Intraspecific variation and evolutionary trends of *Alicornops simorrense* (Rhinocerotidae) in Spain

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The Spanish material of *Alicornops simorrense* constitutes the best representation of the species in Western Europe. It provides interesting data on the metrical and morphological intraspecific variation of *A. simorrense* and its evolutionary trends from late Middle Miocene to the early Late Miocene. From late Aragonian to early Vallesian, a slight increase in size is observed, but without clear limits among series. During the late Vallesian, *A. simorrense* evolved in central Spanish basins into a second species, *A. alfambrense*, greater in size and with more robust proportions. In the Vallés-Penedés basin, *A. simorrense* shows a noticeable increase in size, while maintaining its proportions, during the Vallesian. *A. simorrense* was a very abundant species, an open woodland dweller, with gregarious behaviour, whose extinction was probably linked to the climatic change that took place at the end of the Vallesian and the beginning of the Turolian.

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Introduction

The species *Rhinoceros simorrensis* was described by Lartet (1851) based on some remains from Simorre and Villefranche d'Astarac (France). Hooijer (1966) placed it in the genus *Aceratherium*, but its generic status has subsequently changed several times. Ginsburg (1974) considered the species to belong to the genus *Dromoceratherium*, and Heissig (1976) included it within *Mesaceratherium* (Heissig 1969). Later, Ginsburg & Guérin (1979) created the subgenus *Alicornops* with the type species *Aceratherium (Alicornops) simorrense*, establishing differences with *A. (Mesaceratherium) gaimersheimense*, *A. tetradactylum* and *A. incisivum* (further changes of the generic status of *A. tetradactylum* are given in Cerdeño 1996). The generic status of *Alicornops* was soon accepted by some authors (e.g. Yan & Heissig 1986) and later broadly adopted (e.g. Heissig 1989; Prothero *et al*. 1989). A cladistic analysis of Rhinocerotidae placed *Alicornops* close to the genera *Peraceras* and *Chilotheridium*, and the tribe Alicornopini within Aceratheriinae was proposed for this clade (Cerdeño 1995).

Alicornops simorrense was one of the most widely distributed rhinocerotids during the late Middle Miocene and early Late Miocene in Europe (Fig. 1). It has been recorded in a large number of Western European sites (Guérin 1980), as well as in the late Aragonian and early Vallesian of Romania (Codrea 1992, 1996), the early Vallesian of Moldova (Lungu 1984) and the Middle Miocene of Polonia (Kubiak 1981). Outside Europe, *A. simorrense* was recognized in the Middle Miocene of Turkey (Heissig 1976) and apparently in the Vallesian of the Siwalik deposits (Guérin 1980; p. 387). Nevertheless, it is in Spain where we find the best representation of *A. simorrense*. It constitutes the most abundant species in some fossil assemblages (Cerdeño 1989; Cerdeño & Nieto 1995). Therefore, the aim of this paper is to give detailed information on this small rhinoceros, based on the good Spanish material, which has allowed us to establish intraspecific variation and evolutionary trends in the species.

Materials and methods

Alicornops simorrense has been recovered from the main Tertiary basins in Spain, at the sites listed below (Figs 1, 2). The material is mainly stored in the Museo Nacional de Ciencias Naturales (MNCN, Madrid, Spain).

Tajo Basin

1 *Area of Madrid city*. There are two important sites of late Aragonian, Middle Miocene age: Paracuellos III (Alberdi

Ma	EPOCH	ELMA	MN ZONES	TAJO BASIN	CALATAYUD - TERUEL B.	DUERO BASIN	VALLÉS - PENEDÉS B.	OTHER LOCALITIES
9	LATE MIOCENE	VALLESIAN LATE	10		La Roma-2*		Can Jofresa	Montredon* (F)
10		VALLESIAN EARLY	9	Chiloeches Cendejas	Nombrevilla Carrilanga-1	El Lugarejo LVF Relea	Can Gabarró Can Llobateres Can Ponsic Can Almirall Poble Nou	Moldavia Jassy (R) Sinmihaiu de Padure (R) Yaylacilar (T)
11	MIDDLE MIOCENE	ASTARACIAN (LATE ARAGONIAN)	7/8	Moraleja de Enmedio	Andurriales Daroca area Toril-3	La Cistérniga Coca Cerro del Otero Fuensaldaña	Trinchera Ferro. Can Feliú Can Barberá Hostalets de P. S. Pere de Ribes	Minisu de Sus (R) La Grive (F) Villefranche d'Astarac (F) Simorre (F) Sofça (T)
12								
13			6	Paracuellos III				Przeworno (P)
14		ORLEANIAN (MIDDLE ARAGONIAN)	5		Montejo de la Vega			
15					Armantes-1			

Fig. 1 Chronological distribution of Spanish and other European localities with *Alicornops simorrense* and (*) *A. alfambrense*. ELMA, European Land Mammal Ages (Sen 1997). Absolute chronology follows Daams *et al*. (1998); LVF, Los Valles de Fuentidueña; P., Piérola; (F) France; (P) Poland; (R) Romania; (T), Turkey.

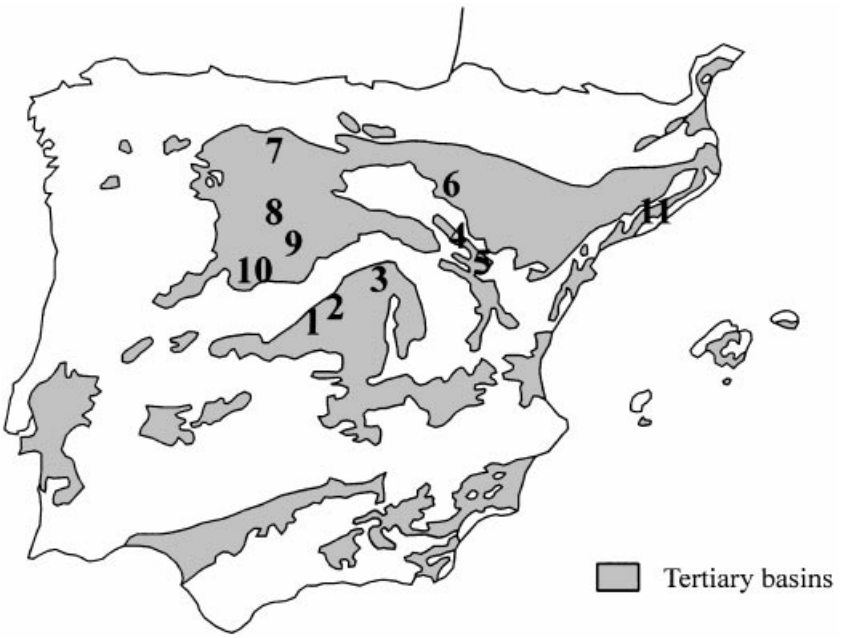

Fig. 2 Geographical distribution of the Spanish localities with *Alicornops simorrense*. Madrid area: 1, Moraleja de Enmedio (MOR) and 2, Paracuellos III (PAIII); 3, Guadalajara area: Chiloeches (CHI) and Cendejas de la Torre (CEN) (= Los Canalizos); 4, Calatayud-Daroca area: Arroyo del Val (AV), Armantes (ARM), Murero (MUR), Solera (SOL), Manchones (MAN) and Carrilanga (CAR); 5, Toril-3 (TO3); 6, Zaragoza area: Los Andurriales (AND), Nombrevilla (NOM); 7, Palencia area: Cerro del Otero (OTE), Relea (REL); 8, Valladolid area: La Cistérniga (CIS), Fuensaldaña (FUE); 9, Segovia area: Los Valles de Fuentidueña (LVF), Coca, Montejo de la Vega de la Serrezuela (MVS); 10, El Lugarejo (LUG); 11, Vallés-Penedés Basin (VP).

et al. 1985), with more than 150 remains of *A. simorrense*, and Moraleja de Enmedio, recently discovered, which has yielded a well-preserved skull and mandible of *A. simorrense*, as well as a number of isolated teeth (some extremely worn) and postcranial bones.

2 *Province of Guadalajara*. Here, two localities of Late Miocene (early Vallesian) age have provided scarce remains of *A. simorrense*: Chiloeches, with only a maxillary fragment with very worn M1–M3 (Royo Gómez 1931; Alberdi *et al*. 1981), and Cendejas de la Torre (= Los Canalizos). The material from Cendejas was originally attributed to *Lartetotherium sansaniense* (Villalta & Crusafont 1948; Guérin 1980), but at least some bones (unciform, McII, McIV and McV) correspond to *A. simorrense* (Cerdeño 1989).

Calatayud-Teruel Basin

1 *Calatayud-Daroca area (Zaragoza)*. *A. simorrense* is present at the sites of Arroyo del Val-1, 3, 4 and 6; Armantes-1, 3 and 6; Murero; Solera; and Manchones-1 and 2; all successions are late Aragonian in age, except Armantes-1, which is middle Aragonian (MN5), and Carrilanga-1, which is early Vallesian (Daams & Freudenthal 1981). The material, stored at Utrecht University, The Netherlands, and the MNCN, is rather scarce (Cerdeño 1989). Not far from Daroca, Toril-3, of late Aragonian age, has provided important micro- and macromammal remains, including several well-preserved skulls, mandibles and most postcranial bones of *A. simorrense* (Cerdeño 1989).

2 *Zaragoza Province*. Here two other sites provided *A. simorrense* remains: Los Andurriales, late Aragonian, in which badly preserved and distorted remains correspond to an adult and a juvenile (Cerdeño 1989), and Nombrevilla, a classic site for the Spanish Vallesian fauna (Hernández Pacheco 1926, 1930; Villalta & Crusafont 1947), where several rhinoceros species have been recovered (Alberdi *et al*. 1981; Santafé *et al*. 1982). A revision of more than 100 remains (mostly isolated teeth) from Nombrevilla (MNCN and Museo Geominero, Madrid) has allowed the recognition of a sample of *A. simorrense*, comparable with that from Los Valles de Fuentidueña, and some doubtful remains of *L. sansaniense* (Cerdeño 1989, 1992).

Duero Basin

1 *Cerro del Otero (Palencia)*. This is another classic site of late Aragonian age (Hernández Pacheco & Dantín 1915), where *A. simorrense* is well represented by a skull, an upper tooth row, some isolated teeth and an astragalus (Cerdeño 1989).

2 *Relea (Palencia)*. This is an early Vallesian site where Guérin (1980) established the presence of *L. sansaniense* and *A. simorrense*. The remains ascribed by this author to *A. simorrense* (mandibular fragment, two tarsals and one metacarpal) are not within the MNCN material revised by Cerdeño (1989), but other specimens were identified as *A. simorrense* (D4, M2, M3, a juvenile mandibular fragment and a patella).

3 *La Cistérniga (Valladolid)*. Early Vallesian in age, it is comparable to Cerro del Otero (Hernández Pacheco 1930). Cranial, dental and postcranial bones of *A. simorrense* have been recognized (Guérin 1980; Alberdi *et al*. 1981; Cerdeño 1989, 1992).

4 *Fuensaldaña (Valladolid)*. Hernández Pacheco (1930) included three fossiliferous sites around Fuensaldaña, the rhinoceros remains coming from El Barredo, of late Aragonian age. The dental material of *A. simorrense* is comparable with other Aragonian series (Cerdeño 1989).

5 *Los Valles de Fuentidueña (Segovia)*. Early Vallesian, it has provided more than 200 remains, on the basis of which Alberdi *et al*. (1981) described the subspecies *A. simorrense duratonense*, based on the greater size of the upper molars. Cerdeño (1989; p. 165) did not consider this subspecies to be fully justified.

6 *Coca area (Segovia)*. A juvenile McIV comparable with those of *A. simorrense* from La Cistérniga appeared near the late Aragonian site of Coca, which provided an incomplete individual of *L. sansaniense* (Cuesta *et al*. 1983; Cerdeño 1986).

7 *El Lugarejo or Arévalo (Avila)*. The fauna from this site is comparable with that from Los Valles de Fuentidueña (Crusafont *et al*. 1968). The rhinoceros material consists of a juvenile partial skull, with some milk molars, and an M3, smaller in size than the other studied specimens (Cerdeño 1989).

8 *Montejo de la Vega de la Serrezuela (Segovia)*. Very recently, Mazo *et al*. (1998) have described two upper teeth of *A. simorrense* among the middle Aragonian fauna of this site.

Vallés-Penedés Basin

Santafé (1978) and Santafé & Casanovas (1978) recognized *A. simorrense* in the late Aragonian deposits of Trinchera del Ferrocarril, Can Feliú, Castell de Barberá and Hostalets de Piérola (lower levels), scantily represented except in Hostalets (22 teeth and 4 metapodials), the early Vallesian beds of Can Ponsic, Can Llobateres and Can Gabarró and the late Vallesian deposits of Can Jofresa. Cerdeño (1989) later considered the remains from Can Almirall, Poble Nou, St. Pere de Ribes and Hostalets de Piérola, determined as *L. sansaniense* by Santafé (1978), to have '*Aceratherium*' morphology. They would likely correspond to *A. simorrense*.

Abbreviations. In text and tables these are: ant., anterior; APD/TD, anteroposterior and transverse diameters; art., articulation; D/d, upper/lower milk molars; dia, diaphysis; dis., distal; epi., epiphysis; H, height; I/i, upper/lower

incisors; isol., isolated; juv., juvenile; L, length; M/m, upper/lower molars; max./min., maximum/minimum; Mc/Mt, metacarpal/metatarsal; P/p, upper/lower premolars; post., posterior; pr., proximal; W, width.

Nomenclature and metrical parameters on teeth and bones. These follow Guérin (1980) and Cerdeño (1989). All dimensions in tables are expressed in millimetres.

Systematic palaeontology

Order PERISSODACTYLA Owen, 1845
Family RHINOCEROTIDAE Owen, 1845
Subfamily ACERATHERIINAE Dollo, 1885
Tribe ALICORNOPINI Cerdeño, 1995
Genus *Alicornops* Ginsburg & Guérin, 1979
Alicornops simorrense (Lartet, 1851)
Rhinoceros simorrensis Lartet, 1851: pl. 1
Ceratorhinus (*Dicerorhinus*) *simorrensis* Osborn, 1900: p. 256, fig. 13(b)
Rhinoceros sansaniensis Hernández Pacheco & Dantín, 1915: pls. 28–30
Rhinoceros indet. Hernández Pacheco & Dantín, 1915: pl. 36; figs 4–7, 9, 12; pls. 8–39; pl. 40 (*p.p.*)
Rhinoceros sansaniensis Hernández Pacheco, 1930: p. 110; p. 115, fig. 27; p. 120, fig. 1
Aceratherium simorrensis Hooijer, 1966: p. 142
Dromoceratherium simorrensis Ginsburg, 1974: p. 599
Mesaceratherium simorrense Heissig, 1976: p. 72
Dicerorhinus sansaniensis Santafé, 1978: p. 364–367, 369–370, 382–385; pl. 18, figs 2–3
Aceratherium (Alicornops) simorrense Ginsburg & Guérin, (1979): p. 115.

