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STEPHANORHINUS ETRUSCUS (FALCONER, 1868) FROM PIRRO NORD (APRICENA, FOGGIA, SOUTHERN ITALY) WITH NOTES ON THE OTHER LATE EARLY PLEISTOCENE RHINOCEROS REMAINS OF ITALY

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Abstract. During the late Early Pleistocene (latest Villafranchian-earliest Galerian), a marked faunal turnover occurred in Italy, with a progressive disappearance of Villafranchian species and the gradual arrival of new species that later characterized the Middle Pleistocene. Two rhinoceros species are reported during this time: *Stephanorhinus etruscus* and *S. hundsheimensis*. The morphological and morphometrical analysis of the rhinoceros remains unearthed in the quarries of Pirro Nord (Pirro Faunal Unit, about 1.3-1.6 Ma) show a great affinity with *S. etruscus*, in particular with its second evolutionary stage. This stage is characterized by a general variation in body size and proportions. Other rhinoceros remains, found in Italian sites chronologically correlated with Pirro Faunal Unit (FU), are also ascribed to the second evolutionary stage of *S. etruscus.* In addition, in Italy, the presence of *S. hundsheimensis* is unknown before the Colle Curti FU (about 1 Ma). This is likely related to the scarcity of sites chronologically referable to the Early-Middle Pleistocene transition or to a delay in the dispersal event of this species in Italy. Furthermore, the occurrence of *S. hundsheimensis* in Europe and in Italy may be related to the climatic deterioration of the latest Early Pleistocene, as may be the variation in proportions and size of *S. etruscus*.

Riassunto. Durante la fine del Pleistocene Inferiore (tardo Villafranchiano - inizio del Galeriano), in Italia si ha un marcato rinnovamento faunistico, con la progressiva scomparsa di specie villafranchiane e il graduale arrivo di nuove specie che caratterizzeranno il Pleistocene Medio. Durante questo periodo di tempo, sono segnalate due specie di rinoceronte: *Stephanorhinus etruscus* e *S. hundsheimensis*. L'analisi morfologica e morfometrica dei resti di rinoceronte rinvenuti nelle cavità carsiche del sito di Pirro Nord (Unità Faunistica di Pirro, circa 1,3-1,6 Ma) ha permesso di riferire gli stessi al secondo stadio evolutivo della specie *S. etruscus*. Questo stadio è caratterizzato da una generale variazione della taglia corporea e delle proporzioni. Alla stessa specie vengono poi riferiti altri resti di rinoceronte rinvenuti in siti italiani cronologicamente correlabili con l'Unità Faunistica di Pirro. Inoltre, in Italia, la presenza di *S. hundsheimensis* sembrerebbe essere certa solo a partire dalla Unità Faunistica di Colle Curti (circa 1 Ma). Ciò è probabilmente da mettere in relazione con la scarsità di siti cronologicamente riferibili alla transizione Pleistocene Inferiore-Medio oppure è da correlare con un ritardo nell'evento dispersivo della specie in questione nella Penisola. Infine, la comparsa di *S. hundsheimensis* in Europa ed in Italia potrebbe essere legata al deterioramento climatico verificatosi dalla fine del Pleistocene Inferiore, così come la variazione di taglia e proporzioni di *S. etruscus*.

Introduction

Rhinoceroses represent a common element of the Plio-Pleistocene faunas of Europe but they are, however, a poorly known taxon. The identification of the different rhinoceros species as well as determining their temporal and spatial distribution is sometimes very difficult. The taxonomy of fossil Rhinocerotidae is still debated and the major reason for this is, according to Heissig (1981) and Fortelius et al. (1993), "that the rhinoceroses are a highly stereotyped group with little morphological divergence".

In the past centuries, all remains of European rhinoceroses not ascribed to the genus *Coelodonta* were referred to the genus *Rhinoceros* and later to the genus *Dicerorhinus*. Guérin (1980) ascribed them to the genus *Dicerorhinus* and the new subgenus *Brandtorhinus*; later, this last was elevated to the genus rank (Guérin 1989). However, according to Groves (1983), the Pleistocene European rhinoceroses show little similarity with the genus *Dicerorhinus*. In fact, among

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the other characters, lost or non-functional incisors and a partially ossified nasal septum distinguish them from the genus *Dicerorhinus*. Despite this, some authors continue to refer them to the present-day genus (McKenna & Bell 1997; Guérin 2004).

The nomenclature used in this work follows by Fortelius et al. (1993) and the European Pleistocene rhinoceroses, except for *Coelodonta* and *Elasmotherium*, are referred to the genus *Stephanorhinus* as previously used by several authors (Heissig 1973, 1981, 1989; Cerdeño 1993, 1995, 1998; Prothero et al. 1986; inter alios). This choice is based on the morphological characters differentiating between *Dicerorhinus* and European fossil rhinoceroses, as already discussed by other authors (see Groves 1983; Fortelius et al. 1993; Lacombat 2005).

During the time span between the Late Villafranchian and earliest Galerian (late Early Pleistocene), two rhinoceros species are known from Europe: *Stephanorhinus etruscus* (Falconer, 1868) and *S. hundsheimensis* (Toula, 1902) but their stratigraphic range is not well-defined. In the Italian literature (Gliozzi et al. 1997; Fortelius et al. 1993; Mazza et al. 1993; Palombo et al. 2002; inter alios), the Etruscan rhinoceros was first present as early as the Montopoli Faunal Unit and lasted until the Tasso FU. The Hundsheim rhinoceros was instead found in the recent Galerian sites. In 1993, Mazza et al. reported small-sized rhinoceros populations in the Farneta, Pirro and Colle Curti FUs (latest Villafranchian-earliest Galerian), and they referred these rhinoceros to *S.* cf. *hundsheimensis*. Small-sized rhinoceroses were subsequently reported to be *S.* aff. *hundsheimensis*, *S.* cfr. *hundsheimensis* and *S. hundsheimensis* (Mazza et al. 1993; Gliozzi et al. 1997; Lacombat 2005), thus extending the stratigraphic range of this last species. In Europe, the occurrence of these two species is still discussed and their chronological ranges are relatively well-defined (Guérin 1980; Fortelius et al. 1993). At present, *S. etruscus* is reported from sites correlated with the Late Villafranchian and the Early Galerian, while the first occurrence of S. *hundsheimensis* is recorded during the latest Villafranchian. Furthermore, Guérin (1980) described two evolutionary stages of *S. etruscus*: the first stage related with the specimens from the Early and Middle Villafranchian sites of Europe and the second one related with the specimens from the Late Villafranchian sites. According to the previous author, the second stage is characterized by a general variation in body size and proportions (Guérin 1980: 598-604). Also, two size variants are recognized for *S. hundsheimensis* (Guérin 1980; Lacombat 2005); they are probably related with geographic and/or climatic factors.

The present study is aimed at the examination of rhinoceros remains found in Italy, in reference to a chronological interval related to the latest Villafranchian and earliest Galerian. It will attempt to clarify the presence of rhinoceros species during this time span and their implications.

Materials and methods

The morphological characteristics considered in this work are those listed as diagnostic by several authors, including Guérin (1980), Mazza (1988), Fortelius et al. (1993) and Lacombat (2005, 2006). The morphometric methodology is based on the work of Guérin (1980), Mazza (1988), Fortelius et al. (1993) and Lacombat (2005, 2006). The metric values obtained for Italian rhinoceroses are compared with those of different European sites.

Simpson ratio diagrams are made, using data on extant *Diceros bicornis* (data from Guérin 1980) as a reference. This reference was chosen to better highlight differences in specimen proportions and avoid errors of attribution derived using fossil species.

The rhinoceros remains found in Pirro Nord are preserved in the museums of Palaeontology of Rome (MPUR), Turin (MPUT) and Florence (MPUF).

The small collection in the Museum of Palaeontology at Sapienza University of Rome contains a lower molar (MPUR s.n.), the fragmented mandible of a young rhinoceros (MPUR s.n.) and a fourth metacarpal bone (MPUR s.n.). These remains were found in the karst cavity present near P10 and later destroyed during the quarry activity.

One D3/ (MPUT PU106664), one M1/ (MPUT PU123658), one P/2 (MPUT PU s.n.), a third metacarpal bone (MPUT PU106398) remains were recovered in the last few years in the karst cavities P10 and P13, located in the Dell'Erba quarry; these remains are preserved in the Museum of Palaeontology of Turin.

The material at the Museum of Geology and Palaeontology of Florence was found in karst cavity (called P80) in limestone quarries in Apricena and was ascribed to *Dicerorhinus etruscus* (De Giuli et al. 1987), *Stephanorhinus* cf. *hundsheimensis* (Mazza et al. 1993), and later to *S.* cf. *S. etruscus* (Abbazzi et al. 1996) and *S.* cfr. *hundsheimensis* (Gliozzi et al. 1997). The material was listed by Mazza et al. (1993).

Description and comparisons

Rhinoceros remains from Pirro Nord

The remains preserved in the Museums of Rome and Turin are in a good state of preservation.

The teeth (Fig. 1) have a number of characteristics in common with *S. etruscus* and *S. hundsheimensis*. However, the following morphological characteristics appear to be more indicative of *S. etruscus*:

- the presence of small cuspids at the outlets of the U-shaped valleys between protocone and hypocone in D3/;
- the absence of the lingual cingulum in the same tooth;
- the presence of a V-shaped posterior valley and a weak mesial cingulum in P/2;
- the great difference of height between the bottoms of the valleys in the M/1;
- the profile of the ectoloph in M1/, slightly convex, lacking a marked paracone fold.

