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Morphological and biometrical differentiation of the teeth from Pleistocene species of *Stephanorhinus* (Mammalia, Perissodactyla, Rhinocerotidae) in Mediterranean Europe and the Massif Central, France

by

FRÉDÉRIC LACOMBAT

With 28 figures and 20 tables in the text

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Zusammenfassung

Die vorliegende Arbeit ist eine Untersuchung eines fossilen Rhinozeros der Gattung *Stephanorhinus* aus dem mediterranen Raum Europas und dem Massif Central in Frankreich. Die Studie basiert auf Material von 19 pleistozänen Fundstellen. Obwohl *Stephanorhinus etruscus*, *Stephanorhinus hunsheimensis*, *Stephanorhinus hemitoechus* und *Stephanorhinus kirchbergensis* eine ähnliche Zahnmorphologie aufweisen, konnten spezifische unterscheidende Merkmale durch die Quantifizierung qualitativer Daten gefunden werden. Die biometrischen Daten zeigen spezifische Unterschiede, und für jede der vier Arten werden morphologische Beschreibungen und präzise Diagnosen für jeden Zahn geliefert.

Schlüsselwörter: *Stephanorhinus* – Morphologie – Biometrie – Pleistozän – Europa.

Summary

This work presents a paleontological study of fossil rhinoceros of the genus *Stephanorhinus* in Mediterranean Europe and in the Massif Central, France, based on the study of material from nineteen sites of Pleistocene age. Although *Stephanorhinus etruscus*, *Stephanorhinus hundsheimensis*, *Stephanorhinus hemitoechus*, and *Stephanorhinus kirchbergensis* have similar tooth morphology, distinctive characters were found by quantifying the qualitative observations. Biometrical data show specific differences according to the results of the morphological description and a precise diagnose of each tooth is proposed for the four species.

Key words: *Stephanorhinus* – Morphology – Biometry – Pleistocene – Europe.

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Introduction

Since the beginnings of paleontological studies, the fossil rhinoceroses have been easily recognizable because of their particular morphology. However, many of the Pleistocene fossil species represent a restricted group, whose morphology is extremely similar. After the precursor works of the nineteenth century and the beginning of the twentieth century (FALCONER 1868, OSBORN 1900, TOULA 1902, 1906 and SCHROEDER 1903, 1906), KRETZOÏ (1942) revised the numerous species that had been created, while in the nineteen sixties and seventies KAHLKE published many reference works on rhinos from the rich German sites (VOIGTSTEDT 1965, SÜSSENBORN 1969, EHRINGSDORF 1975 and TAUBACH 1977). At the beginning of the nineteen eighties, GUÉRIN wrote a synthesis on the Miocene – Recent Rhinocerotidae (GUÉRIN 1980), and numerous other systematic and phylogenic studies have since been published (HEISSIG 1981, 1989, GROVES 1983 and PROTHERO et al. 1986, 1989). MAZZA (1988) redefined precisely the holotype of *Stephanorhinus etruscus* and discussed the nomenclature then in use, and FORTELIUS et al. (1993) proposed the bases for new studies of the genus *Stephanorhinus*.

The goal of the present work is to provide a clear definition of the morphological and biometrical differences between the species of *Stephanorhinus* that followed each other during the Pleistocene based on their dental remains. Collections of rhinoceros have become richer during these last twenty years, and the material has therefore become sufficiently abundant to define the species of the *Stephanorhinus* clearly while concentrating on this geographical area. This restricted area is chosen to limit the influence of paleoclimatic variations.

Abbreviations used

S. etr – *Stephanorhinus etruscus*
S. hun – *Stephanorhinus hundsheimensis*
S. hem – *Stephanorhinus hemitoechus*
S. kirch – *Stephanorhinus kirchbergensis*

Material and Methods

This paleontological study concentrates on Mediterranean Europe and the Massif Central during the whole Pleistocene. The studied material is stored in the following institutions: National Museum of Natural History of Paris (Senèze, Durfort, Soleilhac, Mars cave and Upper Valdarno), Museum of Regional Prehistory of Menton (Vallonnet cave and Tour de Grimaldi), Museo d'Isernia (Isernia la Pineta), European Center of Prehistoric Research of Tautavel (Caune de l'Arago and Orgnac 3), Museum of Natural History of Nice (Cagnes-sur-Mer), Museum Crozatier of Puy-en-Velay (Sainzelles, Ceyssaguet and Soleilhac), Museum of Prehistoric Anthropology of Monaco (Aldène, Prince cave, Cavillon cave, Observatoire cave and Grotte des Enfants), Museum Terra Amata of Nice (Terra Amata) and Museum of Natural History of Florence (Upper Valdarno).