Holotype. Skull fragment with P2–M3 and p2–m3. Simorre, France. Museum National d'Histoire Naturelle, Paris (France).
Stratigraphic and geographical distributions. Middle and Late Miocene; middle Aragonian–late Vallesian. Europe, Anatolian Peninsula (Turkey), and ?Siwalik deposits (Guérin 1980).

Diagnosis (modified from Ginsburg & Guérin 1979 and Cerdeño 1989). Small aceratheriine. Skull with postglenoid apophysis very developed in contact with the post-tympanic one, both slightly oblique anteriorly. Anterior dentition with I1 and i2 developed, the latter as a large tusk (greater in males). Upper cheek teeth with paracone fold strong and little projected. Crochet well developed; sometimes crista also developed. Upper premolars usually with continuous lingual cingulum. Lower premolars with lingual and labial cingula. Postcranial skeleton with shortened legs, fore foot tetradactyl.

The diagnosis of *Alicornops* given by Ginsburg & Guérin (1979) included a tridactyl manus, but Cerdeño (1989) rejected this, based on the well-developed McV found at several Spanish sites. Therefore, in common with other aceratheriine forms of the genera *Acerorhinus* and *Aceratherium*, *A. simorrense* has a tetradactyl manus.

Description

Skull (Table 1) with long nasals, slightly curved in transverse section on the specimen from Toril-3, without horn boss. Frontal bone wide and flat, strongly narrowing backwards. Parietal crests very close or united in sagittal crest, elevating backwards. Occipital crest wide, projected backwards without surpassing the condyle level. Postglenoid and post-tympanic apophyses in contact, not fused. Nasal incision at P4 level. Anterior border of orbit above M1–M2 or anterior part of M2. Anti-orbital apophysis marked as vertical projection, hiding posterior opening of anti-orbital foramen. Median posterior border of palatine bones at M2 level.

Skull from Moraleja de Enmedio with the peculiarity of parietal crests forming short, narrow sagittal groove instead of crest, giving more rounded transverse section in parietal region (Fig. 3A). At present, this feature can be considered as an individual condition, since different from general condition in rhinoceroses.

On juvenile skull from Arévalo, nasal incision at D3 level. Long and narrow, with supraorbital processes little developed. Juvenile specimen from Toril-3 incomplete, dorsally crushed; zygomatic arches weak and narrow; preserving milk molars (right D1–D4 and left D2–D4) and erupting M1.

Table 1 Skull dimensions of *A. simorrense* from Spain. Values in parentheses are approximate.

Skull	Cerro del Otero	Toril-3	Moraleja
L tip of nasal to occipital crest	(470.9)	(448)	—
Distance from M3 to condyle	(214)	—	250.5
Distance nasal incision–orbit	>	(69)	71.4
Zygomatic width	—	(263)	251.4
Width at the parietal level	110	(111)	76.0
Height above P4–M1	114	(128)	—
Width above nasal incision	(107)	—	—
Maximal frontal width	154	(182)	153.2
Palatine width before M3	78	65	66.8
Zygomatic width	—	(263)	251.4
Width of the occipital crest	—	109	112.3
Occipital height	—	161	190.4
Maximal width at the occipital condyle	—	87	94.0
Width of the foramen magnum	—	37	31.4
L P1–M3	—	192	205.5/202.6

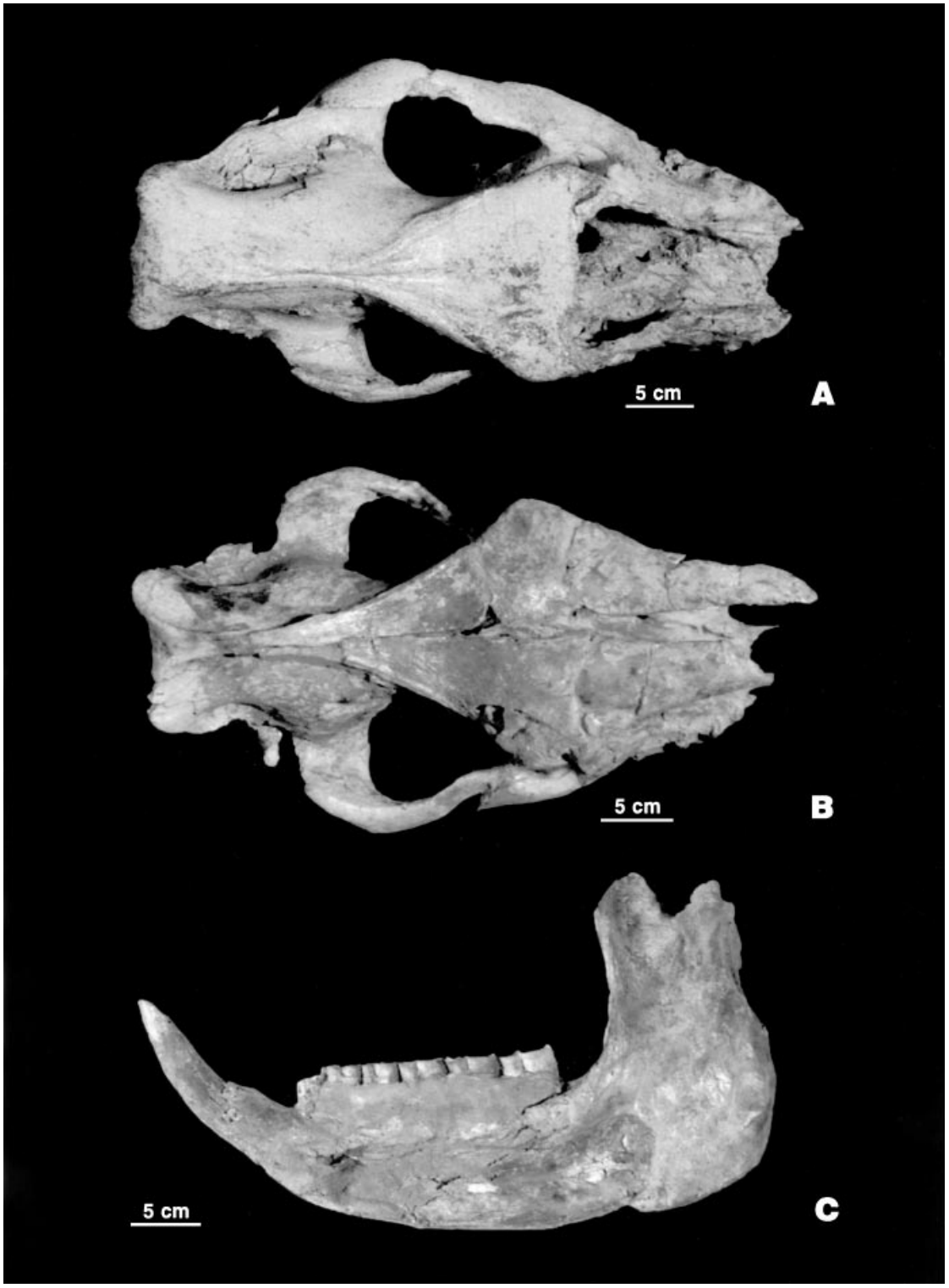

Fig. 3 A–C. *Alicornops simorrense*. —A. Skull from Moraleja de Enmedio, MNCN 30768, dorsal view. —B. Skull from Toril-3, MNCN 33420, dorsal view. —C. Left mandible of a male individual from Toril-3, MNCN 31856, labial view.

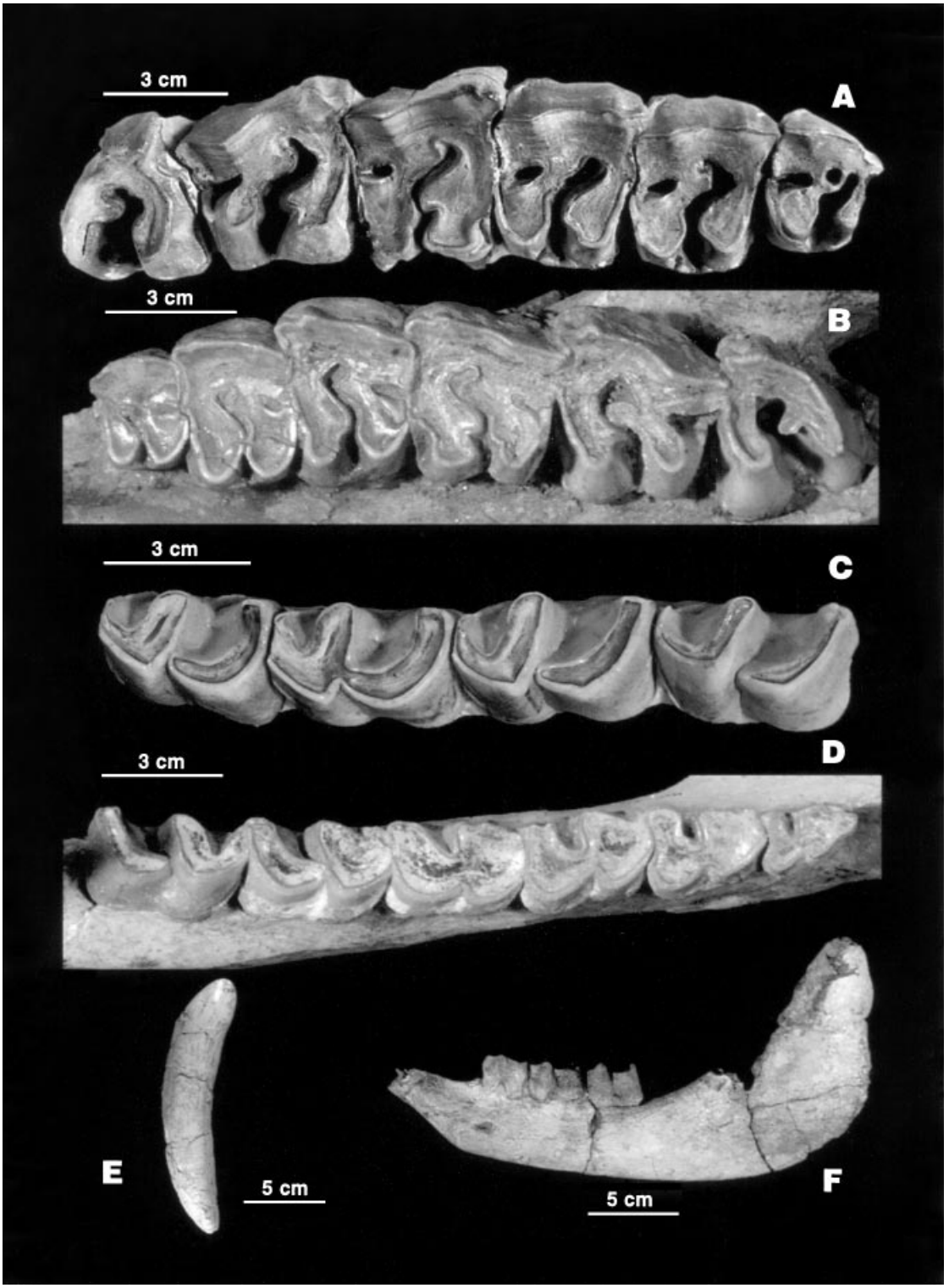

Fig. 4 A–F. *Alicornops simorrense*. —A. Right upper series P2–M3 from La Cistérniga, MNCN 16020, occlusal view. —B. Left upper series P2–M3 from Moraleja de Enmedio, MNCN 30768, occlusal view. —C. Left lower series p2–m3 from Nombrevilla, MNCN 7942, occlusal view. —D. Right lower series p2–m3 from Toril-3, MNCN 31856, occlusal view. —E. Left lower incisor (i2) from Los Andurriales, MNCN 35968. —F. Left mandibular fragment with roots of di1, di2, d1 and the series d2–d4 from Los Andurriales, MNCN 35962, labial view.

Table 2 Mandibular dimensions of *A. simorrense* from Spain.

Mandible	Toril-3	Toril-3	Toril-3 (juv.)	Moraleja	Manchones-2	Nombrevilla
L symphysis (ant.)-angular process	402.5	—	—	401.8		
L symphysis (post.)-angular process	319.4	(378)/—	—	312.0/325.2		
L symphysis	96.0	—	(90)	111.4		
TD symphysis	79.7	—	(55.6)	(> 62)		
H p2–p3 level	—/71.0	(90)/—	(66.6)/63.7	70.3/71.0		70.5 –
H p4–m1 level	83.5/78.0	—/90	63.3/63.7	76.7/75.8	74.0 75.0	80.8 81.0
H behind m3	92.0/92.0	(101)/100	—/—	82.0/82.1		92.5 94.0
TD p4–m1 level	33.0/34.0	(33)/31.0	29.4/30.8	29.2/(28.8)	28.0 (31.5)	
APD ascending ramus	109.5/109.0	130.0/132.5	101.7/102.3	108.4/107.1		
TD condyle	(85.6)/78.4	85.5/85	74.3/69.2	77.2/74.3		
H condyle	(217.5)/219	(236)/(230)	201.5/196.2	196.0/186.6		
H coronoid apophysis	—/272	—/277	(238)/—	(> 207)/(> 206)		
L p2–m3	182	(188)/(187)	(195)	191.4/194.4		

Table 3 Lower incisor dimensions (at the base of the crown of i2) of *A. simorrense* from Spain.

Males	L	A	Females	L	A
Paracuellos III	29.4	27.6	Paracuellos III	19.5	13.0
	32.0	23.6		22.7	13.0
	35.7	24.4		23.3	15.0
	37.0	27.4		20.6	16.2
				21.7	16.2
				20.6	(15.0)
Toril-3	(34.0)	(32.3)	Toril-3 (juv.)	20.5	13.2
Andurriales	34.7	31.5	Moraleja (alveolus)	20.8	17.7
	33.9	33.5			
La Cistérniga	37.5	28.0			
Los Valles de Fuentidueña	41.6	29.0	Los Valles de Fuentidueña	21.0	19.0
	41.0	28.0		21.7	16.6
	44.5	29.4		21.7	16.6
	38.0	(23)		22.5	18.0
	38.5	27.7		22.0	(17.0)

Good mandibular specimens of both sexes (Table 2; Fig. 3C), distinguished by different size of i2 (Table 3), have been recovered from Toril-3. Mandible with smaller i2 would correspond to females (Toril-3, Moraleja). Horizontal ramus high, with ventral border little convex anteroposteriorly. Symphyseal region enlarged because of great root of i2, developed as tusk. Symphysis at a marked angle with horizontal ramus. Posterior symphyseal border at p2–p3 or p3 level. Vertical ramus at rather straight angle; angular process hardly surpassing the condyle posteriorly. Condyle inclined medially; articular facet with median constriction in some specimens. Mandibular foramen at alveolar border level. Toril-3 specimens seem to have higher horizontal rami than those from Paracuellos III, Moraleja and Manchones-2, which are, in turn, shorter than in Simorre (type material). Juvenile mandibles from Los Andurriales (Fig. 4F), Arroyo del Val-4 and Moraleja have horizontal ramus long (APD) and low (H). Metrical data of mandibular fragment from St. Pere de Ribes (Santafé 1978) around the minimum provided by other Spanish remains.