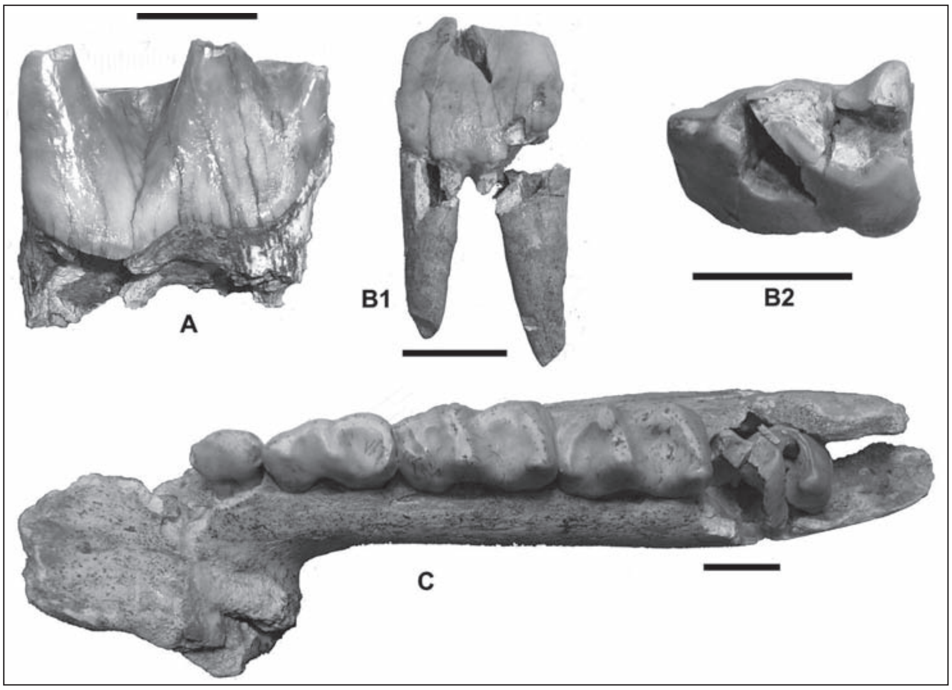


Fig. 1 - Rhinoceros remains from Pirro Nord. (A) First lower molar, lingual view; (B) Second lower premolar, (1) buccal view, (2) occlusal view; (C) Fragmentary right mandible, occlusal view. Scale bar: 2 cm.

D/1		**L max**	**l max**
Pirro Nord		16	8
Senèze (*S. etru.*)		17.52	9.55
Upper Valdarno+Olivola (*S. etru.*)	med	18.34	10.82
	min	18.17	10.67
	max	18.51	10.97
Vallonnet (*S. hund.*)	med	17.86	11.22
	min	16.6	10.48
	max	20.46	12.44
Isernia (*S. hund.*)		19.2	13.8
Untermassfeld (*S. hund.*)	med	18.09	11.5
	min	16	10.4
	max	21	15
D/2		**L max**	**l max**
Pirro Nord		29.5	15
Senèze (*S. etru.*)	med	29.91	15.66
	min	29.28	15.1
	max	30.55	16.62
Upper Valdarno+Olivola (*S. etru.*)	med	38.45	21.66
	min	37.9	21.66
	max	39	21.66
Vallonnet (*S. hund.*)	med	31.12	17.69
	min	28.5	15.46
	max	32.87	18.95
Untermassfeld (*S. hund.*)	med	31.6	17.64
	min	30	16.5
	max	33.1	19.8

Tab. 1 - Comparative dimensions of lower deciduous teeth, D/1 and D/2, from Pirro Nord and of *S. etruscus* (*S. etru.*) (data from Mazza 1988; Lacombat 2006) and *S. hundsheimensis* (*S. hund.*) (data from Kahlke 2001; Lacombat 2006). L max = maximal length; l max = maximal breadth.

D/4		**L max**	**l max**
Pirro Nord		36.2	22
Senèze (*S. etru.*)	med	40.36	
	min	39.5	
	max	41.84	
Upper Valdarno (*S. etru.*)	med	38.47	22.7
	min	37.82	
	max	39.11	
Isernia (*S. hund.*)	med	41.17	24.5
	min	40	
	max	42.39	
Vallonnet (*S. hund.*)	med	40.05	24.29
	min	38.1	23.42
	max	41.99	25.46
Untermassfeld (*S. hund.*)	med	42.13	23.93
	min	39.8	22.8
	max	44.5	25.8

Tab. 2 - Comparative dimensions of the lower deciduous tooth, D/4, from Pirro Nord and of *S. etruscus* (*S. etru.*) (data from Guérin & Heintz 1972; Mazza 1988) and *S. hundsheimensis* (*S. hund.*) (data from Kahlke 2001; Lacombat 2006). L max = maximal length; l max = maximal breadth.

In the lower deciduous teeth, the difference in height between the bottoms of the valleys is large (0.67 in D/3 e 0.72 in D/4), as in *S. etruscus*. Also, the V-shaped posterior valley, the absence of a mesial cingulum and the strong depth of the vestibular syncline in D/4 of Pirro Nord is a typical character of *S. etruscus* (see also Lacombat 2006).

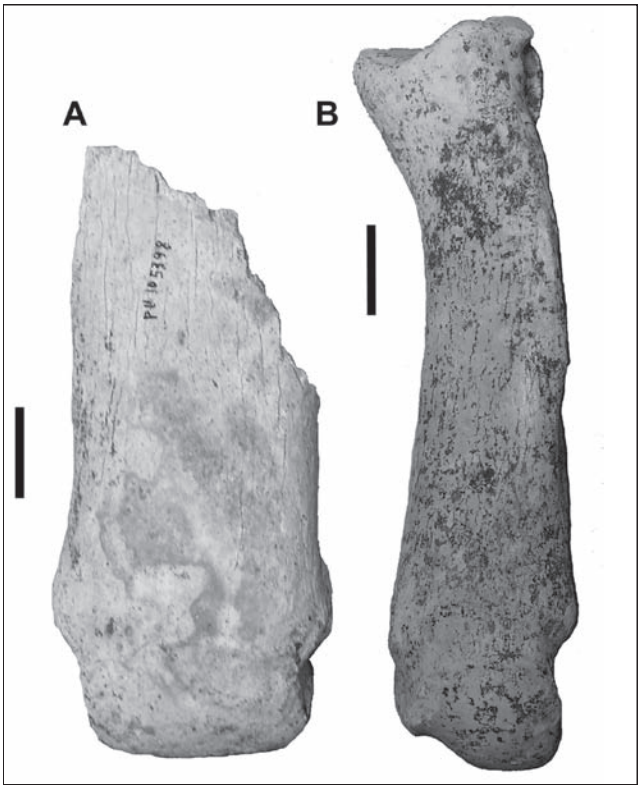


Fig. 2 - Rhinoceros remains from Pirro Nord. (A) Fragmentary third metacarpal bone, anterior view; (B) Fourth metacarpal bone, anterior view. Scale bar: 2 cm.

The dimensions of the lower deciduous teeth are comparable with the minimum values of *S. etruscus* and are smaller than *S. hundsheimensis* (Tab. 1; Tab. 2). In fact, in this last species, the lower deciduous teeth are more developed than in *S. etruscus* (Lacombat 2006).

The dimensions of the distal epiphysis of the third metacarpal bone (Fig. 2A) are also comparable with the minimum values of *S. etruscus* (Tab. 3).

The fourth metacarpal bone (Fig. 2B) has a subtriangular surface at its dorsal end. In medial view, two articular facets are present. The anterior one is stretched along the upper margin of the epiphysis, while the posterior facet is sub-elliptical and much wider than the anterior. These characters are present in *S. etruscus* (see also Mazza 1988; Lacombat 2005).

The dimensions of the fourth metacarpal are comparable to the minimum values of Etruscan rhinoceros (see for example Guérin 1980) and are similar to that of Créspia (Tab. 4). In the Simpson diagram, the curve of the remains of Pirro Nord is close to *S. etruscus* of Senèze and La Puebla de Valverde. It is clearly different from *S. hundsheimensis* of Vallonnet, Isernia, Soleilhac and Untermaßfeld (Fig. 3).

The rhinoceros remains preserved in the Museum of Geology and Palaeontology at the University of

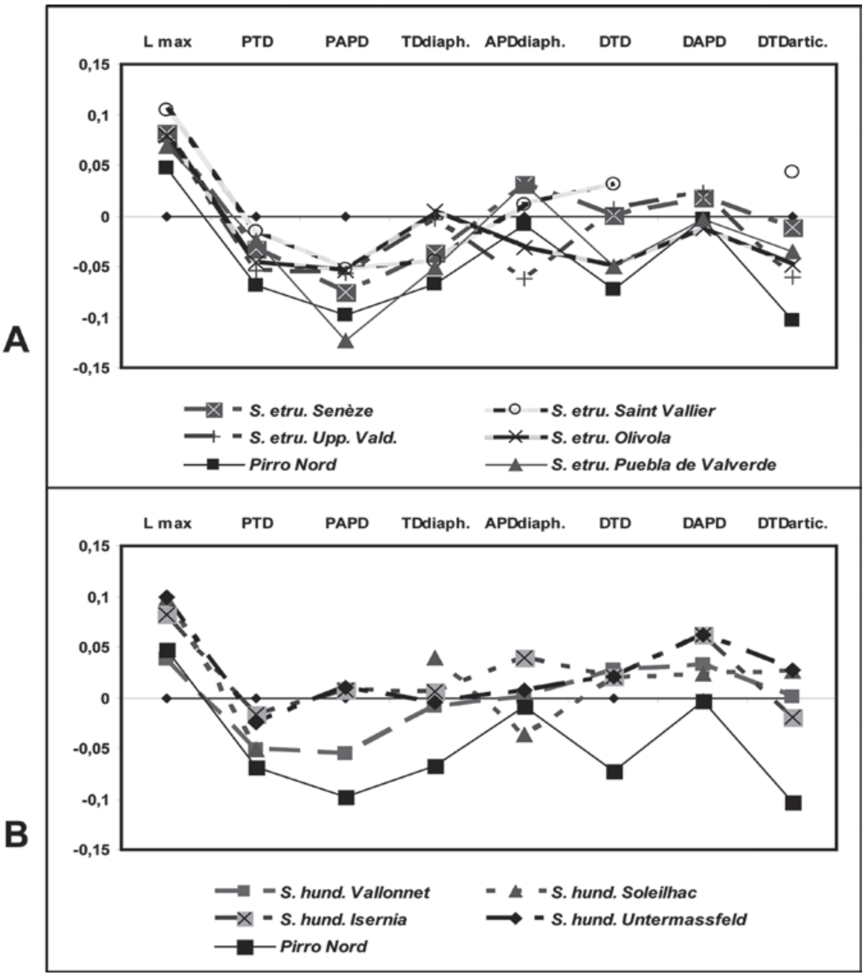


Fig. 3 - Ratio diagrams for the MC IV from Pirro Nord and Pietrafitta (data from Mazza et al. 1993) versus *S. etruscus* (*S. etru.*). (A) (data from Guérin & Heintz 1972; Mazza 1988) and *S. hundsheimensis* (*S. hund.*); (B) (data from Fortelius et al. 1993; Kahlke 2001; Lacombat 2005) (standard *Diceros bicornis*). Abbreviations in Tab. 4.

