	32	36	28.4	27.7	24.7	28.2	22.7
Mean	30.52	32.78	26.92	26.76	23.63	27.1	21.3
S	0.84	1.72	1.1	0.81	0.81	0.95	1.2
First, hind limb Digit II							
N	6	6	6	6	6	5	4
Min	25.4	27.9	24.4	23.8	22	23	19.3
Max	30.2	29.5	26.6	25.6	24	25.1	20.2
Mean	28.3	28.63	25.59	24.42	22.85	24.38	19.77
S	1.71	0.61	1.07	0.73	0.74	0.84	0.44
First, hind limb Digit IV							
N	7	6	7	5	5	5	6
Min	26.9	30.2	24.1	25.4	21.5	23	18.5
Max	30.7	33.6	27.5	26.8	24.6	26.8	20.8
Mean	28.41	31.6	25.37	25.92	22.62	25.24	19.52
S	1.24	1.23	1.18	0.61	1.25	1.42	0.79
Second, fore limb Digit II							
N	4	4	4	4	4	3	3
Min	22.6	29.3	21.6	26.2	26.2	24.9	19.2
Max	24	31.4	23.6	28.2	28.2	28.4	20.3
Mean	23.33	30.53	22.6	27.43	27.43	26.2	19.9
S	0.64	0.9	0.82	0.9	0.9		
Second, fore limb Digit IV							
N	10	10	10	9	10	5	5
Min	22.4	28.5	18.9	25.7	17.9	23.8	18.6
Max	25.7	31.9	21.3	29	19.7	30	20
Mean	23.43	30.13	20.32	27.14	18.7	26.12	19.24
S	1	1.13	0,74	1.18	0.66	2.81	0.62
Second, hind limb Digit II							
N	7	7	6	7	5	4	5
Min	19.3	26.7	18	23.4	17	24.2	15.5
Max	21.3	28.9	19.9	26.4	18.3	25.6	18
Mean	20.33	27.63	18.88	24.76	17.44	24.65	17.22
S	0.86	0.79	0.72	1.04	0.5	0.65	0.99
Second, hind limb Digit IV							
N	6	6	6	6	6	5	4
Min	19.4	26.7	17.6	23.7	17.2	23.7	18.1
Max	22.5	28.3	20.3	28	19	26.1	19.9
Mean	21.23	27.68	19.5	25.77	18.05	24.56	18.74
S	1.09	0.57	0.98	1.52	0.76	1.01	0.83

TABLE 27 - Comparative dimensions of the lateral phalanx of *H. matritense* from Córcoles. References in table 1. *Dimensions comparées des phalanges des doigts latéraux de* H. matritense *de Córcoles.*

Other characters yielded by Fortelius and Heissig (1989) seem to be of lesser importance. The hypsodonty is badly comparable, since there hardly exist unworn teeth of *Hispanotherium*. The differences referred to the depth of the postfossette and the development of the cingulum do not appear to justify a generic distinction.

With respect to *B. caucasica*, it appears within their cladogram in a different clade than *Hispanotherium, Caementodon* and *Begertherium*. The authors state that *B. caucasica* has smaller premolars in relation to the molars, but this statement is not verified when the mean values of the upper teeth of both species are compared (Fig. 15). We do not agree either with their statements concerning the different position of the metaloph of the P^{3-4}, and the straigth hypolophid of the lower molars, since the figures of Borissiak (1938) show a morphology which keeps within the morphological variation of *H. matritense*.

One added problem to this comparison is the lack of good cranial remains of these "elasmotherines".



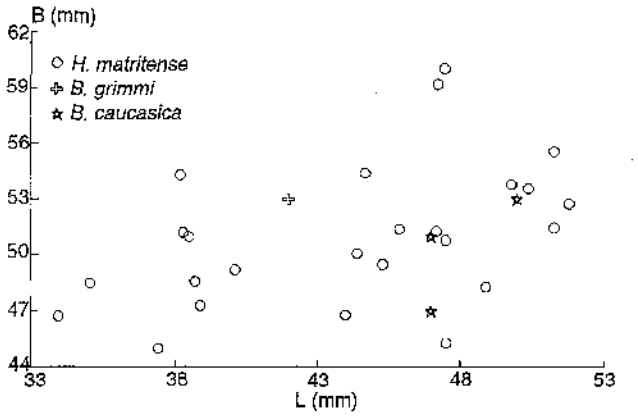
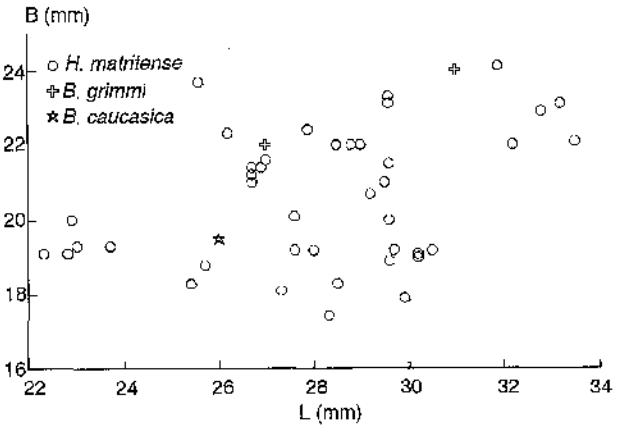