Dental remains of *A. simorrense* (Tables 3–5; Fig. 4) from Spanish sites rather homogeneous and morphologically comparable with type material from Simorre, differing in greater relative width of upper premolars, mainly P3 and P4. Some specimens show cement remains on ectolophs/ectolophids (e.g. Toril-3 and Moraleja; Fig. 4B,D).

In general, upper teeth of *A. simorrense* characterized by constant presence of lingual cingulum on premolars, normally developed as continuity of anterior cingulum, reaching hypocone, separated from the posterior one. Molars sometimes with little tubercle or swelling at entrance of median valley. Constant rounded crochet, progressively developed from P2 to molars (can exist on P1 and maximal on M1–M2). Crista usually present on P1–P2, united or not to crochet, more or less evident on P3–P4. Protocone well marked by two vertical grooves on molars; only posterior

Table 4 Comparative dimensions of the upper teeth of *A. simorrense* from Spain. Size of the sample (*N*), minimum, average and maximum values are provided when there are more than two specimens of each tooth. Values in square brackets correspond to one tooth series. Abbreviations of sites as in Fig. 2 and SIM, Simorre (holotype, data from Alberdi *et al.* 1981). Vallés-Penedés Basin data from Santafé (1978; L at the base of the tooth). Other abbreviations explained in the text.

	P1		P2		P3		P4		M1		M2		M3		
	L	W	L	W	L	W	L	W	L	W	L	W	L	W	D
PAIII															
N	11	11	11	11	6	6	8	8	3	2	4	5	4	4	4
Min.	(15.6)	13.0	(23.5)	28.7	27.0	38.6	31.1	40.5	39.5	46.4	40.0	44.0	(36)	40.7	41.4
Aver.	17.0	15.5	24.5	30.7	29.5	40.2	34.6	45.7	40.5	47.2	43.6	46.4	38.6	43.2	45.6
Max.	18.1	17.9	25.5	(34.5)	33.0	42.3	37.2	48.1	42.0	48.1	47.0	48.5	40.8	46.7	(48.1)
TO-3															
N			5	4	2	1	2	2	3	2	1	1	2	2	2
Min.			(22.5)	30.2	32.9		(33.2)	45.8	(37)	47.0			34.4	40.0	42.3
Aver.			25.7	31.9	32.9		35.5	46.9	41.3	50.0	45.1	48.7	36.8	41.3	44.1
Max.			27.6	33.6	33.0	39.5	37.8	48.0	44.5	(53)			39.3	42.6	46.0
MOR	17.0	13.0	26.4	30.4	31.9	40.5	35.1	46.1	40.0	44.1	43.2	46.2	37.9	42.2	47.0
	18.4	13.0	26.2	30.7	32.3	40.6	35.4	46.4	39.8	44.7	43.7	48.0	37.5	40.8	44.3
(isol.)	16.7	15.9	23.4	30.9	30.5	41.9							41.3	45.7	47.6
CIS															
N			2	2	1	1	1	1	1	1	1	1	2	2	2
Min.			29.0	34.7	33.9	43.0	36.7	45.3					36.7	40.5	43.4
Max.			28.0	33.0					40.2	44.8	45.4	46.1	38.0	42.0	45.7
OTE															
N			1	2	3	3	1	2							
Min.			30.0	32.6	29.2	40.8	38.3	(44)							
Aver.				33.3	31.5	41.8		44.5							
Max.				34.0	35.3	43.2		45.0							
CHI									44.4	50.0	50.0	52.7	42.0	46.0	46.0
REL									50.0	55.5	43.0	49.0	52.0		
SIM			29.3	33.1	33.1	38.6	36.5	43.2	40.0	43.0	41.3	44.8	43.5		41.4
AV4															
N	3	3	3	3	1	1	2	2	1	1			1		
Min.	17.1	14.0	(24)	29.6			37.3	43.3							
Aver.	18.6	15.1	24.8	31.2	37.7	38.5	37.3	44.4	44.7	44.8			39.5		
Max.	20.5	16.6	26.0	32.9			37.4	45.6							
AV3					33.3	45.9	36.3	45.9	42.7	45.6	45.7	48.2			
					34.2	41.8	36.2	48.7	42.4	45.9	43.9	47.1			
(isol.)			26.0	30.6			35.3	46.6					27.3	35.5	39.0
ARM3	[22.0	16.0	31.0	27.0	38.0	35.1	(45)	45.6	46.7	43.7	47.4	44.4	(37)	(43)	46.0]
	[—	—	—	—	37.4	39.8	—	—	47.1	43.5	49.6	40.8	32.3	38.0	48.0]
ARM6															
N													3	3	3
Min.													(36)	43.4	43.1
Aver.													38.4	44.4	45.3
Max.													41.3	46.2	46.6
MUR							38.0	47.8	40.3	40.0	46.0	49.6			
MAN1															
N	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4
Min.	16.7	14.8	24.1	31.7	30.0	40.0	34.5	42.5	39.0	44.0	43.5	46.0	35.8	39.6	41.4
Aver.	17.7	16.5	25.5	32.9	30.5	42.5	34.7	45.0	40.2	45.7	45.7	47.7	38.7	42.2	44.5
Max.	19.1	18.2	27.1	35.0	30.9	45.4	35.0	47.5	42.4	7.0	47.0	49.8	40.6	45.0	47.5

Table 4 *Continued.*

	P1		P2		P3		P4		M1		M2		M3		
	L	W	L	W	L	W	L	W	L	W	L	W	L	W	D
NOM															
N	11	11	9	9	6	4	7	7	7	7	3	3	11	11	11
Min.	18.4	15.7	23.0	30.4	(32)	40.0	(36)	45.0	43.9	47.0	47.4	48.5	35.0	(41)	41.2
Aver.	21.3	18.0	31.1	35.7	35.6	42.9	37.8	46.2	45.4	47.9	48.9	49.5	39.5	44.0	47.7
Max.	24.3	20.4	34.0	37.6	40.6	44.5	39.0	47.0	47.1	49.5	51.5	51.0	42.1	46.7	51.2
LVF															
N	12	11	5	5	2	2	3	3	2	2	2	2	4	4	4
Min.	18.0	15.6	26.0	32.5	(33)	43.6	35.5	44.5	45.0	49.5	49.0	51.7	40.7	43.6	(46.5)
Aver.	20.0	17.3	28.5	34.0	33.5	43.9	36.4	46.0	46.1	50.9	49.8	52.3	42.3	46.3	49.1
Max.	22.5	19.3	30.8	36.0	34.0	44.2	37.0	46.8	47.3	52.3	50.7	53.0	45.0	48.7	50.7
VP															
N	3	3	2	2	5	7	1	2	2	2	4	4	1	1	1
Min.	18.5	15.9	25.0	30.0	31.1	38.0		41.5	39.1	41.5	40.5	42.0			
Aver.	18.7	16.2	27.5	31.2	32.5	38.9	34.6	41.7	39.6	42.5	42.3	44.1	34.0	39.5	43.5
Max.	19.0	16.4	30.1	32.5	33.5	39.5		42.0	40.2	43.2	44.0	45.3			

Table 5 Comparative dimensions of the lower teeth of *A. simorrense* from Spain. Abbreviations in text and Fig. 2.

	p2		p3		p4		m1		m2		m3	
	L	W	L	W	L	W	L	W	L	W	L	W
PAIII												
N	4	4	4	4	4	4	2	3	6	6	2	2
Min.	19.1	14.6	27.8	(16.4)	31.0	21.7	(33.7)	21.6	37.0	21.8	37.3	21.4
Aver.	22.8	15.6	29.21	9.4	32.9	23.2	35.6	21.9	38.0	22.6	38.4	21.4
Max.	23.3	17.0	31.4	21.7	(34.5)	24.63	7.5	22.2	(40.9)	23.43	9.6	21.5
TOR-3												
N	6	6	6	6	7	7	7	7	8	8	8	8
Min.	20.4	15.7	24.7	20.3	28.0	23.2	31.4	22.3	35.3	23.5	38.8	23.0
Aver.	21.5	16.2	27.5	21.4	30.5	24.0	33.8	23.6	37.7	24.3	42.5	25.2
Max.	22.6	17.3	29.3	22.4	31.9	26.5	35.8	26.3	38.9	25.8	47.4	27.2
AV4												
N	2	2	1	1	3	3	5	5	3	3	1	1
Min.	22.7	15.6			32.0	(22.3)	35.5	21.0	41.0	23.3		
Aver.	22.8	15.8	31.0	19.8	33.9	24.6	37.7	22.3	41.8	24.0	39.0	22.0
Max.	23.0	16.0			(35.7)	26.5	40.0	23.9	43.3	25.2		
AV6	21.7	15.0										
	22.0	12.7										
ARM3	22.0	16.0	27.2	20.8	34.0	20.0	38.0	27.0				
			27.0	19.7								
ARM6												
N	2	2	2	2	2	2	2	2	3	3	2	2
Min.	21.5	16.6	31.0	21.9	36.0	25.3	37.3	25.2	39.3	24.4	40.8	25.0
Aver.	23.0	17.3	31.1	21.9	36.1	25.8	37.4	25.9	40.6	25.6	40.9	25.3
Max.	24.5	18.0	31.2	22.0	36.2	26.4	37.5	26.7	41.5	26.7	41.0	25.7
MUR							35.4	22.5	38.6	21.8	40.7	24.7
MAN1	23.2	13.0	29.4	21.7	—	24.5	34.0	24.3			39.0	23.0
	(22.5)	16.3					37.8	26.0			37.4	23.8
MAN2	(22)	15.0			30.4	22.3	34.5	22.1	38.3	22.6	39.0	22.0
	22.5	16.3			31.6	23.0	36.5	23.6	40.0	22.7	39.3	22.3

Table 5 *Continued.*

	p2		p3		p4		m1		m2		m3	
	L	W	L	W	L	W	L	W	L	W	L	W
CAR1											39.0	22.3
AND											35.1	20.4
MOR	24.9	16.7	31.1	23.4	33.5	23.6	33.9	23.2	36.0	22.8	36.2	22.6
	26.0	16.5	29.6	22.3	34.3	24.2	34.5	23.0	36.5	22.8	36.8	22.9
(isol.)								35.3	23.2	36.2	24.9	
CIS												
N	1	1	3	3	5	5	4	4	4	4	4	4
Min.			28.0	21.2	30.6	17.7	32.1	22.0	36.8	(20.5)	35.0	21.3
Aver.	23.5	16.7	29.2	21.7	32.1	20.9	32.9	22.5	37.6	22.6	39.5	23.8
Max.			30.9	22.6	33.8	22.8	34.0	23.0	(39)	25.3	42.3	25.0
OTE	25.5	16.6					37.4	20.6				
							34.7	19.2				
NOM												
N	10	10	16	15	9	8	8	7	12	12	22	22
Min.	23.0	15.5	(31.4)	22.0	32.3	23.4	36.0	23.3	(39.3)	24.7	38.2	21.0
Aver.	27.1	18.4	34.0	23.2	36.1	25.4	38.8	24.5	41.2	26.0	40.9	23.4
Max.	29.6	21.0	36.8	25.3	38.8	27.5	43.4	25.7	43.5	27.0	45.7	25.7
LVF												
N	11	11	6	6	4	4	3	3	5	5	5	5
Min.	22.6	13.0	29.0	22.4	32.0	24.2	37.6	23.4	41.7	25.0	40.4	23.0
Aver.	24.3	16.0	31.1	22.9	32.9	24.7	39.0	24.5	42.5	26.4	43.0	23.5
Max.	27.4	18.0	33.0	24.0	34.0	25.2	40.0	25.4	44.0	27.6	45.7	24.1
VP												
N	7	7	3	4	5	5	3	2	4	2	3	4
Min.	25.5	15.2	26.0	20.0	29.0	21.9	32.0	22.0	34.0	22.4	34.1	21.5
Aver.	26.0	16.9	27.4	20.9	30.1	22.4	32.3	22.1	34.8	22.8	34.9	22.5
Max.	26.9	18.4	29.7	23.0	31.0	23.2	32.6	22.2	36.0	23.8	36.3	23.7
SIM	24.8	18.0	29.2	22.6	30.0	23.7	33.3	22.2	38.5	23.2	39.0	21.8

groove present on P3–P4. Protoloph very markedly enlarged above groove, forming rounded protuberance (not anticrochet) that can reach metaloph. On M3 of skull from Moraleja, this protuberance thin and developed to base of median valley; left P2 with protoloph separated from ectoloph. Hypocone can have anterior vertical groove, mainly on M1. On ectoloph, paracone fold wide and prominent on M1–M2, smoother on other teeth; some convexity corresponding to mesostyle on molars.

Milk molars can show bifurcated cristae and anticrochets; crista frequently united to well-developed crochet. Paracone fold well marked. D1 triangular in shape, with protoloph not developed and small crochet (Toril-3). D2 elongated owing to lengthening of the parastyle.

Table 4 shows some dental size increase from Aragonian specimens to Vallesian ones, mainly for M1 and M2 (Fig. 5).

Lower teeth not easy to characterize. Large tusks (Table 3; Fig. 4E), i2 of male individuals, with large root and rounded section; i2 of females as much smaller tusks, with more flattened cross-section. Great isolated tusks from Los Valles de Fuentidueña or Paracuellos III show marked turn in crown direction from base to tip, curving to inner side.

Lower premolars with labial cingulum, usually continuous. Anterior cingulum continues lingually to base of anterior valley; small cingular rim at base of posterior valley. Molars can have more reduced and discontinuous labial cingulum; lingual cingulum, if present, reduced to short rims or tubercles at base of valleys. Characteristic established by Guérin (1980) for *Aceratherium* (including *Alicornops*), 'false bottom' in anterior valley of cheek teeth, evident on little worn specimens. Lower milk molars long and narrow; paralophid of d2 sometimes bifurcated; protoconid with narrow, flattened fold on ectolophid.