MC III		**DTDmax**	**DAPD**
Pirro Nord	PU106398	54.55	37.2
Upper Valdarno+Olivola (*S. etru.*)	med	56.25	40.25
	min	54	39
	max	59	42
Capitone (*S. etru.*)		58	40
Puebla de Valverde (*S. etru.*)	med	45.5	40
	min	44	39
	max	47	41
Senèze (*S. etru.*)	med	48.3	41
	min	48	40
	max	49	42
Vallonnet (*S. hund.*)	med	58.14	43.5
	min	58.04	41.77
	max	58.24	45.22
Soleilhac (*S. hund.*)		54.6	42.5
		59.17	
Untermassfeld (*S. hund.*)	med	58.1	46.06
	min	52	42
	max	64.6	49.2
Mauer (*S. hund.*)		56.8	43.8
Mosbach (*S. hund.*)		53.7	42.1
Vergranne (*S. hund.*)	med	63.1	45.7
	min	61.5	45
	max	65.5	46.5
Pietrafitta	med	53.4	41.15
	min	51.8	40.3
	max	55	42

Tab. 3 - Comparative dimensions of MC III from Pirro Nord, Pietrafitta (Mazza et al. 1993) and of *S. etruscus* (*S. etru.*) (data from Guérin & Heintz 1972; Mazza 1988) and *S. hundsheimensis* (*S. hund.*) (data from Fortelius et al. 1993; Guérin 1983; Kahlke 2001; Lacombat 2005). DTDmax = maximal breadth of distal epiphysis; DAPD = depth of distal epiphysis.

Florence are well-described and depicted by Mazza et al. (1993). According to these authors, the rhinoceros from Pirro Nord shows similarities with both *S. etruscus* and *S. hundsheimensis*, despite the incomplete and fragmentary state of the remains. According to Mazza et al. (1993), all the teeth have morphology comparable to that of *S. etruscus*, while some postcranial elements show differences from this last species. In particular, these differences are observable in the scapulae, humeri, scaphoid and metapodial bones. Other postcranial elements are morphologically comparable to *S. etruscus* from the Upper Valdarno.

The morphology of the considered scapulae is similar to *S. etruscus* of Créspia (García-Fernandez et al. 2003b) and the dimensions are comparable to those of *S. etruscus* from different European sites and differ from those of *S. hundsheimensis* (Tab. 5). There are few morphological and metric differences between the humeri of *S. etruscus* and *S. hundshemensis* (Guérin 1980; Mazza 1988; Fortelius et al. 1993; Lacombat 2005). However, the morphological characteristics and morphometric values listed by Mazza et al. (1993) are comparable to those of *S. etruscus* (Mazza 1988; Kahlke 2001; Lacombat 2005).

In the remains of the Museum of Florence, only one fragmentary scaphoid is present and its dimensions are comparable to that of *S. etruscus*. In particular, the proximal articular surface allows for it to be distinguished from *S. hundsheimensis* (Lacombat 2005) (Fig. 4). The morphological characters described by Mazza et al. (1993) may fall within the intraspecific variation of the Etruscan rhinoceros.

Only the proximal epiphysis of the third metacarpal is preserved. The Simpson diagram of this last bone shows similarities with *S. hundshemensis* from Vallonnet and *S. etruscus* from La Puebla de Valverde and Senéze (Fig. 5). In addition, the proportions of the fourth metacarpal are comparable to those of *S. etruscus* (Fig. 6).

The metatarsal bones do not greatly differ in proportion between the two species (Figs 7, 8) and the morphological characters, as listed by Mazza et al. (1993), could lie within the intraspecific variation of *S. etruscus*.

Rhinoceros remains from other latest Villafranchian-earliest Galerian sites of Italy

Madonna della Strada (Scoppito, L'Aquila, central Italy)

The sandy-lignitiferous deposits of Madonna della Strada are chronologically related to the latest Early Pleistocene (Magri et al. 2010). At this site, rhinoceros remains were found together with *Mammuthus meridionalis* and were first ascribed to *D. etruscus* and later to *S.* aff. *hundsheimensis* and *S.* cf. *hundsheimensis* (Maccagno 1962; Caloi & Palombo 1995; Palombo et al. 2002). However, the morphological and metric characters of these remains make it possible to ascribe them to *S. etruscus*. P/2 (MPUR s.n.) is characterized by quite smooth enamel. The cingulum, represented by small cuspulae, occurs at the vestibular side of the tooth; this character can be seen also in the premolars of the *S. etruscus* specimens from the Upper Valdarno (Mazza 1988). The astragalus preserved in the Museum of San Giuliano (L'Aquila) (MSG 396), shows in anterior view, a convex, but quite small, trochlear distal side. The articular surface is well defined in medial view, and the medial tuberculum is posterodistally oriented. In posterior view, the mesiodistal articular surface is sub-elliptical. Metatarsal IV (MPUR s.n.) has a sub-triangular medial-anterior articular facet, connected to the proximal side. The corresponding posterior facet is sub-circular and placed at a lower level than the anterior one.

The morphology of these bones is consistent with an attribution to *S. etruscus* following the diagnostic features pointed out by several authors (Guérin

MC IV		**L max**	**PTD**	**PAPD**	**TD diaph.**	**APD diaph.**	**DTDmax**	**DAPD**	**DTD artic.**
Pirro Nord	s.n.	152	38	30	25	22	36	35	30
Pietrafitta		150	38	35.2	29	16	37	35.3	33
Pirro Nord*					32.6	19	36.1	37.8	34
Senèze (*S. etru.*)	med	167	41.3	35.8	31.1	22	42.7	37.9	37
	min	158	40	33	28	20	40	37	34
	max	171	45	38	34	24	46	39	39
Crespia (*S. etru.*)		146.6	38	32.4	23.2	20	35	27	30
Puebla de Valverde (*S. etru.*)		162	42	32	30	22	38	36	35
			44	33					
Saint Vallier (*S. etru.*)	med	176	43	37.75	30.5	21	46		42
	min		41	36	30				
	max		45	40	31				
Upper Valdarno+Olivola (*S. etru.*)	med	166.75	39.75	37.6	34.66	18.83	40	36.5	33.75
	min	157	37	32	32	17	33	34	32
	max	176	43	41	39	20	46	39	36
Vergranne (*S. hund.*)	med	169.41	45.37	41	33.5	23.5	43.58	40.83	38.41
	min	167	43.5	38.5	29.5	22	40	39	37
	max	172.5	47.5	48	37.5	24	45.5	43.5	41
Isernia (*S. hund.*)			41.8	44.3					
			42	44					
		167	45.5	44.5	33.7	22	42.2	42	37
Mosbach (*S. hund.*)	med	174.12	43.26	41.62	36.93	22.36	46.22	39.6	38.02
	min	164	42.8	38.5	34.6	20	42.1	37.2	34
	max	181.3	44	44	39.8	23.1	50.2	41.2	41
Vallonnet (*S. hund.*)		153.2	39.52	37.55	33.22	20.44	45.59	39.2	38.02
Soleilhac (*S. hund.*)		181	41.92		37.06	17.82	47.67		44.54
		165	37.02		37.17	19.67	41.82	38.45	36.37
Sussenborn (*S. hund.*)			43.7	46					
Untermassfeld (*S. hund.*)	med	174.01	42.01	43.68	33.53	20.78	44.78	41.88	40.53
	min	162.9	37.8	41.2	31.6	19	41.5	40.3	35.9
	max	186.3	45.5	48.4	34.8	21.9	48.4	44	44.9

Tab. 4 - Comparative dimensions of MC IV from Pirro Nord (* = data from Mazza et al. 1993), Pietrafitta (data from Mazza et al. 1993) and of *S. etruscus* (*S. etru.*) (data from Guérin & Heintz, 1972; Mazza 1988; García-Fernández et al. 2001) and *S. hundsheimensis* (*S. hund.*) (data from Fortelius et al. 1993; Guérin 1983; Kahlke 1969, 2001; Lacombat 2005). L max = maximal length of the bone; PTD = breadth of proximal epiphysis; PAPD = depth of proximal epiphysis; TD diaph. = breadth of diaphysis; APD diaph. = depth of diaphysis; DTDmax = maximal breadth of distal epiphysis; DAPD = depth of distal epiphysis; DTD artic. = breadth of distal articular surface.

1980; Fortelius et al. 1993; Lacombat 2005). Other remains discovered at this site, as recently described by Magri et al. (2010), consist of some fragmentary teeth and postcranial elements, probably of an old rhinoceros (MPUR s.n.). These remains were ascribed to *S.* cf. *hundsheimensis*, but no diagnostic character is present in the teeth analyzed by Magri et al. (2010). Also, the dimensions of the few and fragmentary postcranial elements fall into size ranges of *S. etruscus* and *S. hundsheimensis* (see Guérin & Heintz 1972; Guérin 1980). Morphological characters given by Magri et al. (2010) for the distal articular face of the cuboid and posterior articular faces of talus are present in *S. etruscus* from the Upper Valdarno (Mazza 1988).

Colle Curti (Umbria, central Italy) and Castagnone (Monferrato, northern Italy)

The early Galerian fauna is not well-know in Italy, because of the limited fossil record of this time span. The Colle Curti local fauna was correlated with the base of Jaramillo subchron (about 1.1 Ma) and is more recent than the Pirro FU (Gliozzi et al. 1997). In this latter local fauna, Ficcarelli & Mazza (1990) ascribed three upper molars to *S. etruscus*, stating: "which can easily be attributed to Falconer's *Dicerorhinus etruscus*" but that "this attribution is not conclusive, since recent observations on fossil rhinoceroses of the latest Early Pleistocene pointed out the occurrence of a new species, equipped with teeth very similar to those of *Dicerorhinus etruscus*". Later, these remains were ascribed to *S.* cf. *hundsheimensis* (Mazza et al. 1993). However, the morphology of the upper molar, as figured by Ficcarelli & Mazza (1990), and, generally, the morphology of the isolated upper molars, seems not to have diagnostic characteristics to distinguish between *S. etruscus* and *S. hundsheimensis* (Guérin 1980;

Scapula		**DTD**	**TDCS**	**LG**	**BG**
Pirro Nord*		108		73	
		104	87	67	51
Pietrafitta		110	87	70	57
Upper Valdarno (*S. etru.*)				72	58
		98	91	76	59
Créspia (*S. etru.*)		115		70	>60
Capitone (*S. etru.*)		111	86	74ca	
Senèze (*S. etru.*)	med	134.91	109.91	84.42	65.63
	min	128	104.95	78.11	60.16
	max	150.88	117.8	91.5	71.3
Cagnes sur Mer (*S. etru.*)		123.64	107.49	76.26	62.12
Vergranne (*S. hund.*)		130	115.5	80	59
			116ca	80	71
Untermassfeld (*S. hund.*)		120.8	108	81.5	75
			108.8		73
Mosbach (*S. hund.*)		127	115	83	72.8
		114		85	65

Tab. 5 - Comparative dimensions of scapulae from Pirro Nord (* = data from Mazza et al. 1993), Pietrafitta (data from Mazza et al. 1993) and of *S. etruscus* (*S. etru.*) (data from Guérin & Heintz 1972; Mazza 1988; García-Fernández et al. 2001) and *S. hundsheimensis* (*S. hund.*) (data from Fortelius et al. 1993; Guérin 1983; Kahlke 2001; Lacombat 2005). DTD = breadth of distal epiphysis; TDCS = breadth of *collum scapulae*; LG = length of the glenoid cavity; BG = breadth of the glenoid cavity.