The morphology of the teeth of the different species of *Stephanorhinus* is extremely similar. Thus, it is necessary to quantify the qualitative data in order to be able to discriminate between them.

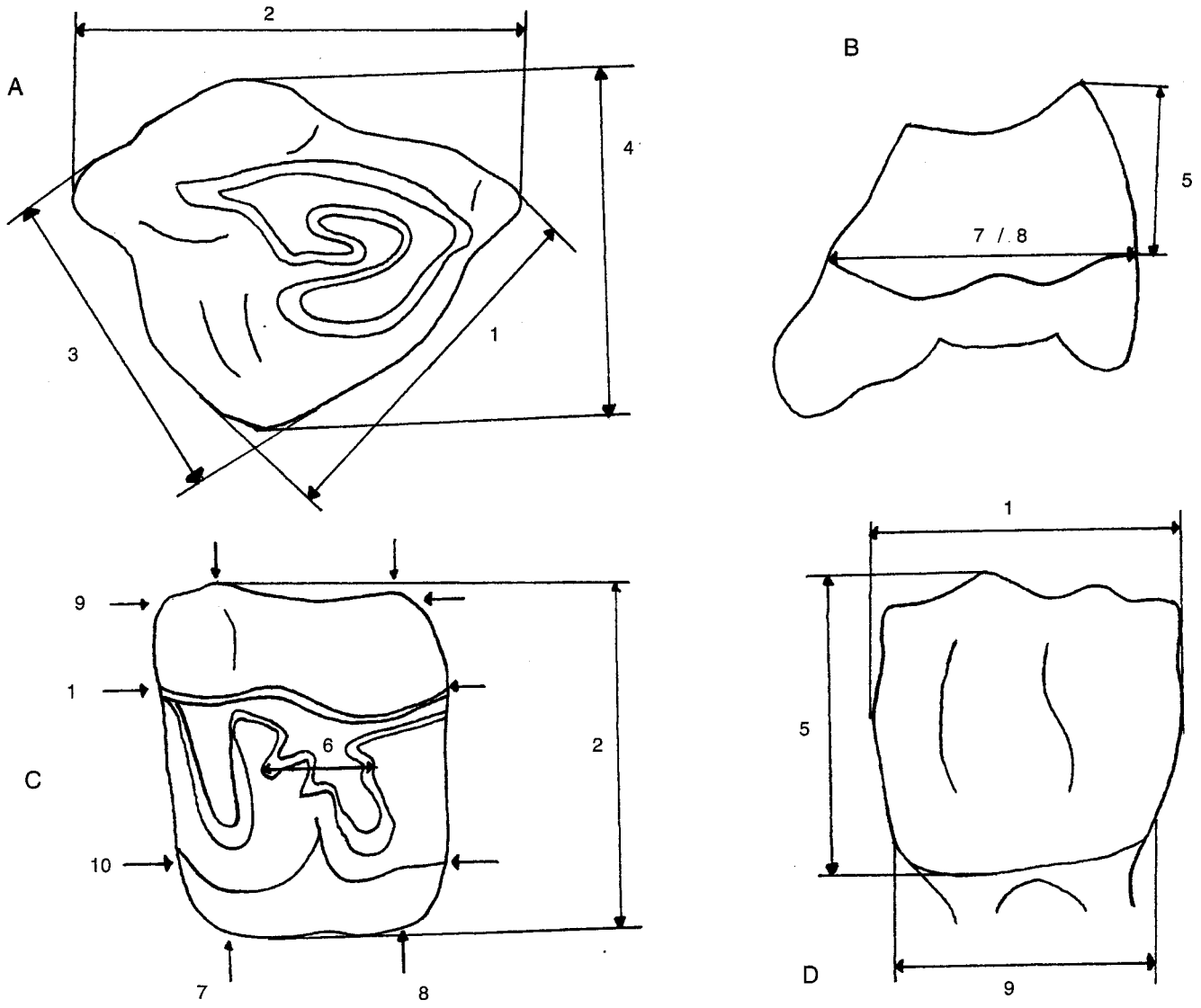

Fig. 1. Biometrical measurements on the upper teeth. A-Upper M3, occlusal view, B-Upper Molar mesial view, C-Upper Molar occlusal view, D-Upper Molar vestibular view.
Measurements of the upper teeth (but the M3): 1. Maximal length. 2. Maximal breadth. 5. Height of the crown. 6. Maximal length of the crochet. 7. Mesial breadth, taken to the level of the collar. 8. Distal breadth, taken to the level of the collar. 9. Vestibular length, taken to the level of the collar. 10. Lingual length, taken to the level of the collar.
Upper M3: 1. L ana - anatomical length. 2. L abs – absolute length. 3. l ana – anatomical breadth. 4. l abs – absolute breadth. 5. Hs – Height of the crown.
Hypsodonty index: (H/Max. length) × 100. Calculated index only on the non worn-out teeth.

The morphological descriptions of the upper teeth are derived extensively from the method established by GUÉRIN (1980).
The internal folds and cingulum are described as follows:
– Single, double or multiple crochet.
– Single, double or multiple crista.
– Single, double or multiple antecrochet.
– Horizontal or oblique, continuous or discontinuous mesial, distal, vestibular and lingual cingulum.
– Open or closed mediofossette.
– Obtuse, right or sharp angle between the crochet and the metacone.
– Strong or light protocone constriction.
– Development and shape of the paracone fold.