Compared to type series from Simorre, premolar series of mandible from Toril-3 appears relatively shorter, but not other specimens from this and other sites (Table 5). For

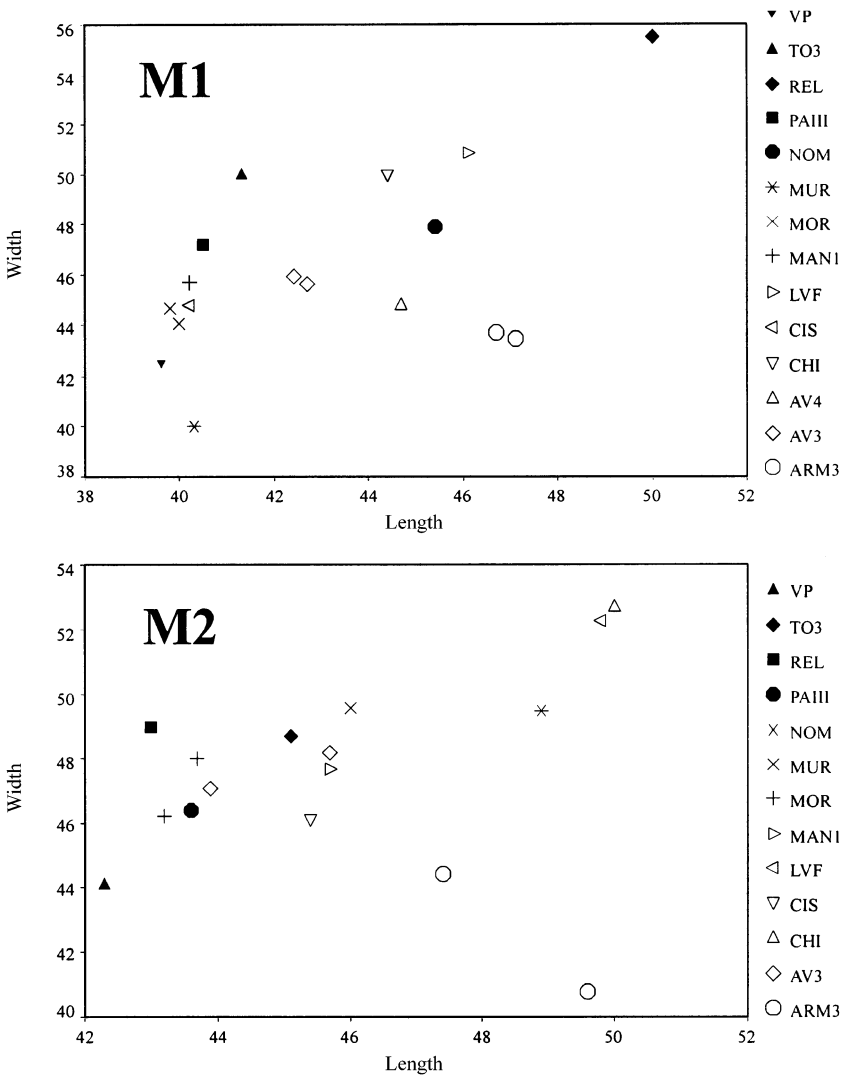

Fig. 5 Dispersion diagrams of M1 and M2 of *Alicornops simorrense*. Abbreviations as in Fig. 2.

instance, premolars from Armantes-6 longer, whereas shorter in Armantes-3; p2 from Paracuellos III shorter and narrower, whereas lower cheek teeth from Los Valles de Fuentidueña tend to be longer than in Simorre, also slightly narrower.

Postcranial skeleton of *A. simorrense* characterized by leg shortening, especially metapodials, which become short and with broad epiphyses, not being massive bones as in teleoceratines (e.g. *Brachypotherium*) owing to lesser relative width. Long bones not so obviously shortened, with gracility indices comparable to other aceratheriine species (Cerdeño 1989). Metapodials, carpal and tarsal bones robust, with very developed rugosities of muscular insertion, indicating strong muscles. In general, *A. simorrense* is small-sized, with variation within samples such as that from Los Valles de Fuentidueña.

Four atlas fragments from Toril-3 and Paracuellos III with transverse foramina close to anterior border. Dimensions in Table 6.

Axis from Paracuellos III wide, short (APD) and high (Table 6). Lateral anterior expansions wide and subrectangular in outline. Odontoid apophysis rounded, narrow, well projected. Ventral crest little marked. Spiny process convex, enlarging posteriorly. Articular caudal processes wide, with ovoid, flat surfaces. Transverse processes long and narrow. Fragment from Toril-3 slightly narrower at cranial articular level.

Scapula represented by few fragments from Toril-3 and Paracuellos III. Diameters of oval articulation: Toril-3, 48.3×60.7 mm; Paracuellos III, 50.1×78.1 mm; 52.7×69.9 mm.

Few specimens of more or less complete long bones exist. Humerus small, with transverse distal diameter relatively wide (Table 7; Fig. 6A). Lesser tubercle as narrow, medially curved apophysis, separated from great tubercle by deep depression extended anteriorly. Olecranian fossa large and

Table 6 Dimensions of the atlas and axis of *A. simorrense* from Spain. Abbreviations in text and Fig. 2.

	Toril-3		Paracuellos III	
Atlas				
Maximal articular width	110	111.0	108.7	112.0
Maximal height	89	90.6	—	—
Vertebral foramen (width)	38	42.3	34.2	44
Vertebral foramen (height)	45	49.3	45.7	52.4
Anteroposterior diameter of the dorsal arch	33		34.5	36.7
Width of the anterior articular facet	53		—	—
Height of the anterior articular facet	36.5		37.5	—
Width of the posterior articular facet	51		—	—
Height of the posterior articular facet	3	5	—	40
Axis				
TD at the level of transverse processes	—		(155)	
TD at the level of cranial articular surfaces	118		132.4	
DT at the level of the caudal articular processes	—		75	
APD maximum	103.5		102.5	
DT × H vertebral fossa	53 × 32		50 × 45	
H vertebral foramen			(31)	

Table 7 A–E. Comparative dimensions of the long bones of *A. simorrense* from Spain. Abbreviations in text and Fig. 2.

(A) Humerus

		pr. epi.		dia.		dis. epi.	
	L	TD	APD	TD	APD	TD	APD
PAIII	290	(103)	(>61)	42.0	39.0	88.0	65.3
						72.0	(70)
						93.0	72.4
AV4				40.0	57.0	—	63.5
(juv.)	>230	—	—	30.2	42.3	(>67)	66.8
MOR	(268)	105.2	—	48.3	48.7	97.6	76.7
CIS						94.0	(>72)
AND	304	(>102)	(97)	50.0	43.0		

(B) Radius

		pr. epi.		dia.		dis. epi.	
	L	TD	APD	TD	APD	TD	APD
PARIII							
N	0	3	3	1	1	2	2
Min.		66.0	35.3			60.3	33.6
Aver.		66.9	36.5	34.7	27.3	60.4	34.3
Max.		68.2	37.3			60.5	35.0
CIS							
N	0	3	3	1	1	2	2
Min.		(62.6)	(38.5)			67.8	37.0
Aver.		66.8	41.8	(39)	30.0	68.4	39.0
Max.		70.5	45.0			69.0	41.0
TOR-3							
N	1	4	4	3	3	1	1
Min.		60.0	32.5	33.6	18.0		
Aver.	242	65.6	38.9	38.2	20.9	58.5	41.0
Max.		74.2	47.7	43.0	23.8		

(C) Ulna

		olecranon		dia.		dis. epi.	
	L	TD	APD	TD	APD	TD	APD
PAIII	327	(>36)	68.0	34.0	36.5	(39)	44.5
			60.0	(32)	(36)	—	—
MOR	311.2	47.8	(72)	35.8	28.1	31.6	43.5

(D) Femur

				dia.		dis. epi.	
	L	TDpr.	TD3tr.	TD	APD	TD	APD
CIS						104	112
TOR-3			(>85)	51.0	44.6		
PAIII			81.5	(54.5)	(40)	106.4	117
AND	(370)	(>110)	(>75)	(44)	(46)	—	—
	322	136	—	(55)	(38)	—	—

(E) Tibia

		prox. epi.		dia.		dis. epi.	
	L	TD	APD	TD	APD	TD	APD
CIS	—	—	—	47.0	35.0	71.7	53.7
	—	100	86.0	—	—	—	—
	—	—	—	—	—	70.0	56.0
PAIII						74.4	55.1
(juv.)						66.2	46.5
TOR-3	282.5	(>83)	(74.5)	45.0	37.0	76.5	52.0
AND	267.0	91.0	—	40.0	37.0	78.9	47.8
	—	—	—	39.0	38.5	(75)	(45)
LVF						73.0	52.8

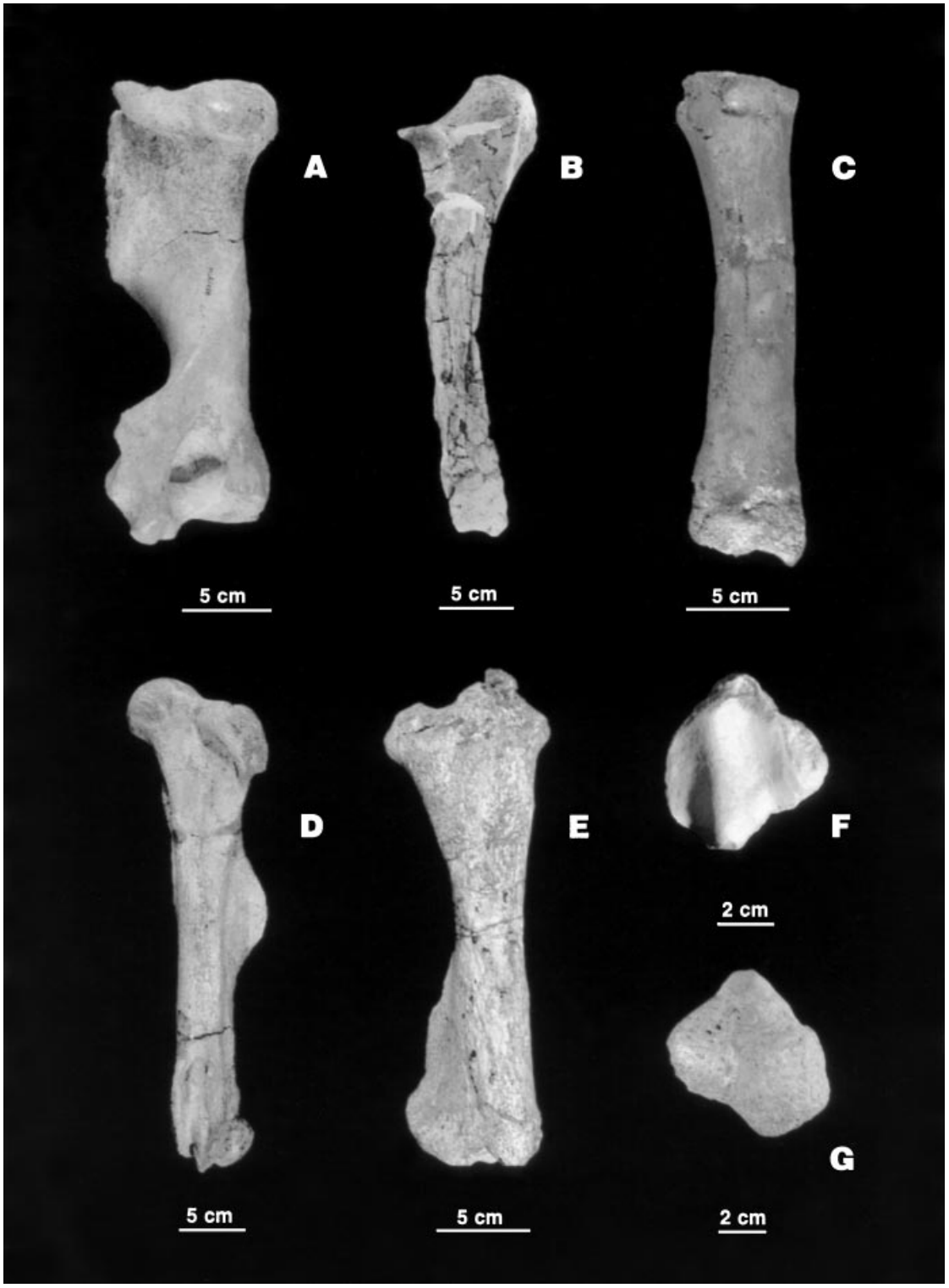

Fig. 6 A–G. *Alicornops simorrense*. —A. Left humerus from Moraleja de Enmedio, MJA/170, posterior view. —B. Left ulna from Paracuellos III, MNCN 7451, lateral view. —C. Right radius from Toril-3, anterior view. —D. Left femur (distorted) from Los Andurriales, anterior view. —E. Right tibia from Los Andurriales, anterior view. —F. Left patella from Toril-3, posterior view. —G. Left patella from Moraleja de Enmedio, MNCN 35722, anterior view.