Fortelius et al. 1993; Lacombat 2006).

The site of Castagnone was also correlated with the Colle Curti FU (Siori & Sala 2007). At this site, rhinoceros remains consist of one M/3 and several fragmentary teeth, ascribed "with some uncertainty" to *S.* cf. *S. hundsheimensis* by Siori & Sala (2007). Also in the site of Castagnone, the morphological and morphometrical characters do not allow for a distinction between *S. etruscus* and *S. hundsheimensis*. In these cases, all the rhinoceros remains should be ascribed to *Stephanorhinus* sp.

Cava Redicicoli (Rome, central Italy)

The site of Cava Redicicoli, discovered by Blanc in the 1950s (Blanc et al. 1955), may be chronologically correlated to the Colle Curti FU. In this site, Caloi et al. (1979) listed a few rhinoceros remains, including a skull fragment, a fragmentary mandible and some teeth. These remains were ascribed to *Dicerorhinus* sp. (*Rhinoceros* sp. in Blanc et al. 1955) and were later reported as *S. hundsheimensis* (Caloi & Palombo 1988; Di Stefano et al. 1998; Palombo et al. 2002). The remains from Cava Redicicoli have morphological characters similar to *S. hundsheimensis*, such as the very small difference in height between the bottoms of the valleys in the lower molars (MPUR 1956 R45a, b), the relatively large and robust horizontal ramus of the mandible (MPUR 1956 R45), the profile of the occipital crest of the skull (MPUR 1956 s.n.), convex in posterior view and slightly concave in dorsal view (Pandolfi, unpublished data). The faunal list of the site includes typical Villafranchian taxa and taxa more frequently recorded in Galerian faunas or closely related to the Galerian ones. Due to the composition of the Redicicoli fauna, Caloi et al. (1979) and Di Stefano et al. (1998) suggest the presence of two different faunal assemblages, which are believed to have come from two different levels. The first level is correlated with the Pirro FU and the second one with the Isernia FU. According to Di Stefano et al. (1998) the rhinoceros remains come from this second level. Caloi & Palombo (1995, 1997), Palombo et al. (2002) and Milli & Palombo (2005) suggest that the taxa are coeval and that the Redicicoli faunal assemblage should be ascribed to the Colle Curti FU only. Unfortunately, the fossiliferous deposit does not exist anymore and the problem is difficult to resolve.

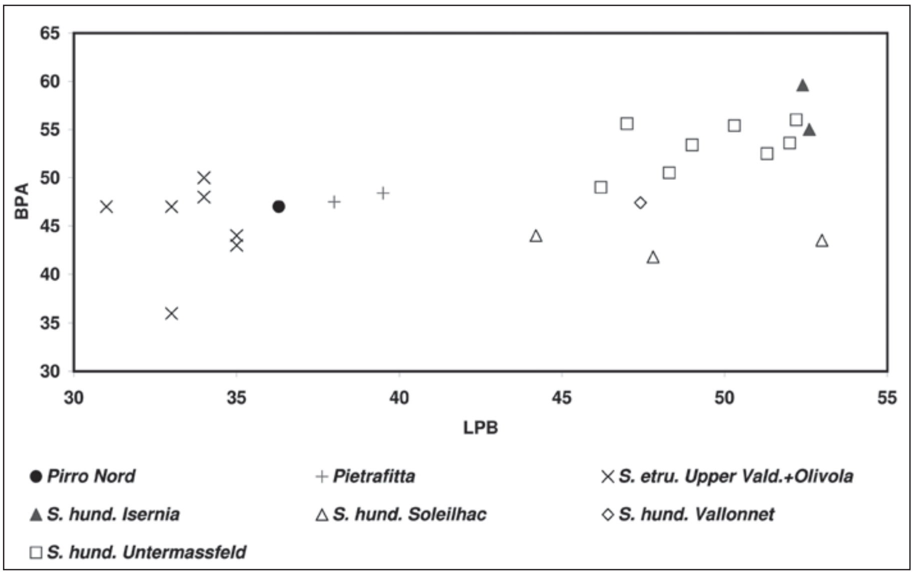


Fig. 4 - Bivariate diagram of scaphoids from Pirro Nord and Pietrafitta (data from Mazza et al. 1993), *S. etruscus* (*S. etru.*) (data from Mazza 1988) and *S. hundsheimensis* (*S. hund.*) (data from Kahlke 2001; Lacombat 2005). LPB = length of the proximal articular surface; BPA = breadth of the proximal articular surface.

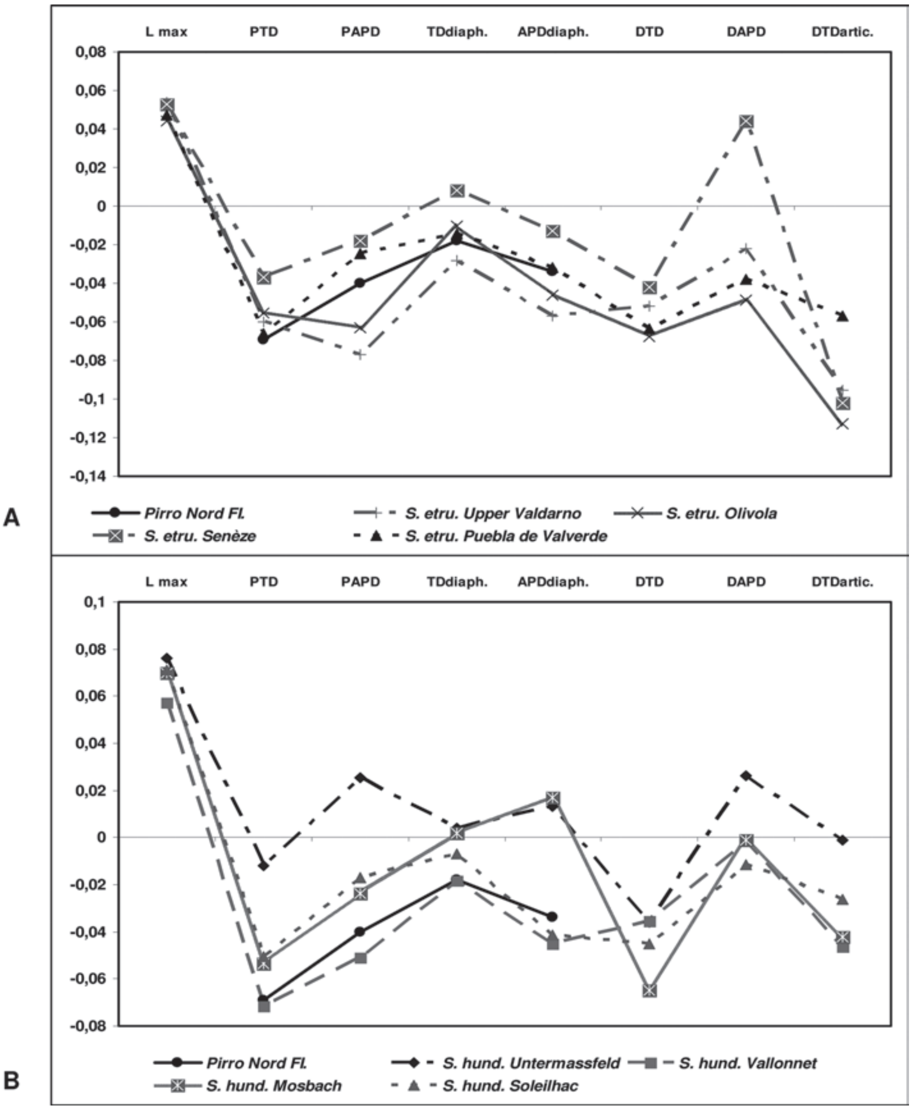


Fig. 5 - Ratio diagrams for MC III from Pirro Nord (FI = preserved in the Museum of Palaeontology of Florence, data from Mazza et al. 1993), Pietrafitta (data from Mazza et al. 1993), *S. etruscus* (*S. etru.*) (data from Guérin & Heintz 1972; Mazza 1988) and *S. hundsheimensis* (*S. hund.*) (data from Fortelius et al. 1993; Kahlke 2001; Lacombat 2005) (standard *Diceros bicornis*). Abbreviations in Tab. 4.

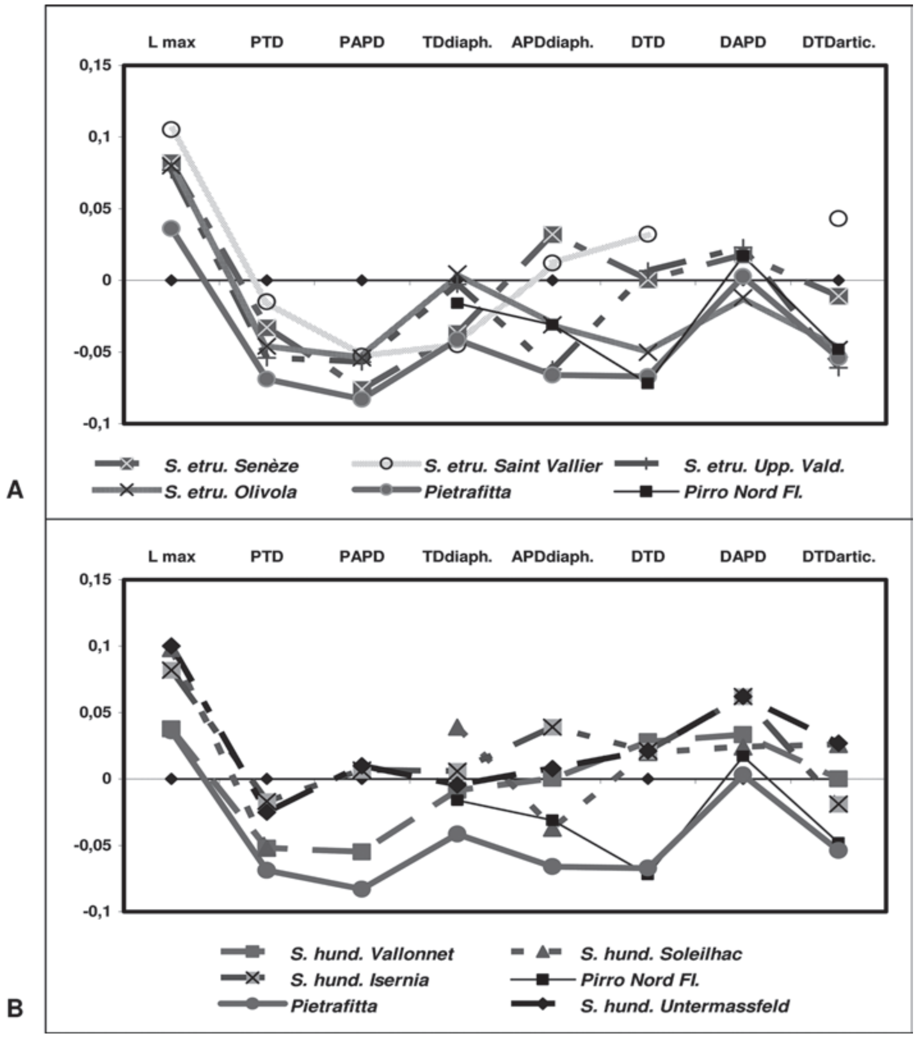
Imola basin (Imola, northern Italy)