FIGURE 12-13 - **12.** Scatter diagram of the McIII of *H. matritense, B. grimmi* and *B. caucasica.* **13.** Scatter diagram of M^{1-2} of *H. matritense, B. grimmi* and *B. caucasica.* ***12.*** *Diagramme de dispersion des McIII (Longueur maximale/indice de gracilité) de* H. matritense, B. grimmi *et* B. caucasica. ***13.*** *Diagramme de dispersion des* M^{1-2} *de* H. matritense, B. grimmi *et* B. caucasica.



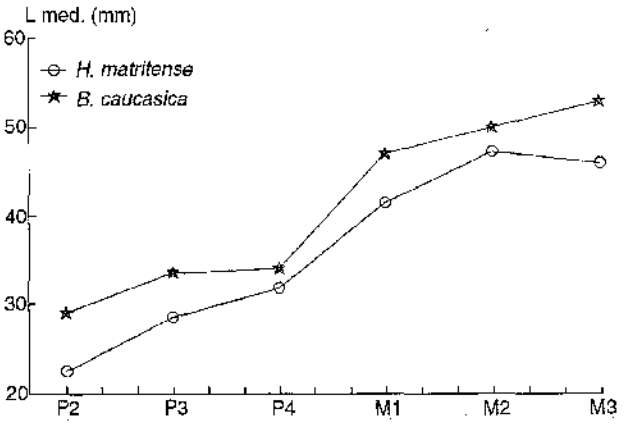


FIGURE 14-15 - **14.** Scatter diagram of P_{3-4} of *H. matritense, B. grimmi* and *B. caucasica.* **15.** Comparative relationship of the mean length of the upper teeth of *H. matritense* and *B. caucasica.* ***14.*** *Diagramme de dispersion des* P_{3-4}. ***15.*** *Relation comparative des longueurs moyennes des dents supérieures de* H. matritense *et* B. caucasica.

The debated position of the horn is quite speculative. Only two fragmentary nasal bones of *Hispanotherium* are known: one of *H. matritense* (unpublished, Paseo de las Acacias, Madrid) and other of *H. grimmi* from Sofça 4 (Heissig 1976; revised by E.C.). None of them show a trace of horn rugosity. Nevertheless, both *B. borissiaki* and *B. caucasica* present a well developed nasal horn boss. Since we establish *B. borissiaki* as synonym of *H. matritense,* this fact leads to consider a possible sexual dimorphism concerning the presence of nasal horn (Cerdeño 1995), as it happens in other rhinocerotid taxa (e.g., *Hoploaceratherium, Teleoceras, Menoceras* and others).

PALAEOENVIRONMENTAL AND BIOCHRONOLOGICAL REMARKS

Besides the morphometric characteristics of the *H. matritense* from Córcoles, there are several interesting points concerning its palaeobiology and temporal distribution.

H. matritense is a characteristic species of the MN4b or D biozone (Mein, 1975; Daams & Meulen 1984). Most of the Spanish and Portuguese sites with *H. matritense* correspond to this biozone within the Middle Miocene (in Portugal it continues later into the MN5, and it also appears in France in the MN5). Besides, at the Spanish localities it is the only species of rhinoceros known at that time (Cerdeño 1989; Cerdeño & Nieto 1995). Therefore, the presence of *H. matritense* at Córcoles implies, on one hand, the extension of its temporal range, since Córcoles corresponds to the older MN4a or C zone (Moyá & Alférez 1988); and, on the other hand, it coexists with another rhinoceros species, *Protaceratherium platyodon* (Iñigo 1994). These differences could probably be due to climatic and environmental changes. The MN4b /

Stages		Mein 1975	Daams & Freudental 1981	EUROPEAN SITES	ASIAN SITES
VALLESIAN	LOWER	9	I H		Yaylacilar
ARAGONIAN	UPPER	7/8	G	CHINJI FORMATION	Sofça Catakbagyaka Bielometchetskaya Candir Pasalar
		6	F		
	MIDDLE	5	E	Quintanelas Lisbon, Hommes Dehesa de Caballos Pte de Toledo Tarazona Torrijos	
		4b	D	Munébrega I Torralba V	
	LOWER	4a	C	La Retama Córcoles	
			B		

FIGURE 16 - Chronostratigraphic distribution of the sites with *Hispanotherium*. *Répartition chronostratigraphique des gisements miocènes à* Hispanotherium.