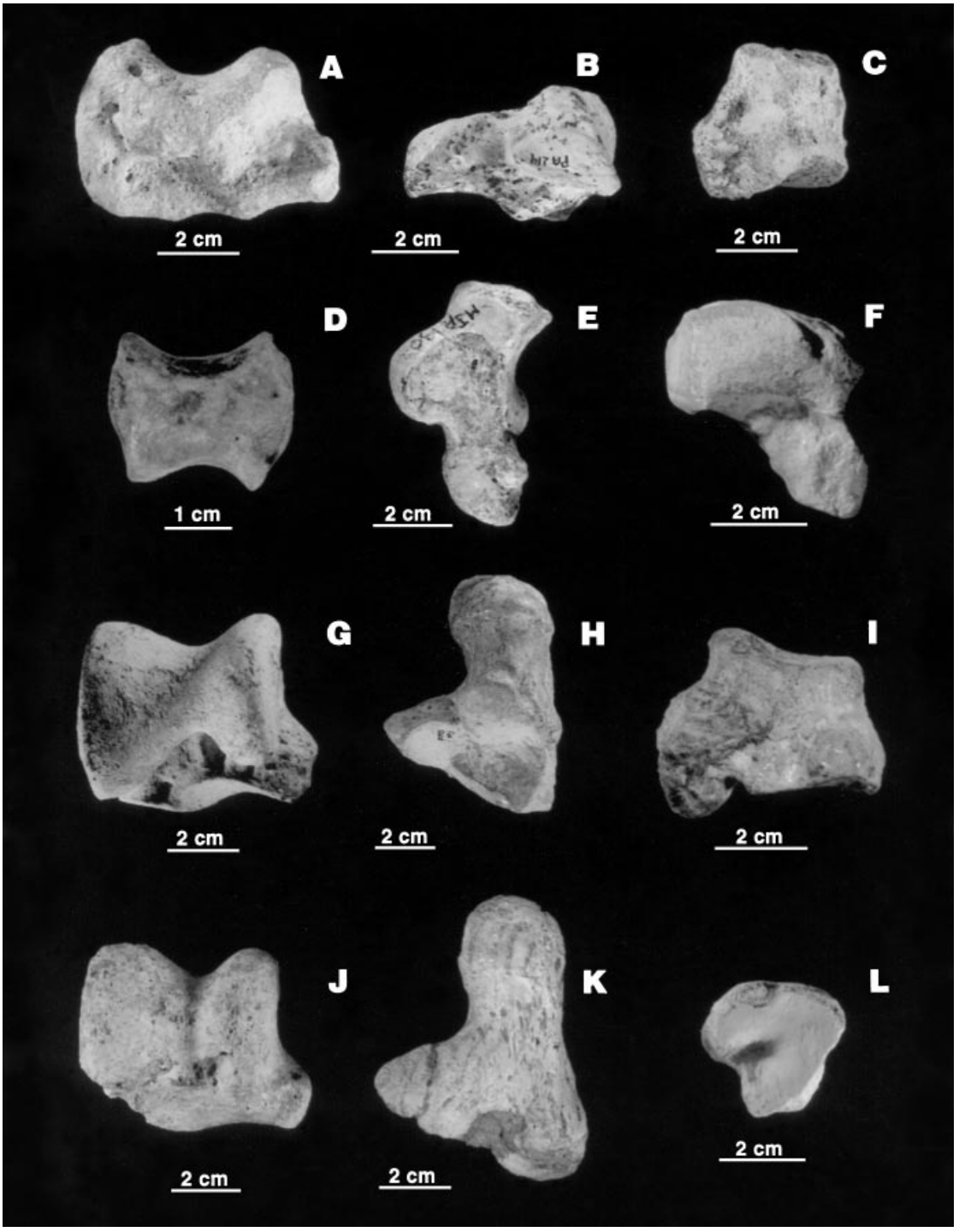

Fig. 7 A–L. *Alicornops simorrense*. —A. Right scaphoid from Los Valles de Fuentidueña, MNCN 3884, lateral view. —B. Left semilunate from Paracuellos III, MNCN 8120, medial view. —C. Right pyramidal from Moraleja de Enmedio, MJA 2/11, anteromedial view. —D. Right trapezoid from Toril-3, medial view. —E. Right magnum from Moraleja de Enmedio, MJA 130, lateral view. —F. Right unciform from Los Andurriales, proximal view. —G. Right astragalus from Los Valles de Fuentidueña, MNCN 4058, anterior view. —H. Left calcaneum from Paracuellos III, MNCN 7172, anterior view. —I. Right cuboid from Toril-3, lateral view. —J. Right astragalus from Moraleja de Enmedio, MJA/43, anterior view. —K. Right calcaneum from Los Andurriales, MNCN 35963, posterior view. —L. Right ectocuneiform from Los Andurriales, proximal view.

deep. Gracility index: Paracuellos III, 14.4; Los Andurriales, 16.4; Moraleja, 18.0.

Radius with proximal epiphysis relatively narrow and little thickened (Table 7; Fig. 6C). Posterior margin of proximal inner facet rather straight. Posterior medial facet usually separated from posterior ulnar facet, but united in a specimen from La Cistérniga. Insertion of biceps brachial muscle as deep hole on medial half of anterior face, in proximal position. Complete radius from Toril-3 with gracility index of 15.7.

Ulna robust, with olecranon tuberosity wide and thick (Table 7; Fig. 6B). Distal epiphysis narrow, with convex articulation slightly extended posteriorly. Gracility index: Paracuellos III, 10.4; Moraleja, 11.5.

Two complete femora from Los Andurriales distorted, showing differences in length (Table 7; Fig. 6D). The trochanter major forms a posterior rounded protuberance and an anterior, laterally inclined crest. Third trochanter little projected. Well-preserved distal epiphyses from Paracuellos III and La Cistérniga show narrow, very asymmetric trochlea, with little projecting epicondyles.

Diaphysis of tibia triangular in cross-section, with strong lateral edge (Fig. 6E). Distal inner facet narrow, very concave. Variation in size given in Table 7. Gracility index of most complete specimens from Los Andurriales and Toril-3, 14.9 and 15.9.

Fibula fragment from Los Andurriales with very narrow diaphysis, greatly enlarged distally. Mediodistal facet for astragalus subrectangular, almost flat. Dimensions of fragment: diaphysis, 11 × 16.7 mm; distal epiphysis, 15 × 36.5 mm; facet, 28 × 15 mm.

Patella (Fig. 6F,G) with narrow articulation, straight lateral border and well-developed proximal tuberosity. Specimens from Los Valles de Fuentidueña, Relea and Moraleja higher than those from Los Andurriales, Paracuellos III and Toril-3 (Table 8). Most specimens do not reach minimum values indicated by Guérin (1980) for *A. simorrense*.

In general, carpal bones short in height relative to width (Fig. 7A–F). Scaphoid long (APD), with short posterior border and short anterior apophysis. Trapezium facet particularly small on specimen from Toril-3. Lateral inferior facet long and partly subdivided on its dorsal border on Los Andurriales specimen, which differs from others in its greater maximum length (APD) and distal articular length (Table 9).

Semilunate with wide anterior face and short and robust posterior apophysis. Distally, anterior part of magnum facet at strong angle to unciform facet. Medially, dorsal facet for scaphoid not extended over apophysis. Size of semilunates rather homogeneous (Table 9), Can Llobateres specimen (Santafé 1978) being relatively longer and higher.

Pyramidal as a 'chubby' bone, that from La Cistérniga being the shortest (Table 9). Proximal facet wide anteroposteriorly. Pisiform facet very narrow on upper half. Medial facets for semilunate long, with irregular border. Two specimens from Los Valles de Fuentidueña with laterodistal extension, implying lengthening of distal facet in that area. This zone would articulate with extension of proximal facet of unciform. This condition seen only in specimens from Los Valles de Fuentidueña and Los Andurriales.

Two incomplete pisiforms recovered from Los Andurriales and Los Valles de Fuentidueña (Table 9).

Trapezoids short in H and APD, those from Los Valles de Fuentidueña being somewhat longer and wider. Among these, three especially long and high (Table 9), considered as representative of intraspecific variation (Cerdeño 1989). However, it is necessary to bear in mind their possible correspondence to other species recognized at this site, *A.* cf. *incisivum* (Alberdi *et al.* 1981).

Magnums from Paracuellos III, Moraleja and Los Valles de Fuentidueña with wide and short anterior face, with acutely projected sides; La Cistérniga and Nombrevilla specimens slightly narrower (Table 9). Proximal tuberosity with semilunate facet very convex. Posterior apophysis narrow and not very long (Fig. 7E). Distal facet narrows posteriorly with medial notch.

Unciform (Table 9) with anterior face transversely convex, especially on NM-1375 from La Cistérniga. Posterior apophysis short and robust. Distally, metacarpal facets as continuous surface with smooth limiting crests. Specimens from Los Andurriales and Los Valles de Fuentidueña with

Table 8 Comparative dimensions of the patella of *A. simorrense* from Spain. Abbreviations in text and Fig. 2.

Patella	TD	APD	H
AND	59.0	35.0	(63)
	55.4	36.0	60.3
PAIII			
N	2	4	4
Min.	60.0	29.5	(>66)
Aver.	60.0	31.8	67.9
Max.	(60)	33.0	71.8
TOR-3	55.4	33.0	(65.1)
REL	68.0	36.4	69.0
CIS	58.9	29.5	62.7
	63.5	36.6	64.3
MOR	68.5	36.1	74.5
	70.0	36.9	68.9
	63.0	(32.5)	68.8
LVF			
N	3	3	3
Min.	62.0	(34)	69.0
Aver.	67.9	35.7	74.4
Max.	74.8	37.3	83.3

Table 9 A–E. Comparative dimensions of the carpus of *A. simorrense* from Spain. Abbreviations in text and Fig. 2.

(A) Scaphoid

				art. prox.		art. dis.	
	TD	APD	H	TD	APD	TD	APD
AND	34.6	58.1	42.5	32.4	33.6	23.2	48.7
TOR-3	33.1	55.5	40.4	31.3	34.0	24.3	43.6
PAIII	37.2	56.0	41.8	35.7	36.0	22.3	44.6
	34.6	—	—	32.0	—	26.0	—
MOR	31.0	53.1	43.3	30.5	26.2	20.3	(46)
LVF							
N	3	4	5	3	4	4	4
Min.	32.1	60.1	(38)	25.8	(34.5)	(20.1)	(42)
Aver.	34.8	63.9	41.6	28.4	37.4	22.7	47.7
Max.	37.5	66.8	44.5	31.6	40.1	25.4	52.0

(B) Semilunate and pyramidal

Semilunate	TD	APD	H	Hant.	Pyramidal	TD	APD	H	prox. APD
CIS	35.0	51.0	34.3	36.1	CIS	30.0	33.3	34.0	24.3
PAIII					PAIII	31.5	32.3	39.7	25.7
N	4	2	4	3					
Min.	31.5	48.5	30.2	32.6					
Aver.	34.8	50.0	33.2	34.2					
Max.	(37)	51.5	34.7	37.1					
TOR-3	28.1	47.0	29.0	32.0	AV4	(28)	31.3	(35)	22.0
						(31.5)	28.5	(33)	22.0
CLL	36.0	55.0	42.0		ARM1	37.0	31.8	40.1	24.0
					MOR	31.7	33.8	36.3	23.3
						36.5	35.0	(37.9)	26.2
LVF					LVF				
N	3	1	4	4	*N*	8	8	8	7
Min.	25.7		30.6	31.0	Min.	28.0	(>28)	36.4	21.5
Aver.	30.2	48.5	33.5	35.0	Aver.	31.7	30.8	38.9	24.0
Max.	(33)		(38)	40.0	Max.	35.7	33.0	42.6	26.0

(C) Pisiform

	TDart.	Hart.	APD	H
AND	19.0	21.0	48.4	35.0
LVF	21.2	26.6	—	—

(D) Trapezoid and magnum

Trapezoid	TD	APD	H	Hmin.	Magnum	TD	APD	H	Hart.
PAIII					PAIII				
N	6	6	6	5	*N*	4	1	2	2
Min.	17.7	25.4	19.4	13.5	Min.	32.8		40.0	36.4
Aver.	19.2	28.2	21.2	15.3	Aver.	35.6	63.0	43.2	38.7
Max.	22.6	29.6	24.4	16.2	Max.	37.7		46.4	41.1

Table 9 *Continued.*

Trapezoid	TD	APD	H	Hmin.	Magnum	TD	APD	H	Hart.
TOR-3	20.5	28.3	23.0	15.6	CIS	31.5	—	—	—
	20.5	30.1	25.6	17.1					
					MOR	34.6	61.6	39.1	38.5
					NOM	29.2	—	—	(40)
LVF					LVF				
N	9	9	9	9	*N*	3	1	1	2
Min.	(17)	30.0	20.4	15.7	Min.	32.5			(36)
Aver.	20.3	34.1	24.2	17.2	Aver.	34.2	66.4	(>43)	40.0
Max.	22.8	38.0	29.0	20.0	Max.	35.6			44.0

(E) Unciform

	TD	Hant.	abs. L	anat. L
PAIII				
N	4	4	0	0
Min.	(41.4)	32.7		
Aver.	43.6	34.6		
Max.	44.9	36.0		
TOR-3	42.5	34.0	56.0	47.3
MOR	43.0	35.0	61.8	46.4
CIS				
N	3	3	3	3
Min.	44.2	31.6	59.0	44.7
Aver.	44.5	33.9	60.0	48.0
Max.	45.0	35.3	61.0	52.0
AV4	42.2	37.1	59.0	42.6
ARM1	46.3	39.0	—	—
AND	43.0	33.0	58.3	50.7
LVF				
N	3	3	2	2
Min.	40.4	(33)	57.8	49.0
Aver.	41.5	34.2	59.9	49.5
Max.	43.2	35.8	62.1	50.0

narrow extension of proximal facet reaching lateral border, in contact with McV facet.

Both astragalus and calcaneum of *A. simorrense* easily identifiable as small, short, robust bones (Fig. 7G,H,J,K). Calcaneum with strong rugosities of muscular insertion on lateral and posterior faces. Tuber calcis is broad and short, less developed on specimens from Los Andurriales. Sustentaculum well developed, at right angle to major axis of bone; on Toril-3 specimen, sustentaculum is flattened and concave posteriorly; others convex. Astragalus facets usually separated; facets 2 and 3 (anterolateral and anterodistal) united on specimen from Paracuellos III.

Astragalus very short, with very convex and deep trochlea, and great APD. Separating groove between trochlea and distal articulation short, deep. Medial tubercle and distal facet well projected medially from trochlea. Both distal facets forming strong angle. Cuboid facet not visible in anterior view. Calcaneum facets separated; facet 1 (posterolateral) wider and united to facet 2 (posteromedial) on specimen from Toril-3. Distal area of facet 1 usually long and rounded, some variation observed.

Size of astragali and calcanea very homogeneous among different sites (Table 10). Specimen from Trinchera del Ferrocarril (Vallés-Penedés) the highest one, after Santafé (1978).

Navicular short and rhomboidal. Posterior tuberosity rounded, slightly projected. Laterally, anterior facet continues

Table 10 A–E. Comparative dimensions of the tarsus of *A. simorrense* from Spain. Abbreviations in text, Fig. 2, and CP, Can Ponsic; TFE, Trinchera del Ferrocarril (from Santafé 1978).