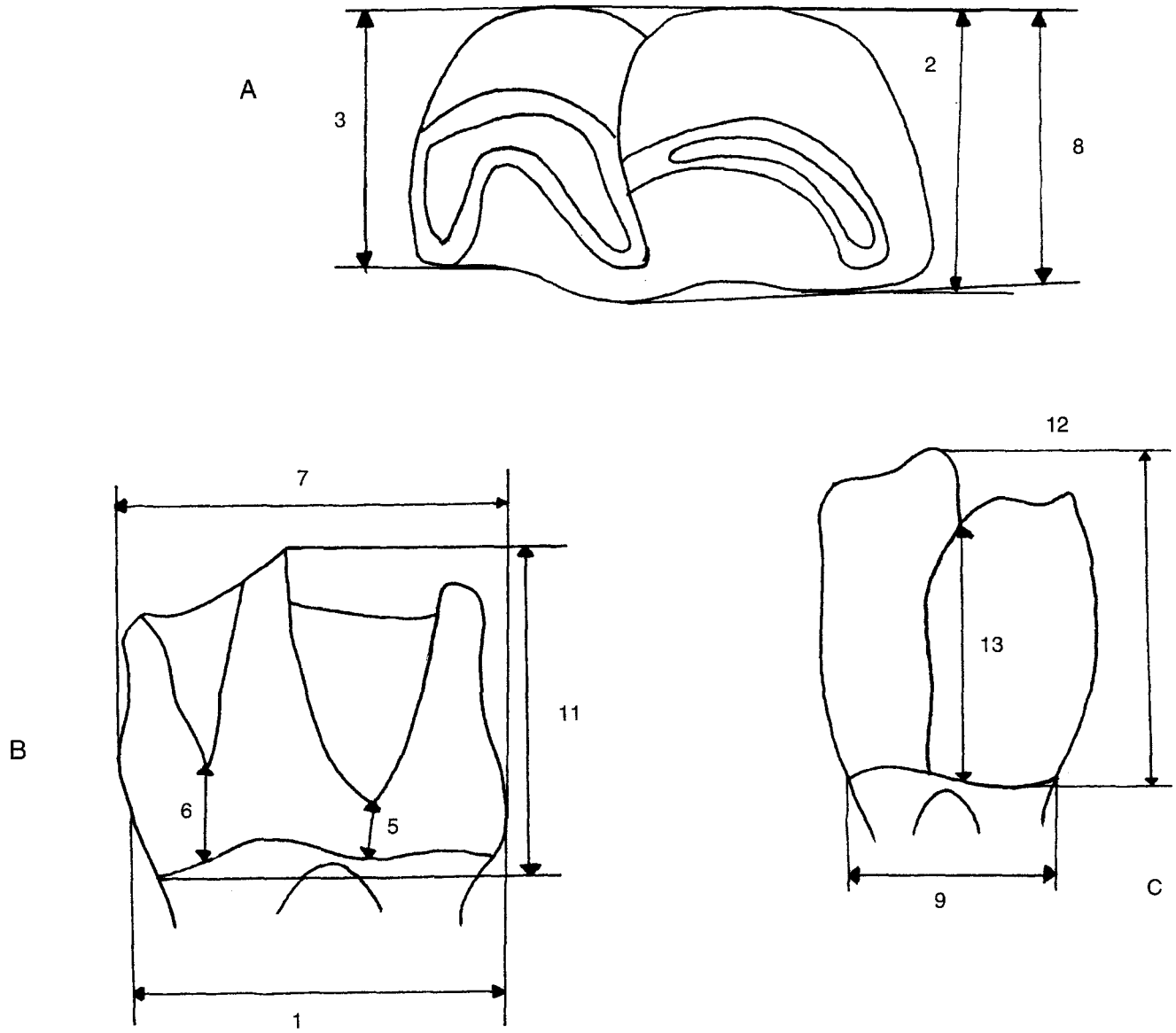

Fig. 2. Biometrical measurements on the lower teeth. A – Lower Molar occlusal view, B – Lower molar lingual view, C – Lower Premolar vestibular view.
Measurements on the lower teeth: 2. Distal breadth, taken to the collar. 3. Mesial breadth, taken to the collar. 5. Difference of height between the bottom of the posterior valley and the collar. 6. Difference of height between the bottom of the previous valley and the collar. 7. Maximal length. 8. Maximal breadth, taken to the collar. 9. Vestibular length, taken to the collar. 10. Lingual length, taken to the collar. 11. Height of the crown, take lingual face. 12. Height of the crown, take vestibular face.
Hypsodonty index: (H/Max. length) × 100. Calculated index only on the non worn-out teeth.

The morphological descriptions of the lower teeth are derived from the works of GUÉRIN (1980) and FORTELIUS et al. (1993). The relevant morphological features are:
– Anterior valley: V-shaped, broad V-shaped or U-shaped.
– Posterior valley: V-shaped, broad V-shaped or U-shaped.
– The difference in height between the bottoms of the two valleys: null, small, high.
– Horizontal and/or oblique, continuous or discontinuous mesial, distal, vestibular and lingual cingulum.
– The opening of the vestibular syncline: closed (sharp angle), orthogonal or open (obtuse angle).
– The depth of the vestibular syncline: null, shallow or deep.

The biometrical method which is defined here is a synthesis of different methods. The measurements of the upper (Fig. 1) and lower teeth (Fig. 2) are based on the work of GUÉRIN (1980), MAZZA (1988) and FORTELIUS et al., (1993), to wich we have added our own measurements (LACOMBAT 2003, 2005).