Rhinoceros remains discovered in the Imola basin (referred to the Late Villafranchian-Early Galerian) were ascribed to *Rhinoceros leptorhinus* by Falconer (1868) and to *Dicerorhinus* cf. *etruscus* by Azzaroli & Berzi (1972). Later, they were reported as *S.* cf. *hundsheimensis* (Palombo et al. 2002). The upper toothrow, preserved in the Museum of Imola and figured in Falconer (1868) and in Azzaroli & Berzi (1972), has a number of common characteristics with *S. etruscus* and *S. hundsheimensis*. However, some characters allow to the remains to be ascribed to Falconer's species, such as the general profile of the vestibular wall in the molars and premolars, the absence of the crista and the presence of a single crochet in P3/, the presence of a crista, a single crochet and a mesial cingulum in P4/, the absence of the antecrochet and the presence of a protocone constriction in M1/, a well developed single crochet and the absence of the antecrochet in M2/ (see also Lacombat 2006). In addition, the upper toothrow shows many similarities in morphology and dimension with *S. etruscus* from Capitone (Terni, Central Italy) (Fig. 9).

*Mugello basin (Mugello, central It*aly)

Specimens with *S. hundsheimensis* affinities were reported in the Mugello basin; in particular, a deformed and damaged skull from Grezzano (IGF 12728) preserved in the Museum of Geology and Paleontology of the University of Florence (Mazza 1988). The characters of the teeth and the skull from Grezzano are more similar to Toula's species, even if the dorsal profile angle (n) is more quite similar to that of *S. etruscus* (n = about 150) than *S. hundsheimensis* (n >170) (see also Lacombat 2005). Also, in the skull of Grezzano the anterior border of the orbital cavity overlies the anterior half of M2/ and the posterior border of the narial notch lies at the level of P4/, but these characters are similar to that of the skull of *S. etruscus* from Capitone (in which the anterior border of the orbital cavity lies at

Fig. 6 - Ratio diagrams for the MC IV from Pirro Nord (FI = preserved in the Museum of Palaeontology of Florence, data from Mazza et al. 1993), Pietrafitta (data from Mazza et al. 1993) versus *S. etruscus* (*S. etru.*). (A) (data from Guérin & Heintz 1972; Mazza 1988) and *S. hundsheimensis* (*S. hund.*) (B) (data from Kahlke 2001; Lacombat 2005) (standard *Diceros bicornis*). Abbreviations in Tab. 4.



the level of M2/ and the posterior border of the narial notch at the anterior half of P4/). Unfortunately, the remains were found in fluvio-lacustrine deposits with a very long chronological range and they have no direct stratigraphic control. From the same localities, typical Early Galerian mammal remains have been found as well (Masini et al. 1994; Abbazzi et al. 1995).

Discussion and Conclusions

The proportions, morphology and dimensions of the rhinoceros remains from latest Villafranchian sites in Italy are comparable to those of *S. etruscus*. According to Guèrin (1980), during the Late Villafranchian, this species is inclined towards a general variation in body size and proportions. Guérin (1980) considers the populations of this time span as “second evolutionary stage”. The same proportions and size of the latter are evident in the Capitone sample and in the remains from Senéze, well as in the specimens from Pirro Nord. In Italy, *S. etruscus* is reported from several Villafranchian sites (Ambrosetti 1972; Ambrosetti & Cremaschi 1975; Mazza 1988; Petronio et al. 2002); according to various authors, its last occurrence is at the beginning of the Late Villafranchian (Tasso-Olivola FUs; Gliozzi et al. 1997). In the present study, however, the occurrence of the Etruscan rhinoceros is confirmed until the Villafranchian-Galerian transition.

During the latest Villafrachian and earliest Galerian, the presence of *S. etruscus* has been reported from several European sites, for example Cueva Victoria, Incarcal, Venta Micena, Huéscar-1, Cúllar de Baza 1, Atapuerca (Gran Dolina TD4-8 and Sima del Elefante TE14), La Sartanette, Blassac-La-Girondie and Peyrolles (Heintz et al. 1974; Cerdeño 1993; van der Made 1998; Rosas et al. 2001; Garcìa-Fernandez et al. 2003a; van der Made et al. 2003; Palombo & Valli 2003; Lacombat 2005) (Fig. 10). *Stephanorhinus etruscus* was also initially reported from the Spanish sites of Fuente Nueva-3 and Barranco León-5 (1.3-1.1 Ma), where lithic artefacts have been found (Turq et al. 1996; Martínez Navarro et al. 1997; Gibert et al. 1999; Oms et al. 2000). The rhinoceros remains of these sites were later ascribed to *S.* cf. *hundsheimensis* (Martínez Navarro et al. 2003). In Europe, the first occurrence of *S. hundshe-*

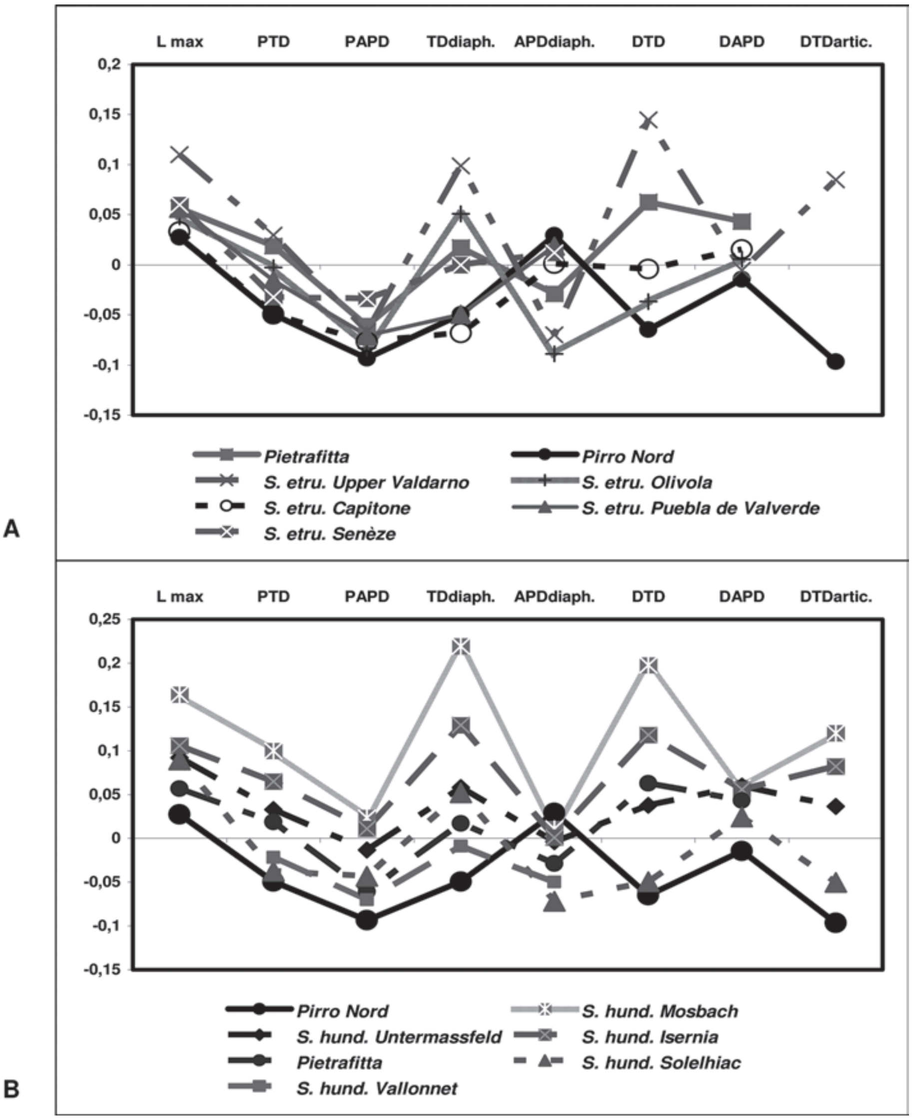


Fig. 7 - Ratio diagrams for MT IV from Pirro Nord (data from Mazza et al. 1993), Pietrafitta (data from Mazza et al. 1993). *S. etruscus* (*S. etru.*) (data from Guérin & Heintz 1972; Mazza 1988) and *S. hundsheimensis* (*S. hund.*) (data from Fortelius et al. 1993; Kahlke 2001; Lacombat 2005) (standard *Diceros bicornis*). Abbreviations in Tab. 4.

imensis is reported during the latest Early Pleistocene and early Middle Pleistocene. It is present in sites such as Vallonnet, Sainzelles, Tour de Grimaldi, Ceyssaguet, Saint-Prest, Durfort, Untermaßfeld, Dorn-Dürkheim 3 and Trlica (Guérin 1980; Radulescu & Samson 1985; Codrea & Czier 1991; Codrea & Dimitrijević 1997; Franzen et al. 2000; Kahlke 2001; Palombo & Valli 2003; Guérin et al. 2003; Lacombat 2005) (Fig. 10). Recently, *S. hundsheimensis* was reported from the Spanish site of Vallparadís (1-0.800 Ma) (Alba et al. 2008).

Thus, during the latest Early Pleistocene – earliest Middle Pleistocene, *S. etruscus* and *S. hundsheimensis* seem to be coeval in Europe.