FIGURE 17 - Geographic distribution of the Iberian and French sites with *H. matritense*. 1=Córcoles. 2=La Retama. 3=Puente de Toledo. 4=Torrijos. 5=Dehesa de los Caballos. 6=Lisbon area. 7=Quintanelas. 8=Torralba de Ribota V. 9=Munébrega I. 10=Tarazona. 11=Hommes. *Distribution géographique des gisements* H. matritense *ibériques et français*.

D zone corresponds to a dry and warm period (Meulen & Daams 1992) where only *H. matritense*, with its anatomical characteristics (high teeth with much cement; slender limbs), would be favoured to bear the arid conditions (Cerdeño & Nieto 1995), while *P. platyodon* became extinct.

During the MN4a/C zone, other Spanish site such as Buñol (Valencia, Belinchón 1987) has yielded three different rhinocerotid species, *P. platyodon* among them, but *H. matritense* is not present there. This could be due to the much more humid conditions of the Mediterranean basins at that time with respect to the internal basins (Agustí et al. 1983; Sesé 1988; Iñigo 1993), and such conditions would not favor the development of *H. matritense*. This rhinoceros mainly inhabited the central basins, and it reached the Lisbon area through the Tagus basin. The Portuguese localities have also provided other rhinocerotid species together with *H. matritense* (Antunes & Ginsburg 1983), and they remain there longer than in central Spain.

These climatic variations among different localities could also probably explain the differences in the relative abundance of *H. matritense* with respect to the equid *Anchitherium*. In several occasions a direct competition between these two perissodactyls has been proposed. Both are well runner ungulates, with clear differences on their dental features. The brachydont teeth of *Anchitherium* were adapted to a shofter vegetation than the subhypsodont teeth of *Hispanotherium;* the former was a browser, while the latter was mainly a grazer. So they would not be direct competitors, but their distribution would depend on the vegetational landscape.

The Córcoles site is actually formed by two near fossiliferous outcrops, where these two perissodactyls are inversely represented in relative proportions. From a taphonomic point of view, this difference has been interpreted as a palaeoecological succession (Iñigo 1993).

From a chronological point of view, the age of Córcoles (MN4a/C) implies the arrival of *Hispanotherium* in Spain to be earlier than supposed before. Antunes (1979) proposed a migration way through the Mediterranean, during a marine regression previous to the Serravallian transgression. The Iberian sites with *H. matritense* belong to the Tagus, Ebro and Calatayud-Teruel basins, and the farther from Córcoles the younger they are (Figs 16-17). This suggest two different dispersion ways from the upper Tagus basin: one following this basin, reaching Lisbon area, and the second to the North, reaching the Ebro basin (Zaragoza province).

The presence of *H. matritense* in France (Ginsburg et al. 1987) is more recent, corresponding to the MN5 zone, and it would have arrived there from Spain (Cerdeño 1989).

CONCLUSIONS

A great amount of rhinocerotid remains from Córcoles (Guadalajara, Spain) are described and identified as *Hispanotherium matritense*. This is the best sample of this species at a single site, and some bones are described for the first time. The size of the sample provides a good idea about the morphological and metrical intraspecifical variation.

Within the Córcoles sample, the frequency of a constricted metaconid on the lower cheek-teeth is very low, and therefore we propose to exclude this character from the diagnosis of the species *H. matritense*.

The comparison with other Iberian remains of *H. matritense* makes evident minor differences referred to the articular surfaces, and a slightly larger general size, more detached with respect to the Torrijos sample. The most interesting morphological particularity of the *H. matritense* from Córcoles concerns the semilunar, which does not present the usual external groove limiting posteriorly the pyramidal-facet, which is in turn quite long.

With respect to the Asian "elasmotherines", the material from Córcoles comes to fade out the differences previously established between *H. matritense* and *H. grimmi*. We confirm the synonymies proposed before for the species *C. oettingenae, B. borissiaki* and *B. tekkayai*, adding now *H. grimmi*. This synonymy is not so clear for *B. caucasica*, whose postcranial skeleton presents metrical differences, and therefore we propose the new combination *Hispanotherium caucasicum* for it.

The age of Córcoles, corresponding to the MN4a or D biozone implies the oldest record of *H. matritense* in Europe, and supposes the arrival of this immigrant to be earlier than thought before. Córcoles is also the only Spanish site where *H. matritense* appears together with other rhinoceros species (*P. platyodon*).

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