(A) Astragalus

				art. dis.			
	TD	H	max. TDdis.	TD	APD	DL	int. APD
AND	62.0	51.0	55.0	49.8	—	41.0	(39.2)
PAIII							
N	8	9	7	8	4	9	8
Min.	(50)	(49.9)	53.0	(48.5)	(25)	40.0	36.4
Aver.	60.4	53.1	55.7	52.7	30.3	42.2	42.5
Max.	66.4	56.0	59.0	56.3	33.8	44.2	(53)
TOR-3	69.3	57.3	63.7	59.8	33.1	46.5	45.6
MOR	67.6	52.1	(60.8)	—	(28.5)	42.3	(35.5)
CIS							
N	4	4	4	4	4	5	5
Min.	66.5	51.0	57.2	54.0	31.2	44.0	(36.3)
Aver.	67.5	55.2	59.3	56.1	33.1	46.1	40.0
Max.	69.0	(58)	62.5	59.7	34.0	48.0	44.0
AV4	63.7	52.5	55.5	51.3	28.5	38.3	35.8
TFE	(60)	59.0	(51)	47.0	(30)	40.0	44.0
LVF							
N	6	6	6	6	6	6	6
Min.	58.9	48.3	(52.8)	(45.3)	(22)	40.0	48.4
Aver.	63.4	52.1	56.2	51.4	27.8	42.5	51.5
Max.	66.3	55.0	59.3	56.6	35.0	46.2	54.5

(B) Calcaneum

		tuber				
	H	TD	APD	TDsus.	beak APD	post. APDmin.
AND	82.0	31.0	42.0	58.0	45.0	27.0
AV4	—	—	—	47.1	—	—
ARM6	—	(42.6)	43.2	—	—	29.7
MAN1	85.0	34.2	45.8	—	43.5	(28)
TOR-3	93.0	36.2	50.8	55.6	46.3	28.9
PAIII						
N	5	5	5	5	4	5
Min.*	76.7	(25)	41.5	41.2	40.0	23.0
Aver.	80.5	31.4	45.7	51.7	43.9	27.6
Max.	83.7	34.4	50.4	59.3	50.1	31.0
*Except for H, minima correspond to a juvenile						
MOR	(79.1)	32.2	51.8	54.0	(44.7)	31.8
	80.7	36.1	47.8	58.2	45.4	33.6
CIS						
N	3	3	3	2	3	3
Min.	82.5	(34)	46.0	56.7	47.8	29.0
Aver.	84.4	35.6	47.6	59.1	48.6	31.5
Max.	86.0	37.2	50.4	61.5	50.0	33.6

Table 10 *Continued.*

		tuber				
	H	TD	APD	TDsus.	beak APD	post. APDmin.
LVF						
N	4	7	7	0	7	8
Min.	79.0	33.3	(47.5)		44.0	25.2
Aver.	80.9	35.0	50.1		46.2	27.3
Max.	82.7	37.0	53.2		49.3	29.0

(C) Cuboid

					art. prox.	
	TD	APD	H	Hant.	TD	APD
AND	28.4	42.3	(>38)	27.7	27.0	—
PAIII						
N	4	4	4	5	4	4
Min.	28.0	44.1	(>36)	27.5	28.0	30.5
Aver.	29.2	45.9	42.5	29.3	28.8	32.6
Max.	31.5	48.5	45.8	31.6	31.2	36.7
AV4	29.8	48.1	44.0	31.0	25.1	30.3
MAN1	25.7	40.3	32.3	24.4	24.8	28.0
	29.8	(>50)	(35.5)	29.4	(25.5)	33.0
TOR-3	29.5	44.7	38.8	28.0	—	(29.4)
	32.3	53.4	40.8	28.7	30.4	30.7
CP	36.0	56.2	(46.5)	—	—	34.0
LVF						
N	4	4	4	4	4	4
Min.	29.0	47.4	30.0	27.9	(26.4)	(26)
Aver.	31.5	50.9	32.9	29.4	28.3	29.1
Max.	32.6	55.5	36.0	30.9	29.6	32.8

(D) Navicular

	TD	APD	H	Hmin
AND	37.0	43.6	20. 0	15.5
	(34.5)	41.2	19.3	15.5
PAIII				
N	5	5	5	5
Min.	33.0	40.8	20.0	14.0
Aver.	36.7	42.8	21.7	15.7
Max.	41.0	46.9	23.9	17.2
AV4	(31)	(38)	17.5	13.5
TOR-3	32.5	(39)	(19.5)	16.0
NOM	(36.7)	(46.5)	(22.5)	—
LVF				
N	6	6	6	6
Min.	33.0	45.0	18.5	14.3
Aver.	35.4	47.6	20.6	16.1
Max.	37.8	51.4	25.0	18.4

Table 10 *Continued.*

(E) Entocuneiform, mesocuneiform and ectocuneiform

	TD	APD	H	ant. Hmin.
Entocuneiform				
AND	(14.3)	(>22)	—	38.0
LVF	16.3	32.9	40.6	33.5
Mesocuneiform				
AND	19.0	18.0	10.6	
	18.2	23.0	12.3	
PAIII	21.3	23.6	11.8	
	18.7	21.7	10.0	
Ectocuneiform				
AND	29.0	30.0	17.6	
PAIII				
N	3	2	3	
Min.	32.6	33.5	18.8	
Aver.	33.4	34.2	20.6	
Max.	34.3	35.0	22.9	
CP	37.0	41.0	23.5	
LVF				
N	3	3	3	
Min.	32.6	(34)	17.4	
Aver.	32.7	36.4	17.9	
Max.	33.0	39.6	18.7	

in posterior one, with narrower median zone. Distally, entocuneiform facet displaced posteriorly. Specimens from Los Valles de Fuentidueña are relatively longer than the others (Table 10).

Cuboid from Los Valles de Fuentidueña longer (APD) and shorter (H) than others (Table 10), with posterior apophysis broader and more robust. In general, cuboid has wide and short anterior face. Two specimens from Los Andurriales have lateral tuberosity from the anterior face backwards, giving greater anterior width. Medially, ectocuneiform facets small, high and narrow. Proximal facet for astragalus placed more posteriorly than calcaneum facet. Distal articulation pear-shaped.

Ectocuneiform broad and short, mainly Los Andurriales and Paracuellos III specimens compared with Los Valles de Fuentidueña; that from Can Ponsic (Santafé 1978) larger than others (Table 10).

Mesocuneiform represented by two specimens from Paracuellos III and Los Andurriales, triangular in outline. The latter shorter and wider (Table 10), with entocuneiform facet occupying whole height of medial facet.

Entocuneiform of *A. simorrense* only known from Los Andurriales and Los Valles de Fuentidueña. Lateral articulation placed on acute protuberance. Proximal facet continuous with mesocuneiform facet, this one united to MtII facet.

As noted above, *A. simorrense* has shortened, not massive, metapodials (Tables 11, 12; Fig. 8). Gracility index similar among different studied samples. On specimens from Los Valles de Fuentidueña, diaphysis slightly wider than those from older sites, implying some loss of gracility (Fig. 9).

McII with rough proximal tuberosity on anterior face. Lateral facets with smooth crest between them, smoother on McII from Los Valles de Fuentidueña. Magnum facet almost flat, slightly longer than McIII facet, slightly concave. McIII facet with well-marked median, inferior notch (Los Valles de Fuentidueña). Proximal facet extended in small medial facet, usually well developed, except on C3/2,38 from Los Valles de Fuentidueña. Diaphysis broader in Vallesian specimens. Gracility indices calculated for McII of *A. simorrense* show progressive decrease of gracility from early late Aragonian (Paracuellos III, Toril-3, Moraleja) to late late Aragonian (La Cistérniga) and Vallesian (Los Valles de Fuentidueña): Paracuellos III, 25.1; Toril-3, 24.6; Moraleja, 25.9; La Cistérniga, 29.4; Los Valles de Fuentidueña, 31.4, 31.1 (Fig. 9).

Proximal facets (for magnum and unciform) of McIII forming strong crest between them; whole articulation hardly wider than thick, except on Toril-3 specimens. Medial McII facet well developed, convex anteroposteriorly, with marked notch on distal border, absent on two of

Table 11 Comparative dimensions of the metacarpus of *A. simorrense* from Spain. Abbreviations in text, Fig. 2, and CJO, Can Jofresa (from Santafé & Casanovas 1978).

		prox. epi.		**dia.**			**dis. art.**	
	L	TD	APD	TD	APD	dis. Tdmax.	TD	APD
McII								
AND	—	26.8	28.5	—	—	—	—	—
PAIII								
N	1	3	4	2	2	1	1	1
Min.		26.5	27.6	25.9	10.4			
Aver.	102.9	27.5	28.3	26.5	10.7	(35.2)	25.1	27.5
Max.		28.2	29.0	27.0	11.0			
AV6	—	27.8	26.7	21.5	(22)	—	—	—
CIS	102.0	29.0	30.6	30.0	11.3	—	—	—
	—	24.8	29.6	(23.6)	10.5	—	—	—
TOR-3	101.6	25.3	(26.2)	25.0	11.5	27.4	25.0	27.0
MOR	101.2	27.7	26.2	26.2	11.7	28.0	25.7	25.6
LVF								
N	2	4	3	3	3	2	2	2
Min.	102.6	27.5	29.3	32.0	(11. 5)	33.8	27.6	29.5
Aver.	103.3	30.3	33.3	32.5	12.8	34.4	28.8	29.6
Max.	104.0	33.7	38.7	32.8	13.8	(35)	30.0	29.7
McIII								
AND	126.7	(41.5)	—	35.0	(12)	35.5	—	—
	—	41.0	—	35.5	(11.8)	—	—	—
PAIII	110.3	35.4	30.5	31.0	14.3	37.2	—	—
AV4	—	41.5	31.3	—	—	—	—	—
MAN1	119.0	43.0	36.7	35.1	15.0	44.2	39.0	33.3
	—	41.3	36.0	33.0	16.0	—	—	—
TOR-3								
N	2	3	2	3	3	2	2	2
Min.	111.0	39.0	32.3	31.1	14.0	38.9	(33.9)	27.5
Aver.	112.2	40.6	32.4	31.7	14.8	38.9	34.2	28.7
Max.	(113.5)	41.8	32.6	33.0	16.0	39.0	34.5	30.0
CIS	117.0	43.7	36.0	35.0	14.8	42.5	31.0	38.4
MOR	—	43.9	37.2	(32.4)	(14.7)	—	—	—
	123.2	45.9	38.0	35.7	16.1	42.5	39.0	31.0
	—	43.3	33.6	30.9	15.4	—	—	—
LVF	—	46.5	33.9	—	(16.5)	—	—	—
McIV								
AND	—	25.0	26.8	24.4	13.8	—	—	—
AV3	—	26.9	28.0	25.7	12.9	—	—	—
AV4	112.0	29.8	30.2	24.2	13.4	29.3	27.5	28.4
TOR-3	—	24.6	27.0	—	—	—	—	—
	89.7	24.0	29.4	21.2	17.7	28.0	25.0	25.6
PAIII	—	26.0	29.0	23.1	15.0	—	—	—
	—	28.3	31.1	—	—	—	—	—

Table 11 *Continued.*

		prox. epi.		dia.			dis. art.	
	L	TD	APD	TD	APD	dis. Tdmax.	TD	APD
MOR	—	27.4	30.6	(22.1)	—	—	—	—
CIS								
N	1	3	3	2	2	1	1	1
Min.	26.0	30.2	23.6	13.6				
Aver.	99.2	26.6	31.2	24.3	13.8	28.0	27.3	29.0
Max.		27.0	32.0	25.0	14.0			
CJO	122.5	(31)	37.5	27.5	17.0	38.5	32.0	35.0
CP	—	31.5	36.0	23.0	17.5	—	—	—
LVF								
N	2	6	7	5	5	2	2	2
Min.	88.7	(27)	27.0	23.5	12.9	30.5	25.0	(25.5)
Aver.	95.3	31.4	31.0	26.2	14.4	33.7	28.3	25.6
Max.	102.0	35.0	35.8	29.3	16.3	37.0	(31.7)	25.8
McV								
AV4	49.0	12.8	17.5	12.0	9.0	18.2	14.5	—
TOR-3								
N	2	2	2	3	3	3	1	3
Min.	51.4	12.4	21.0	10.3	6.5	16.0		16.4
Aver.	53.8	14.4	22.1	11.2	8.7	18.1	13.4	16.5
Max.	56.2	16.4	23.3	12.2	9.9	(20.2)		16.6
LVF	65.2	16.0	22.4	14.9	10.1	26.6	19.6	18.4

Table 12 Comparative dimensions of the metatarsus of *A. simorrense* from Spain. Abbreviations in text, Fig. 2, and HPI, Hostalets de Piérola (from Santafé 1978).

		prox. epi.		dia.			dis. art.	
	L	TD	APD	TD	APD	dis. TDmax.	TD	APD
MtII								
AND	99.5	(17.7)	—	—	—	—	27.1	22.2
AV4	—	19.0	29.0	—	—	—	—	—
MAN1	87.3	19.3	(26.5)	20.0	14.0	25.0	(22.6)	26.0
PAIII								
N	2	4	3	3	3	2	2	2
Min.	99.0	19.0	28.0	18.3	14.2	(24.9)	24.2	26.3
Aver.	99.3	19.5	29.7	19.4	16.6	25.7	24.6	27.1
Max.	99.6	20.3	32.7	20.4	(18)	26.5	25.0	28.0
TOR-3	101.0	22.3	31.3	18.0	16.0	26.2	26.2	29.0
MOR	102.4	21.4	33.7	21.8	18.7	26.7	26.7	30.7
	—	20.6	29.0	20.8	17.9	—	—	—

Table 12 *Continued.*

		prox. epi.		dia.			dis. art.	
	L	TD	APD	TD	APD	dis. TDmax.	TD	APD
HPI	108.5	27.0	37.5	—	21.0	33.5	30.0	33.5
LVF								
N	2	7	7	4	4	2	2	2
Min.	93.6	(19.7)	31.0	19.4	18.3	29.0	25.6	30.0
Aver.	96.1	20.9	32.6	21.1	19.0	29.6	25.8	30.0
Max.	98.6	22.4	35.9	23.6	20.5	30.2	26.0	30.0
MtIII								
MAN1	—		33.6	30.0	—	—	—	—
CIS	—	37.0	34.4	29.4	16.0	—	—	—
(juven.)	103.6	35.7	30.3	30.0	15.7	36.5	34.7	(30)
PAIII	—	33.1	—	31.3	(15.3)	—	—	—
MOR	—	32.9	28.1	—	—	—	—	—
HPI	122.0	—	(42)	39.0	18.0	47.0	40.0	37.0
CLL	120.0	44.2	39.6	41.5	20.0	48.3	41.6	39.5
LVF								
N	1	4	1	5	5	1	0	0
Min.		35.4		32.0	13.0			
Aver.	108.3	35.9	27.0	34.3	15.1	(42.6)		
Max.		37.0		39.0	17.5			
MtIV								
AND	94.5	29.8	—	22.6	17.8	25.0	(23.4)	23.1
ARM1	—	25.8	35.6	—	—	—	—	—
ARM6	—	31.6	36.0	—	—	—	—	—
	—	37.3	33.0	—	—	—	—	—
MAN1	—	25.4	—	17.4	13.4	—	—	—
	—	30.0	30.0	—	—	—	—	—
MAN2	—	34.4	34.9	24.0	19.0	—	—	—
PAIII								
N	2	3	3	2	2	2	3	3
Min.	93.2	27.6	28.5	20.4	16.5	24.7	22.0	26.0
Aver.	94.0	29.5	30.2	21.1	17.6	25.5	23.1	28.4
Max.	94.8	30.7	32.0	21.7	18.7	26.3	25.0	31.6
MOR	—	29.6	29.7	20.6	17.4	—	—	—
CIS								
N	2	4	3	4	3	3	3	3
Min.	98.0	26.0	30.7	21.0	18.7	25.0	23.7	27.8
Aver.	99.0	28.1	32.2	21.6	19.4	25.6	24.5	29.4
Max.	100.0	29.5	34.4	(22.5)	20.1	25.9	25.4	30.8
HPI	112.0	35.0	30.0	25.0	22.0	30.0	26.5	34.5
CLL	115.0	41.0	38.5	27.4	19.0	32.2	29.0	37.5
LVF								
N	0	5	5	3	3	0	0	0
Min.		(27)	(30.7)	22.2	16.7			
Aver.		28.9	32.8	23.0	17.8			
Max.		(30.8)	34.4	(24)	(19)			