However, in agreement with van der Made (2000), the typical early Middle Pleistocene *S. hundsheimensis* appears to be more primitive than the Early Pleistocene *Stephanorhinus*; this last is represented by an evolutionary stage of *S. etruscus* (second evolutionary stage).

S. hundsheimensis may have been an immigrant that replaced *S. etruscus* at the end of the Early Pleistocene. This is in line with the model of Fortelius et al. (1993), which does not derive *S. hundsheimensis* from *S. etruscus*, rather than with Guérin's (1980) model.

Stephanorhinus hundsheimensis probably reached Europe from Asia between 1.3-1.1 Ma and gradually replaced *S. etruscus*; at the same time, populations of the latter species were fragmented into isolated demes.

In Italy, the occurrence of *S. hundsheimensis* in the Late Villafranchian sites (Pirro Nord, Madonna della Strada) is not considered reliable at present time. In the lignitiferous deposit of Pietrafitta (Perugia, Central Italy), chronologically earlier than Pirro Nord site (Farneta FU), several rhinoceros remains were found as early as 1900. At first, Ugolini (1921) ascribed some teeth to *Rhinoceros etruscus* and later, other rhinoceros remains were ascribed to *Dicerorhinus etruscus* (Ambrosetti et al. 1987) and *S.* cf. *hundsheimensis* (Mazza et al. 1993). Some morphological and morphometrical considerations of the rhinoceros remains from Pie-

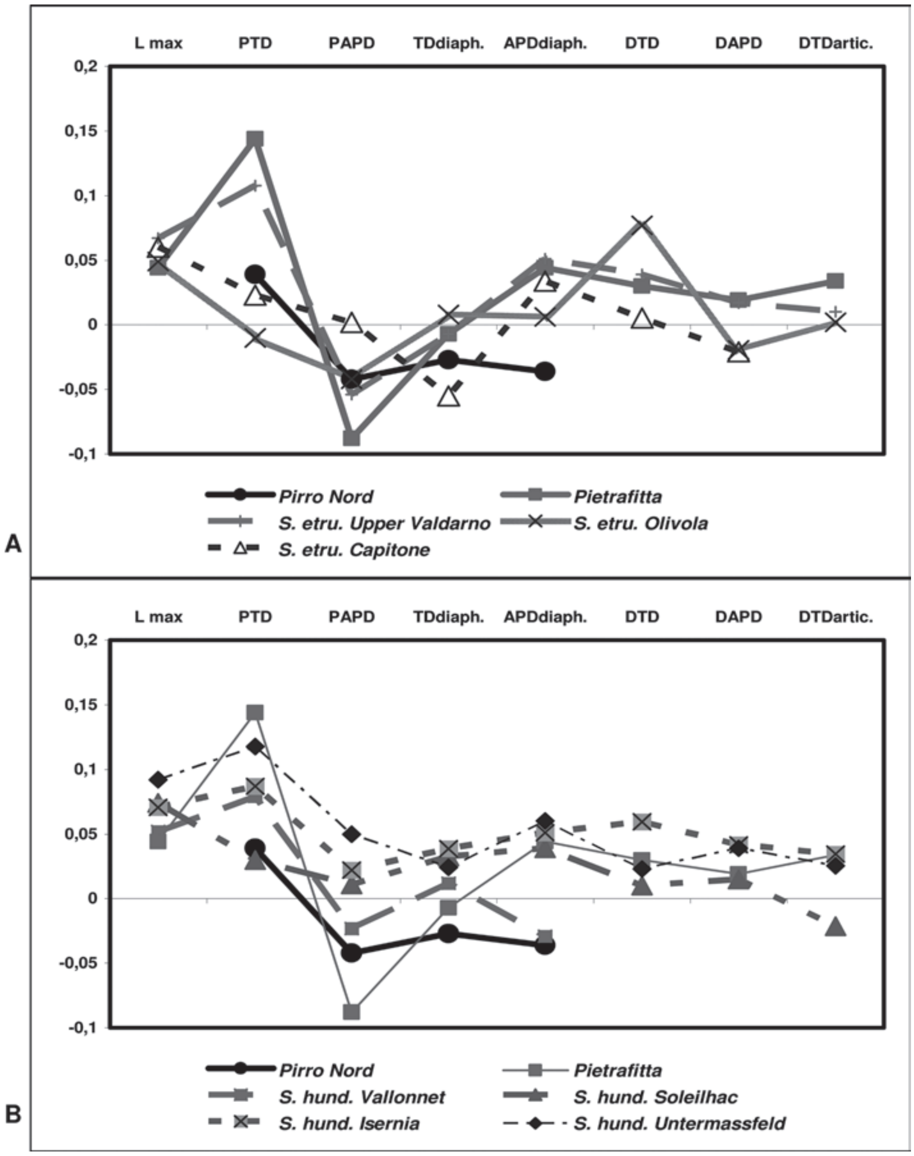


Fig. 8 - Ratio diagram for MT II from Pirro Nord (data from Mazza et al. 1993), Pietrafitta (data from Mazza et al. 1993). *S. etruscus* (*S. etru.*) (data from Mazza 1988) and *S. hundsheimensis* (*S. hund.*) (data from Kahlke 2001; Lacombat 2005) (standard *Diceros bicornis*). Abbreviations in Tab. 4.

trafitta, listed by Mazza et al. (1993), are reported as evolutionary trends of *S. etruscus* by Guérin (1980: 599-603). Furthermore, the small late Early Pleistocene rhinoceroses, very likely identical to that was assigned to *S.* cf. *hundsheimensis* by Mazza et al. (1993), are reported from Spain as *S. etruscus* (Cerdeño 1993; van der Made 1998). However, the remains from Pietrafitta are proportionally more similar to those of *S. etruscus* than *S. hundsheimensis* (for example see Figs 6-8). Besides this, some morphological and metrical differences in the Pietrafitta remains may fall within the intraspecific range of variation of the Etruscan rhinoceros; they may also be the result of adaptation to a particular habitat (see also García-Fernandez et al. 2001). However, a more detailed analysis is needed.

Other rhinoceros remains discovered in Italian sites chronologically related to the Villafranchian-Galerian transition (Mugello basin) have close affinities with *S. etruscus*. Also, remains attributable to *S. hundsheimensis* from the earliest Galerian sites (Colle Curti, Castagnone) are uncertain and scarce, and no more data is available on the origin of the remains of Cava Redicicoli. Thus, *S. hundsheimensis* seems to be present in Italy only after 1 Ma (Slivia FU). This species is certainly present during the Middle Galerian (Middle Pleistocene). It is found in Cesi (about 0.7 Ma) (Mazza 1996; Ficcarelli et al. 1997), in the lower levels of Ponte Galeria (about 0.8 Ma) (Petronio 1988; Petronio & Sardella 1999; Pandolfi, unpublished data) and in Isernia La Pineta (about 0.6-0.55 Ma) (Sala & Fortelius 1993; Coltorti et al. 2005).

The dispersal event of *S. hundsheimensis* into Europe and Italy may be related to the climatic deterioration of the latest Early Pleistocene. The same may be true of the variations in proportions and size of *S. etruscus*. In fact, during this time, the passage to a phase characterized by long glaciations with 100.000-year cycles occurs. The difference between the temperatures

Fig. 9 - Upper toothrows of *S. etruscus* from the Imola basin (A) (after Azzaroli & Berzi, 1972; not in scale) and Capitone (B) (scale bar: 5 cm).

during glacial and interglacial phases becomes more pronounced (Leroy 2007). In Italy, more arid conditions, during the Pirro FU, are testified to by the occurrences of *Bison degiulii* and a lightly build, medium-sized horse, *Equus altidens*. Also, typical African taxa, such as *Hystrix refossa*, *Megantereon whitei* and *Theropithecus* sp. disperse on the Peninsula (Petronio et al. in press). Concurrently, the disappearances of *Leptobos* and *Eucladoceros* were recorded. However, at Pirro Nord, woody areas and humid patches must have been still present at some point, as indicated by the presence of *Apodemus flavicollis*, as well as the presence of amphibians and insectivores. At other sites related to the Pirro FU, in which *S. etruscus* was discovered, lacustrine basins or ponds were present (for example in the Scoppito site; Maccagno 1962).

Later, a very arid-steppic phase is recorded during the Colle Curti FU. In the Ranica site in northern Italy, a cold, steppic phase with *Cervalces latifrons* is well documented (Ravazzi et al. 2005). Nevertheless, trees remain present at the foot of the Alps even during this phase. In contrast, in central Italy, the pollen diagrams of Colle Curti and Cesi (Bertini 2000) show high percentages of herbaceous forms, a clear evidence of more open vegetation. Among the mammals, presence of a cold microfauna represented by *Prolagurus pannonicus* and *Predicrostonyx* sp. is reported in the blue-clay layer of the Ponte Galeria area (Roma, central Italy) (Kotsakis et al. 1992). These finds testify a very cold phase, correlated with the Marine Isotopic Stage 24-22. During this time, *S. etruscus* disappeared from Italy and the occurrence of *S. hundsheimensis* is reported. Other Asian taxa, such as *Praemegaceros verticornis* and *Bison schoetensacki*, co-occur with *S. hundsheimensis*.

The diffusion of *S. hundsheimensis* can be also related to a greater capacity of the species to adapt to the climatic conditions and diet (with highly flexible feeding, Kahlke & Kaiser in press) than *S. etruscus*. Moreover, the distribution of the latter seems to be more influenced by humidity (Guérin 1980).

In Italy, the absence of remains definitely attributable to *S. hundsheimensis* before 1 Ma may be due to the conformation of the Italian Peninsula. This may have played a decisive role in the delay of the dispersal event when compared to the rest of continental Europe. In fact, delayed dispersal events are common in

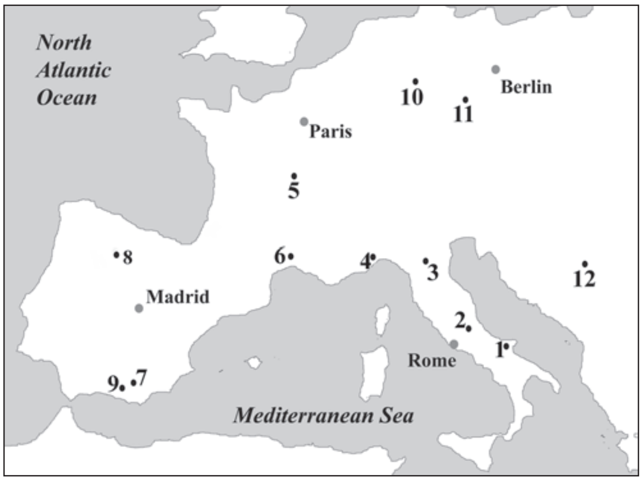


Fig. 10 - Location map of selected late Early Pleistocene sites of Europe and Italy with remains of *S. etruscus* and *S. hundsheimensis*.
Sites with *S. etruscus*: 1 = Pirro Nord (1.3-1.6 Ma); 2 = Scoppito (1.3-1.1? Ma); 3 = Imola basin (latest Early Pleistocene); 6 = Lézignan-le-Cèbe (about 1.5 Ma); 8 = Atapuerca Gran Dolina TD4-8 (about 0.800 Ma) and Sima del Elefante TE14 (1.4-1.1 Ma); 9 = Cueva Victoria (about 1 Ma);
Sites with *S. hundsheimensis*: 4 = Vallonnet (about 1 Ma); 5 = Soleilhac (about 0.750 Ma); 7 = Fuente Nueva-3 and Barranco León-5 (1.3-1.1 Ma); 10 = Dorn-Dürkheim 3 (about 0.800 Ma); 11 = Untermaßfeld (about 1 Ma); 12 = Trlica (latest Early Pleistocene).

Italy during the Pleistocene, in particular for species that arrive from Asia (for example *Coelodonta antiquitatis* is not present before MIS 4 and *Praemegaceros solilhacus* is present during the Isernia FU, about 0.600-0.550 Ma) (Petronio et al. in press). Some African or southwest Asian taxa seem instead to be present first in Italy and later in central Europe. This is the case of *Dama clactoniana* and perhaps *Homo*.

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REFERENCES

Abbazzi L., Benvenuti M., Rook L. & Masini F. (1995) - Biochronology of the Mugello intermontane basin (northern Apennines, Italy). *Il Quaternario*, 8: 5-10.

Abbazzi L., Benvenuti M., Boschian G., Dominici S., Masini F., Mezzabotta C., Rook L., Valleri G. & Torre D. (1996) - The Neogene and Pleistocene succession, and the mammal faunal assemblages of an area between Apricena and Poggio Imperiale (Foggia, Italy). *Mem. Soc. Geol. Ital.*, 51: 383-402.

Alba D.M., Aurell J., Madurell J., Gómez M., Moyà- Solà S. & Beràstegui X. (2008) - Paleontologia i geologia del jaciment del Pleistocè inferior de Vallparadís (Terrassa, Vallès Occidental). *Trib. Arqueol.*, 2008: 29-44.

Ambrosetti P. (1972) - Lo scheletro di *Dicerorhinus etruscus* (Falc.) di Capitone (Umbria meridionale). *Geol. Romana*, 11: 177-198.

Ambrosetti P. & Cremaschi M. (1975) - Segnalazioni di una fauna villafranchiana superiore con *Libralces gallicus* nei livelli fluviolacustri soprastanti alle faune calabriane ad *Arctica islandica* nei dintorni di Reggio Emilia. *Boll. Soc. Geol. Ital.*, 94: 1361-1374.

Ambrosetti P., Faraone A. & Gregori L. (1987) - Pietrafitta: un museo di paleontologia in Umbria. *Museol. Sci.*, 4(1-2): 99-118.

Azzaroli A. & Berzi A. (1972) - On a Upper Villafranchian fauna at Imola, northern Italy, and its correlation with the marine Pleistocene sequence of the Po plain. *Palaeontogr. Ital.*, 66 : 1-12.

Bertini A. (2000) - Pollen record from Colle Curti and Cesi: Early and Middle Pliestocene mammal sites in the Umbro-Marchean Apennine Mountains (central Italy). *J. Quat. Sci.*, 15(8): 825-840.

Blanc A.C., Lona F. & Settepassi F. (1955) - Ricerche sul Quaternario Laziale. 1°. Una torba ad Abies, malacofauna montana e criosedimenti nel Pleistocene inferiore di Roma. Il periodo glaciale Cassio. *Quaternaria*, 2, 151-158.

Caloi L. & Palombo M.R. (1988) - Le mammalofaune del Plio-Pleistocene dell'area laziale; problemi biostratigrafici ed implicazioni paleoclimatiche. *Mem. Soc. Geol. Ital.*, 35: 99-126.

Caloi L. & Palombo M.R. (1995) - Le mammalofaune del Pleistocene inferiore nell'Italia centrale. *Studi Geologici Camerti*, vol. spec. 1994(B), 487-501.

Caloi L. & Palombo M.R. (1997) - Biochronology of large mammals of Italian peninsula in the Early and Middle Pleistocene. *Hystrix*, 9: 3-12.

Caloi L., Palombo M.R. & Petronio C. (1979) - Cenni preliminari sulla fauna di Cava Redicicoli (Roma). *Boll. Serv. Geol. Ital.*, 100: 189-198.

Cerdeño E. (1993) - Remarks on the spanish Plio-Pleistocene *Stephanorhinus etruscus* (Rhinocerotidae). *C. R. Acad. Sci.*, 317: 1363-1367.

Cerdeño E. (1995) - Changes in Western European Rhinocerotidae related to climatic variations. *Palaeogeogr., Palaeoclimat., Palaeoecol.*, 114: 325-338.

Cerdeño E. (1998) - Diversity and evolutionary trends of the family Rhinocerotidae (Perissodactyla). *Palaeogeogr., Palaeoclimat., Palaeoecol.*, 141: 13-34.

Codrea V. & Czier Z. (1991) - *Dicerorhinus etruscus brachycephalus* (Perissodactyla, Mammalia) from the Pleistocene of Subpiatra (Tetchea Village, Bihor County, Romania). *Studia Universitatis Babes-Bolyai, Geologia*, 36(2): 27-33.

Codrea V. & Dimitrijević V. (1997) - *Stephanorhinus* cf. *hundsheimensis* (Toula) (Rhinocerotidae, Mammalia) from Trlica near Pljevlja (Montenegro). *Geol. anali Balk. Poluos.*, Beograd, 61(2): 161-177.

Coltorti M., Feraud G., Marzoli A., Peretto C., Ton-That T., Voinchet P., Bahain J.J., Minelli A. & Thun Hohenstein U. (2005) - New ^{40}Ar/^{39}Ar, stratigraphic and palaeoclimatic data on the Isernia La Pineta Lower Palaeolithic site, Molise, Italy. *Quat. Inter.,* 131: 11-22.

De Giuli C., Masini F. & Torre D. (1987) - The latest Villafranchian faunas of Italy. The Pirro Nord Fauna (Apricena, Gargano). *Palaeontogr. Ital.*, 74: 51-62.

Di Stefano G., Petronio C. & Sardella R. (1998) - Biochronology of Pleistocene mammal faunas from Rome urban area. *Il Quaternario*, 11: 191-199.

Falconer H. (1868) - On the European Pliocene and Postpliocene species of the genus *Rhinoceros. Paleontol. Mem. and Notes*, 2: 309-403.

Ficcarelli G. & Mazza P. (1990) - New fossil findings from the Colfiorito basin (Umbria-Marchean Apennine). *Boll. Soc. Paleont. Ital.*, 29(2): 245–247.

Ficcarelli G., Abbazzi L., Albianelli A., Bertini A., Coltorti M., Magnatti M., Masini F., Mazza P., Mezzabotta C., Napoleone G., Rook L., Rustioni M. & Torre D. (1997) - Cesi, an early Middle Pleistocene site in the Colfiorito Basin (Umbro-Marchean Apennine), central Italy. *J. Quat. Sci.*, 12(6): 507-518.

Fortelius M., Mazza P. & Sala B. (1993) - *Stephanorhinus*

(Mammalia, Rhinocerotidae) of the western European Pleistocene, with a special revision of *Stephanorhinus etruscus* (Falconer, 1868). *Paleontogr. Ital.*, 80: 63-155.

Franzen J.L., Gliozzi E., Jellinkek T., Scholger R. & Weidenfeller M. (2000) - Die spätpleistozäne Fossillagerstätte Dorn- Dürkheim 3 und ihre Bedeutung für die Rekonstruktion der Entwicklung des rhenishen Flusssystems. *Senkenbergiana Lethaea*, 80(1): 305-353.

García-Fernández D., Cerdeño E., Galobart A. & Ros X. (2001) - *Stephanorhinus etruscus* (Rhinocerotidae) del Plioceno superior de Crespià (Gerona, NE de España). *Rev. Esp. Paleontol.*, 16(1): 145-160.

García-Fernández D., Galobart A. & Cerdeño E. (2003a) - Perisodáctilos del Pleistoceno inferior de los yacimientos de Incarcal (Girona, NE de la Península Ibérica). *Paleontol. Evol.*, 34: 175-183.

García-Fernández D., Galobart A., Ros X. & Cerdeño E. (2003b) - *Stephanorhinus etruscus* (Rhinocerotidae) en el Villafranquiense de Crespià (Girona, NE de la Península Ibérica). *Paleontol. Evol.*, 34: 279-296.

Gibert L., Maestro E., Gibert J. & Albaladejo S. (1999) - Plio-Pleistocene deposits of the Orce region (SE Spain): Geology and Age. In: Gibert J., Ribot F., Sánchez F. & Gibert L. (Eds) - The hominids and their environment in the middle and lower Pleistocene of Eurasia. *Museo de Prehistoria y Paleontología «J. Gibert», Orce, Granada*: 127-144, Orce.

Gliozzi E., Abbazzi L., Argenti P., Azzaroli A., Caloi L., Capasso Barbato L., Di Stefano G., Esu D., Ficcarelli G., Girotti O., Kotsakis T., Masini F., Mazza P., Mezzabotta C., Palombo M.R., Petronio C., Rook L., Sala B., Sardella R., Zanalda E. & Torre D. (1997) - Biochronology of selected mammals, molluscs and ostracods from the middle Pliocene to the late Plesitocene in Italy. The state of the art. *Riv. It. Paleont. Strat.*, 103 (3): 369-388.

Groves C.P. (1983) - Phylogeny of the living species of rhinoceros. *Zeitschr. f. zoo. Systematik u. Evolutionsforsch*, 21: 293-313.

Guérin C. (1980) - Les rhinocéros (Mammalia, Perissodactyla) du Miocène terminal au Pléistocène supérieur en Europe occidentale. Comparaison avec les espèces actuelles. *Doc. Lab. Géol. Lyon*, 79(1-2-3) : 1-1185.

Guérin C. (1983) - Les Rhinocéros (Mammalia, Perissodactyla) du gisement Pléistocène Moyen de Vergranne. *Ann. Sci. Univ. Franche-Comté-Besançon, Géol.* 5, 4ème série: 47-67.