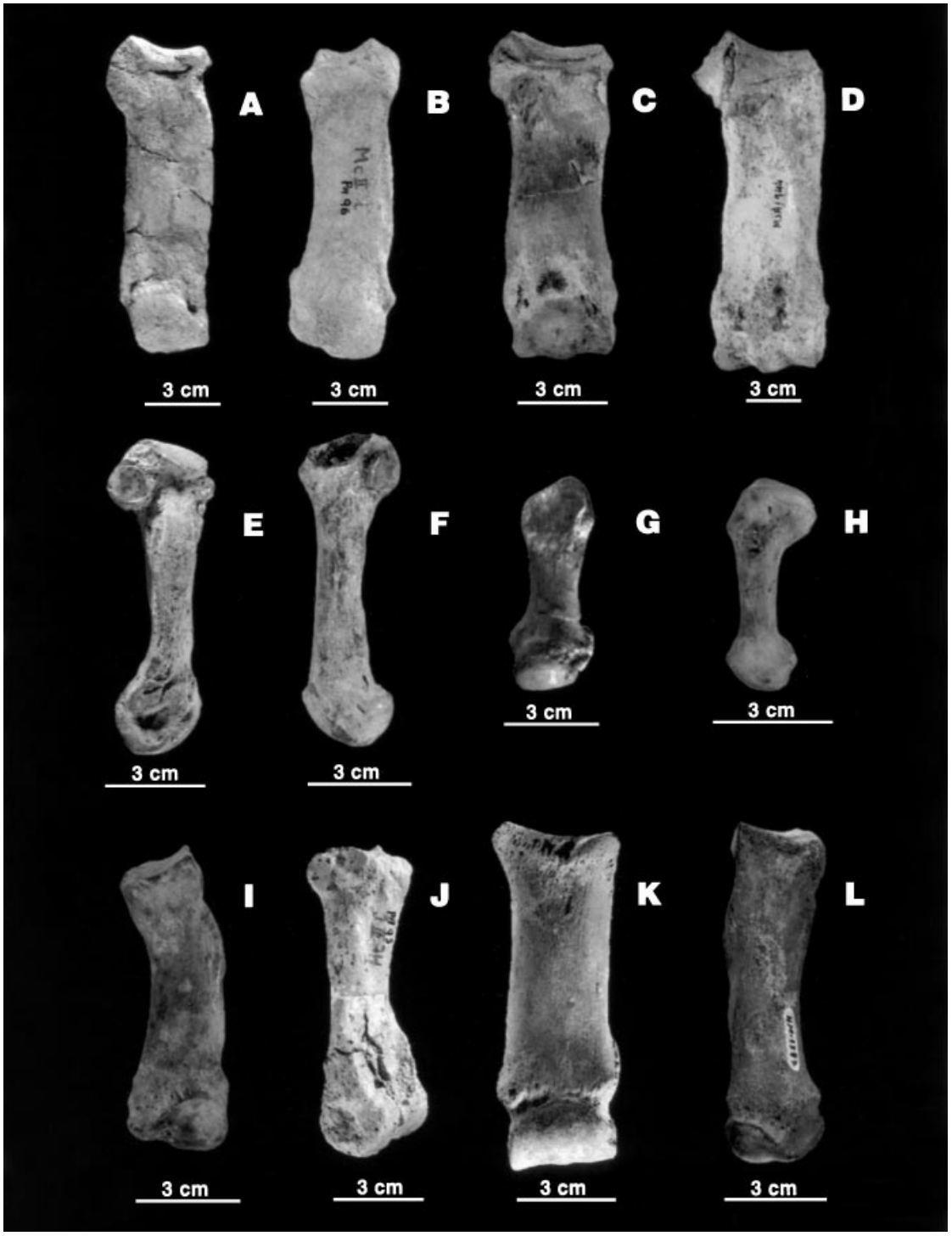

Fig. 8 A–L. *Alicornops simorrense*. —A. Right McII from Los Andurriales, MNCN 35965, anterior view. —B. Left McII from Paracuellos III, MNCN 7164, anterior view. —C. Right McIII from Toril-3, anterior view. —D. Left McIII from Moraleja de Enmedio, MJA/144, posterior view. —E. Left McIV from La Cistérniga, CI/15561, medial view. —F. Right McIV from Toril-3, medial view. —G. Left McV from Los Valles de Fuentidueña, MNCN 4031, anterior view. —H. Right McV from Toril-3, medial view. —I. Left MtII from Toril-3, anterior view. —J. Left MtII from Paracuellos III, MNCN 7163, posteromedial view. —K. Right MtIII from La Cistérniga, MNCN 4156, anterior view. —L. Left MtIV from La Cistérniga, MNCN 4158, anterior view.

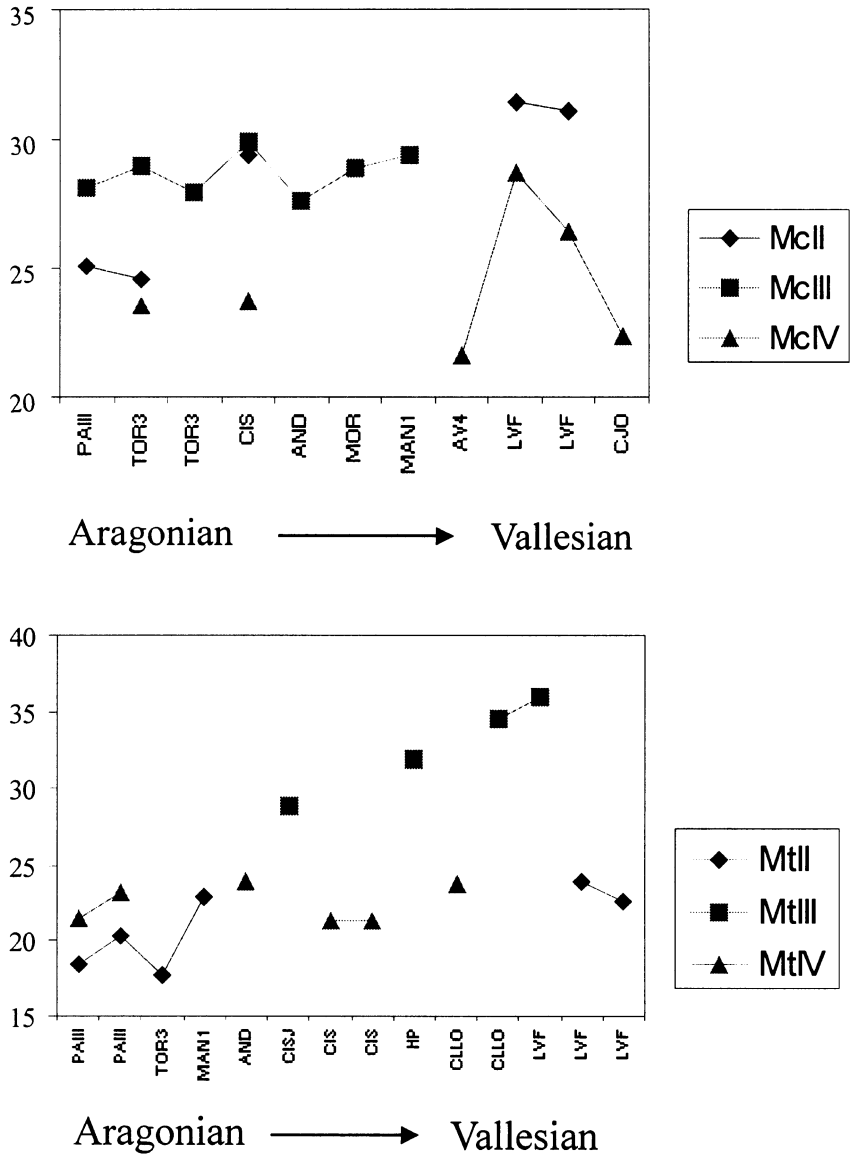

Fig. 9 Distribution of the metapodial gracility indices of *A. simorrense*. Abbreviations as in Fig. 2 except HP, Hostalets de Pierola and CLLO, Can Llobateres.

three McIII from Toril-3. Laterally, anterior McIV facet large and trapezoid in outline; posterior one small and ovoid; both separated by wide, shallow depression. On Toril-3 and Paracuellos III specimens, anterior lateral facet smaller and posterior one higher and placed more vertically. Diaphysis with two deep posterior depressions, above distal articulation; less marked on McIII from Toril-3. Gracility indices: Manchones-1, 29.4; Toril-3, 29.0, 28.0; Paracuellos III, 28.1; Los Andurriales, approximately 27.6; Moraleja, 28.9; La Cistérniga, 29.9.

Some individual variability concerning the proximal facet of McIV, clearly shorter on one specimen from La Cistérniga, and more separated from the posterior medial articulation, in turn, more detached from rest of epiphysis. Width of proximal facet greater on McIV from Paracuellos III than on those from La Cistérniga, even greater on those from Los Valles de Fuentidueña. Two complete specimens from the latter show great difference in size: LVF 1163 even shorter than McIV from La Cistérniga, and B3/1-59 higher and wider (Table 11). Medial McIII facets hardly vary among specimens; posterior one ovoid and shorter in Paracuellos III, Toril-3 and one specimen from La Cistérniga. Laterally, no well-developed McV facet but an extension of proximal facet (very neat in Toril-3).

Specimen from Arroyo del Val-4 notably higher than other McIV, with narrow diaphysis, rather slender. Proximal

epiphysis of this McIV more triangular in outline, with shorter proximal facet; anterior medial facet more semicircular and posterior one more rounded. Vallesian specimen from Can Jofresa (Santafé & Casanovas 1978) longer than any other, but with greater diameters, similar to those of McIV of *Alicornops alfambrense* from La Roma-2 (Cerdeño & Alcalá 1989). Gracility indices for McIV: Toril-3, 23.6; Arroyo del Val-4, 21.6; La Cistérniga, 23.7; Los Valles de Fuentidueña, 28.7, 26.4; Can Jofresa, 22.4.

McV poorly known for *A. simorrense*. Ginsburg & Guérin (1979) indicated this species with tridactyl manus. However, well-developed McV have been found at Arroyo del Val-4, Toril-3 and Los Valles de Fuentidueña (Cerdeño 1989). Their dimensions vary (Table 11). Diaphysis very short, large epiphyses. Large proximal articulation for unciform, forming strong angle (close to 90°), extended dorsally and medially to very small facet for McIV (only evident on Toril-3 and Arroyo del Val-4 specimens). Distal epiphysis broad, with very projecting supra-articular tubercles. Diaphysis elliptical in cross-section, more ovoid on complete specimens from Toril-3; distal fragment from this site with narrower diaphysis and more rounded in cross-section.

MtII varies in proximal facet morphology; shorter and wider on Aragonian specimens. The MtII from Toril-3 shows this facet more ovoid in outline and more detached from epiphysis. On specimens from Los Valles de Fuentidueña, facet more elongated posteriorly in relation with epiphysis (Table 12). Entocuneiform facet variable, generally elliptical, in contact with, or well separated from, proximal facet. Lateral facets for ectocuneiform and MtIII high and slightly subdivided; two inferior subfacets (for MtIII) very reduced on MtII from Los Valles de Fuentidueña. Diaphysis enlarged distally; more robust on MtII from Manchones-1 and Los Valles de Fuentidueña than on those from Paracuellos III and Toril-3, reflected in gracility indices: Paracuellos III, 18.4, 20.4; Toril-3, 17.8; Manchones-1, 22.9; Los Valles de Fuentidueña, 23.9, 22.7 (Fig. 9).

Best preserved MtIII from La Cistérniga with different inclination of lateral posterior facet, more rounded and vertically placed on juvenile specimen. This with very small facet between lateral anterior facet and proximal one that would contact with cuboid. Medially, juvenile has small anterior MtII facet. Gracility indices: La Cistérniga (juvenile), 28.9; Los Valles de Fuentidueña, 36; Can Llobateres, 34.5; Hostalets de Piérola, 31.9. Specimens from Can Llobateres and Hostalets (Santafé 1978) more slender than that from Los Valles de Fuentidueña owing to greater length despite greater diameters.

MtIV with roughly quadrangular proximal epiphysis, more triangular in outline on specimens from Moraleja and La Cistérniga because of lesser development of lateroposterior tuberosity, with proximal facet narrower and longer. MtIV from Paracuellos III and Los Valles de Fuentidueña with lateral notch of proximal facet more marked, with bilobed aspect. Medial anterior MtIII facet semielliptical, posterior one more irregularly rounded. Diaphysis very twisted with respect to proximal epiphysis, but slightly bent. Gracility indices: Paracuellos III, 21.5, 23.2; Los Andurriales, 23.9; La Cistérniga, 21.4, 21.3; Can Llobateres, 23.8.

Dimensions of phalanges of *A. simorrense* in Table 13. Small, subcylindrical first phalanx from Toril-3 seems to correspond to McV. Dimensions: TD, 14.2 mm; APD, 14.4 mm; H, 15.3 mm.