Guérin C. (1989) -La familles des Rhinocerotidae (Mammalia, Perissodactyla): systématique, historie, évolution, paléoécologie. *Cranium*, 6(2): 3-14.

Guérin C. (2004) - Les rhinocéros (Mammalia, Perissodactyla) du gisement villafranchien moyen de Saint-Vallier (Drôme). *Geobios*, 37: 259-278.

Guérin C. & Heintz E. (1972) - *Dicerorhinus etruscus* (Falconer, 1859), Rhinocerotidae, Mammalia, du Villafranchien de La Puebla de Valverde (Turuel, Espagne). *Bull. Mus. Natl. Hist. Nat.*, 18(2): 13-22.

Guérin C., Dewolf Y. & Lautridou J.P. (2003) - Revision of a famous site: Saint-Prest (Chartres, France). *Geobios*, 36: 55-82.

Heintz H., Guérin C., Martin R. & Prat F. (1974) - Principaux gisements villafranchiens de France: liste faunique et biostratigraphique. *Mém. Bureau Rech. Géol. Min.*, 78(1): 169-182.

Heissig K. (1973) - Die Unterfamilien und Tribus der rezenten und fossilen Rhinocerotidae (Mammalia). *Säugetierkundl Mitt.*, 21: 25-30.

Heissig K. (1981) - Probleme bei der cladistischen Analyse einer Gruppe mit wenigen eindeutigen Apomorphien: Rhinocerotidae. *Paläontol. Z.*, 55: 117-123.

Heissig K. (1989) - Rhinocerotidae. In: Prothero D.R & Schoch R.M. (Eds) - The evolution of Perissodactyls. *Oxford University Press*: 399-417, Oxford.

Kahlke H.D. (1969) - Die Rhinoceotiden-Reste aus den Kiesen von Süssenborn bei Weimar. *Paläontol. Abh. A*, 3(3/4): 667-709.

Kahlke R.D. (2001) - Die Unterpleistozäne Komplexfundstelle Untermaßfeld – Zusammenfassung Des kenntnisstandes Sowie Synthetische Betrachtungen Zu Genesemodell, Paläoökologie und Stratigraphie. In: Kahlke R.D. (Ed) - Das Pleistozän von Untermaßfeld bei Meiningen (Thüringen). *Monographien des Römisch-Germanischen Zentralmuseums, Band* 40, 2: 931-1030, Mainz.

Kahlke R.D. & Kaiser T.M. (in press) - Generalism as a subsistence strategy: advantages and limitations of the highly flexible feeding traits of Pleistocene *Stephanorhinus hundsheimensis* (Rhinocerotidae, Mammalia). *Quat. Sci. Rev.,* Elsevier, doi: 10.1016/j.quascirev.2009.12.012.

Kotsakis T., Esu D. & Girotti O. (1992) - A post-Villafranchian cold event in central Italy testified by continental Molluscs and Rodents. *Boll. Soc. Geol. Ital.*, 111: 335-340.

Lacombat F. (2005) - Les rhinocéros fossiles des sites préhistoriques de l'Europe méditerranéenne et du Massif central. Paléontologie et implications biochronologiques. *BAR International Series*, 1419: 1-175.

Lacombat F. (2006) - Morphological and biometrical differentiation of the teeth from Pleistocene species of *Stephanorhinus* (Mammalia, Perissodactyla, Rhinocerotidae) in Mediterranean Europe and Massif Central, France. *Paläont. Abh. A*, 274: 71-111.

Leroy S.A.G. (2007) - Progress in palynology of the Gelasian-Calabrian Stages in Europe: ten messages. *R. Micropaléontol.*, 50: 293-308.

Maccagno A.M. (1962) - L'*Elephas meridionalis* Nesti di Contrada "Madonna della Strada" Scoppito (L'Aquila). *Atti Acc. Sci. Fis. Nat. Napoli*, 4: 1-129.

van der Made J. (1998) - Ungulates from Gran Dolina (Atapuerca, Burgos, Spain). *Quaternaire*, 9(4): 267-281.

van der Made J. (2000) - A preliminary note on the rhinos from Bilzingsleben. *Praehist. Thuringica*, 4(S): 41-64.

van der Made J., Aguirre E., Bastir M., Fernández Jalvo Y., Huguet R., Laplana C., Marquez B., Martínez C., Martinón M., Rosas A., Rodríguez J., Sánchez A., Sarmiento S. & Bermúdez de Castro J.M. (2003)

- El registro paleontológico y arqueológico de los yacimientos de la Trinchera del Ferrocarril en la Sierra de Atapuerca. *Coloquios de Paleontología,* Vol. Ext. 1: 345-372.

Magri D., Di Rita F. & Palombo M.R. (2010) - An Early Pleistocene interglacial record from an intermontane basin of central Italy (Scoppito, L'Aquila). *Quat. Inter.*, 225(1): 106-113.

Martínez-Navarro B., Turq A., Agustí J. & Oms O. (1997) - Fuente Nueva-3 (Orce, Granada, Spain) and the first human colonization of Europe. *J. Hum. Evol.*, 33: 611-620.

Martinez-Navarro B., Espigares M.P. & Ros S. (2003) - Estudio preliminar de las asociaciones de grandes mamiferos de Fuente Nueva-3 y Barranco Leon-5 (Orce, Granada, Espaa). In: Toro I., Agustí J. & Martinez-Navarro B. (Eds) - El Pleistoceno inferior de Barranco León y Fuente Nueva 3, Orce (Granada). Memoria cientifica campañas 1999-2002. *Arqueologìa Monografìas, Consejerìa de Cultura, Junta de Andalucìa*: 115-136, Sevilla.

Masini F., Ficcarelli G. & Torre D. (1994) - Late Villafranchian and the earliest Galerian mammal Faunas from some intermontane basins of north-central Italy. *Mem. Soc. Geol. Ital.*, 48: 381-389.

Mazza P. (1988) - The Tuscan Early Pleistocene rhinoceros *Dicerorhinus etruscus*. *Paleontogr. Ital.*, 75: 1-87.

Mazza P. (1996) - The Middle Pleistocene rhinoceros remains from Cesi (Colfiorito Basin, Macerata, central Italy). *Boll. Soc. Paleont. Ital.*, 35(3): 349-355.

Mazza P., Sala B. & Fortelius M. (1993) - A small latest Villafranchian (Late Early Pleistocene) rhinoceros from Pietrafitta (Perugia, Umbria, central Italy), with notes on the the Pirro and Westerhoven rhinoceroses. *Paleontogr. Ital.*, 80: 25-50.

McKenna M.C. & Bell S.K. (1997) - Classification of Mammals above the species level. V. of 631 pp., Columbia University Press, New York.

Milli S. & Palombo M.R. (2005) - The high-resolution sequence stratigraphy and the mammal fossil record: a test in the Middle–Upper Pleistocene deposits of the Roman Basin (Latium, Italy). *Quat. Inter.*, 126/128: 251–270.

Oms O., Parés J. M., Martínez-Navarro B., Agustí J., Toro I., Martínez-Fernández G. & Turq A. (2000) - Early human occupation of Western Europe: Paleomagnetic dates for two Paleolithic sites in Spain. *Proc. Natl. Acad. Sci. USA*, 97(19): 10666–10670.

Palombo M.R., Azanza B. & Alberdi M.T. (2002) - Italian mammal biochronology from Latest Miocene to Middle Pleistocene: a multivariate approach. *Geol. Romana*, 36: 335-368.

Palombo M.R. & Valli A.M.F. (2003) - Remarks on the biochronology of mammalian faunal complexes from the Pliocene to the Middle Pleistocene in France. *Geol. Romana*, 37: 145-163.

Petronio C. (1988) - Una mandibola di rinoceronte di Ponte Galeria (Roma). *Atti Soc. Ital. Sci. Nat. Mus. Civ. St. Nat. Milano*, 129(2-3): 173-178.

Petronio C. & Sardella R. (1999) - Biochronology of the Pleistocene Mammal Fauna from Ponte Galeria (Rome) and remarks on the Middle Galerian Faunas. *Riv. It. Paleont. Strat.*, 105: 155-164.

Petronio C., Argenti P., Caloi L., Esu D., Girotti O. & Sardella R. (2002) - Updating Villafranchian mollusc and mammal faunas of Umbria and Latium (central Italy). *Geol. Romana*, 36: 369-387.

Petronio C., Bellucci L., Martinetto E., Pandolfi L. & Salari L. (in press) - Biochronology and Palaeoenvironmental Changes from the Middle Pliocene to the Late Pleistocene in central Italy. *Geodiversitas*.

Prothero D.R., Manning E. & Hanson C.B. (1986) - The phylogeny of Rhinocerotoidea, *Zool. J. Linn. Soc.*, 87: 341-366.

Radulescu C. & Samson P. (1985) - Pliocene and Pleistocene mammalian biostratigraphy in southeastern Transylvania (Romania). *Trav. Inst. Speol. "Emile Racovitza"*, 24 :85-95.

Ravazzi C., Pini R., Breda M., Martinetto E., Muttoni G., Chiesa S., Confortini F. & Egli R. (2005) - The lacustrine deposits of Fornaci di Ranica (late Early Pleistocene, Italian Pre-Alps): stratigraphy, palaeoenvironment and geological evolution. *Quat. Inter.*, 131: 35-58.

Rosas A., Pérez-Gonzáles A., Carbonell E., van der Made J., Sánchez A., Laplana C., Cuenca-Bescós G., Parés J.M. & Huguet R. (2001) - Le gisement pleistocene de la «Sima del Elefante» (Sierra de Atapuerca, Espagne). *L'Anthropologie*, 105: 301-312.

Sala B. & Fortelius M. (1993) - The rhinoceroses of Isernia la Pineta (early mid Pleistocene, Southern Italy). *Paleontogr. Ital.*, 80: 157-174.

Siori S. & Sala B. (2007) - The mammal fauna from the late Early Biharian site of Castagnone (northern Monferrato, Piedmont, NW Italy). *Geobios*, 40(2): 207-217.

Turq A., Martínez-Navarro B., Palmquist A., Arribas A., Agustí J. & Rodríguez-Vidal J. (1996) - Le Plio-Pléistocène de la région d´Orce, province de Grenade, Espagne: bilan et perspectives de recherche. *Paléo*, 8: 161-204.

Ugolini R. (1921) - Sopra alcuni resti di rinoceronte del Pliocene lacustre di Pietrafitta in Prov. di Perugia. *Riv. It. Paleont.*, 27(1-2): 15-18.