Discussion

The Spanish material of *Alicornops* shows an evolutionary trend for the species from the late Aragonian to the last Vallesian representatives. From late Aragonian to early Vallesian, differences among series of *A. simorrense* are few, although there is some general increase in size both in dentition and postcranial skeleton in the specimens from Los Valles de Fuentidueña, Chiloeches and Nombrevilla. With respect to the bones, this increase in size is more evident in the maximum APD of different bones and the APD of the metapodial diaphysis (e.g. Los Valles de Fuentidueña vs. Paracuellos III, La Cistérniga). As previously mentioned, we do not justify the subspecies *A. s. duratonense* created by Alberdi *et al.* (1981) for the sample from Los Valles de Fuentidueña. It would simply show a trend of increasing size and robustness without limits among assemblages clear enough to establish different subspecies. On the other hand, the Spanish record has also provided some late Vallesian remains from La Roma-2 (Teruel) which permitted the recognition of a second species of *Alicornops*, *A. alfambrense* (Cerdeño & Alcalá 1989). This is well differentiated by its greater size and robustness, showing a clear change of proportions that would have occurred between the early and the late Vallesian (Fig. 10). On the other hand, *A. simorrense* is also present in the early and late Vallesian deposits of the Vallés-Penedés Basin (Santafé 1978), but does not show the same tendency towards greater proportions observed in the other sites of this age. The metapodials from Hostalets de Piérola (late Aragonian), Can Ponsic, Can Llobateres and Can Jofresa (Vallesian) present similar diameters (TD and APD) to the specimens from La Roma-2, but with a greater length, which implies that they do not reach a great robustness (Cerdeño 1989). We suggest that the Aragonian *A. simorrense* followed two different evolutionary trends: (i) in the central basins, they became progressively more robust, giving rise to *A. alfambrense* (Fig. 10); and (ii) in the Vallés-Penedés Basin, they increased in size overall, but maintained their proportions.

The abundance of *A. simorrense* remains in Spain permits an estimation of its general size, even though it is calculated

Table 13 A–C. Comparative dimensions of the phalanges of *A. simorrense* from Spain. Abbreviations in text and Fig. 2.

(A) First central phalanx and first lateral phalanx

First central phalanx	TD	APD	H	First lateral phalanx	TD	APD	H
				TOR-3	(>26)	25.4	23.2
PAIII				PAIII			
N	3	3	3	*N*	8	8	8
Min.	31.2	(22)	19.6	Min.	23.4	22.8	19.7
Aver.	34.3	24.9	20.6	Aver.	27.1	25.2	21.2
Max.	37.0	26.8	22.4	Max.	29.0	27.0	23.5
LVF				LVF			
N	5	5	5	*N*	3	3	3
Min.	37.4	(25.5)	20.8	Min.	30.0	26.6	22.0
Aver.	39.5	26.7	23.2	Aver.	33.3	28.9	22.9
Max.	41.0	29.5	26.0	Max.	38.4	31.6	24.2

(B) Second central phalanx and second lateral phalanx

Second central phalanx	TD	APD	H	Second lateral phalanx	TD	APD	H
AV4	38.4	19.8	20.0	CIS	(>26)	28.0	20.6
ARM6	45.0	26.4	29.8	MAN	31.8	25.1	22.9
				TOR-3	25.0	(>15)	16.9
					28.7	18.3	17.1
PAIII				PAIII			
N	3	3	3		32.0	20.1	16.3
Min.	(34)	17.2	16.0		26.3	18.8	17.7
Aver.	35.4	18.4	16.8				
Max.	37.3	19.3	17.3				

(C) Third central phalanx and third lateral phalanx

		art.				art.	
Third central phalanx	TD	TD	APD	Third lateral phalanx	TD	TD	APD
MAN2	(59)	31.3	14.5	PAIII			
MOR	—	32.6	13.3	*N*	0	4	4
				Min.		22.0	13.0
				Aver.		22.7	14.8
				Max.		23.5	17.0

from different series (Cerdeño 1989; and new data). The average length of the fore legs would be around 75 cm, and that of the hind legs around 85 cm. These estimations indicate an animal not reaching 1 m in height in anatomical position. On the other hand, the relationship skull/legs would be similar to that of the extant *Rhinoceros unicornis*, *Dicerorhinus sumatrensis* and *Diceros bicornis* (after data from Guérin 1980). The average body mass of *Alicornops simorrense* has been estimated to be 967.5 kg (Cerdeño & Nieto 1995; Cerdeño 1998), following Legendre's formula, based on the area of m1 and some constants established for perissodactyls (Legendre 1986; Alcalá 1994).

Comparing with other series of *A. simorrense* elsewhere, a general similarity is established, with small differences that can be attributed to intraspecific variation. Out of the 22 European localities listed by Guérin (1980), 12 are from Spain, nine from France and one from Germany. Only in a few cases (Simorre, La Grive and Montredon) is the material abundant, the teeth always better represented than the postcranial skeleton. Comparing data, we have observed that, only when Spanish specimens are included in Guérin's (1980) tables, will our data fall within the variation range of the species given by this author, and always around the minimum values or even below them. Only the specimens

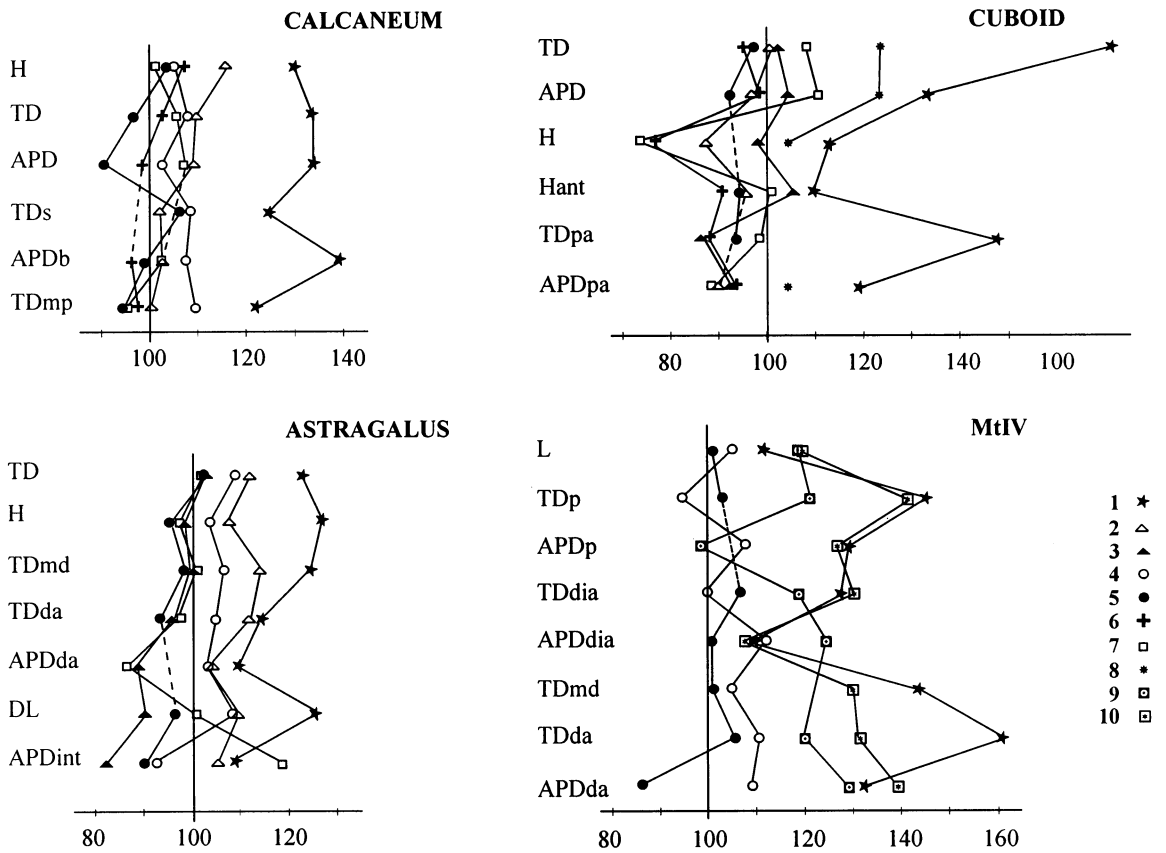

Fig. 10 Comparative proportions of calcaneum, astragalus, cuboid and MtIV of *A. simorrense* and *A. alfambrense* (modified from Cerdeño & Alcalá 1989). 1, La Roma-2; 2, Toril-3; 3, Arroyo del Val-4; 4, La Cistérniga; 5, Los Andurriales; 6, Manchones-1; 7, Los Valles de Fuentidueña; 8, Can Ponsic; 9, Hostalets de Piérola; 10, Can Llobateres. Abbreviations in text and b, beak; da, distal articulation; int, internal; md, maximal distal; mp, maximal posterior; p, proximal; pa, proximal articulation; s, sustentaculum. Value 100 corresponds to Paracuellos III.

of *A. alfambrense* from La Roma-2 reach and occasionally surpass the maximum values, while maintaining a greater robustness. On the other hand, the great metric range of variation recorded by Guérin (1980) for *A. simorrense* led us to consider the possibility that part of that material might really correspond to *A. alfambrense*. However, this cannot be tested satisfactorily using the data in Guérin's tables, because they are not separated by sites, and therefore it is not possible to know whether all maximum values correspond to the same bones or whether there is a proportional difference between them. The presence of *A. alfambrense* beyond Spain was confirmed in Montredon (France) and Dorn-Dürkheim (Germany) (Cerdeño 1997).

As noted by Codrea (1992), P4 from the Aragonian of Romania, described as aff. *A. simorrense*, has a link between the hypocone and the protocone which is not characteristic of *Alicornops* but of other genera such as *Protaceratherium* and *Aceratherium*, among others (Cerdeño 1995, 1996; character 35). Its dimensions are similar to those of the Spanish specimens of *A. simorrense*, especially two P4 from Manchones-1 (Table 4), although in general the Spanish teeth are slightly larger and relatively wider.

The *A. s. orientalis* from early Vallesian deposits in Moldavia (Lungu 1984) has shorter nasals than the Spanish skulls. The positions of the nasal incision and the anterior border of the orbit are very similar, over the end of P4 and M2, respectively (according to Lungu's fig. 5). The size of its teeth is similar to those of the largest Spanish specimens, the premolars being relatively larger than the molars.

Concerning the Polish Middle Miocene remains from Przeworno, we agree with Kubiak (1981) in considering the remains described by Sulimski (in Glazek *et al.* 1971) as *Aceratherium silesiacum* to be *A. simorrense*. The diagnostic characters indicated by Sulimski are common to *A. simorrense*. Among them, the 'undeveloped protoloph' of P2 is usual in unworn specimens (Kubiak 1981; Cerdeño 1989);

in fact, the protoloph is developed, but not fused to the ectoloph until some wear degree is achieved (both P2 of the skull from Moraleja show different condition). P2 and P3 described by Sulimski (in Glazek *et al*. 1971) are larger than the Spanish remains, and relatively longer; the two P2 described by Kubiak (1981) are a little wider than the former P2, and are close to the largest Spanish specimens. Among the lower teeth described by these authors, we disagree with the assignation of m3 MF/1717/80-2 (Kubiak 1981; pl. 2) to *A. simorrense*. We think this m3 corresponds to *Brachypotherium brachypus*, a species also present in Przeworno, since its dimensions are too large for *A. simorrense* and very similar to the French remains of *B. brachypus* (Cerdeño 1993). In addition, this tooth shows the labial groove less marked than in *A. simorrense* and closer to the condition in the brachypotheres.

The Turkish material of *A. simorrense* comes from three sites in the Anatolian Peninsula (Heissig 1976), of late Aragonian (Sofça, Catakbagyaka I and IV) and early Vallesian (Yaylacilar) age, but represented by only nine dental fragments and five bones. All these Turkish remains are of similar dimensions to the Spanish Aragonian specimens of *A. simorrense*. However, Ginsburg & Guérin (1979; p. 116) considered that P4 and M3 from Sofça belong to *A.* aff. *tetradactylum*, which is also present in the area (Heissig 1976). It is true that the junction of crochet and crista is not as usual in P3–4 of *A. simorrense* as it is in P2, but it happens (e.g. at Nombrevilla). In any case, P4 from Sofça could actually belong to *A. tetradactylum*; more debatable is the determination of M3 whose size fits well with that of *A. simorrense*.

Final remarks

Alicornops simorrense appears to be abundant in the late Aragonian deposits in Western Europe. Ginsburg & Guérin (1979) considered as *Alicornops* sp. the remains from Wintershof-West (Germany) of early Aragonian age (MN 3), which might represent the origin of the species. *A. simorrense* is well known from beds of late Aragonian to late Vallesian age (Fig. 1), MN 6 to MN 10, although it has also been identified in the Spanish middle Aragonian (MN 5) of Armantes-1 (Cerdeño 1989) and Montejo de la Vega (Mazo *et al*. 1998).

It is in Spain where *A. simorrense* is better and more widely represented, and where its evolutionary trend can be followed from the early late Aragonian (Paracuellos III, Toril-3, Moraleja, Calatayud-Daroca area) to the early and late Vallesian (Los Valles de Fuentidueña, Nombrevilla, Vallés-Penedés area) (Fig. 1). In Spain, after a period of rather low diversity within rhinocerotids, four new species are present in the late Aragonian (Cerdeño & Nieto 1995). At the end of the Middle Miocene, the previously dry and cold climate became wetter, and *A. simorrense* appears as the most abundant rhinoceros during the late Aragonian and early Vallesian. At some localities, such as Paracuellos III, it is one of the most abundant species (Cerdeño & Nieto 1995). In general, *A. simorrense* coexists with other rhinocerotid species (*Acerorhinus tetradactylum*, *Aceratherium incisivum*, *Lartetotherium sansaniense* or *L. schleiermacheri*), and is usually better represented than these, except in the Vallés-Penedés localities where it is relatively scarce. Differences between the faunas from the Vallés-Penedés and other basins are evident for different faunal groups (Agustí 1978; Forsten 1991). These are mainly explained by the relative isolation of the former, its greater relation with the rest of Europe and local climatic conditions (Meulen & Daams 1992; Daams *et al*. 1999). During the Middle Miocene, the climate of the Vallés-Penedés Basin was warm and dry, tropical or subtropical. This changed in the Late Miocene to temperate and more humid conditions, with clear seasonal differences (Sanz de Siria 1993). Agustí *et al*. (1997) stated that, 'The Vallesian bioevents recorded in the Vallés-Penedés Basin reflect a trend of widespread palaeomastological changes recognized all over the peri-mediterranean areas'.

At the end of the Vallesian and the beginning of the Turolian, there was a further climatic change towards an increase in temperature and a decrease in humidity (Calvo *et al*. 1993; Cerdeño & Nieto 1995). The environment became more arid, which possibly contributed to the decline of *Alicornops* and of rhinoceroses in general (Cerdeño & Nieto 1995; Cerdeño 1998). *A. simorrense* is associated with open woodlands, with lacustrine or marshy areas (Guérin 1980; p. 396), which would have altered as the climate changed. The anatomical type of *Alicornops*, with shortened limb bones and robust epiphyses (especially the metapodials), would provide a better adaptation to soft soils than the longer and straighter metapodials of other rhinoceroses (Cerdeño 1998).

Due to the abundance of its remains at some sites, a gregarious behaviour for *A. simorrense* is assumed. This would have provided a means of partial defence against predators, taking into account the relatively small size and the absence of horns in this species (Cerdeño & Nieto 1995).

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