The biometrical data are compared between the species, the specific differences, using Simpson's ratio diagram (1941). The reference chosen is the present day *Diceros bicornis* (studied collections from the Laboratory of Compared Anatomy of the National Museum of Natural History of Paris and the Museum of Prehistoric Anthropology of Monaco). This method allows us to highlight the differences in proportions of every type of tooth, and the use of a present day reference eliminates the uncertainties about sexual dimorphism and representativeness of the sample that stem from using a fossil species for this purpose.

Results

Upper P2

(Figs. 3 and 4, Table 1)

The crochet is always single in *S. hemitoechus* and *S. etruscus* (Fig. 3), it can be double in *S. hundsheimensis* (27,3 %) and *S. kirchbergensis* (50,0 %).

The crista is always present and single in *S. hemitoechus* and *S. kirchbergensis*, it can be absent in *S. hundsheimensis* (27,3 %) and when it exists, it can be double (9 %) or multiple (9 %). The upper P2 of *S. etruscus* studied present a crista on 40 % of the observations.

The antecrochet can be observed on the P2 of *S. hundsheimensis* (33 %) and *S. hemitoechus* (20 %). It does not exist on the upper P2 of *S. kirchbergensis* and *S. etruscus.*

The mediofossette is always open in *S. etruscus.* It is open or closed in different percentages in the three other species.

The angle between the crochet and the metacone is obtuse to right-angled for *S. hundsheimensis* and *S. kirchbergensis.* It is very variable on the populations of *S. hemitoechus.* It is sharper in the Etruscan rhinoceros.

The protocone constriction is always absent for this tooth and for all species of the study.

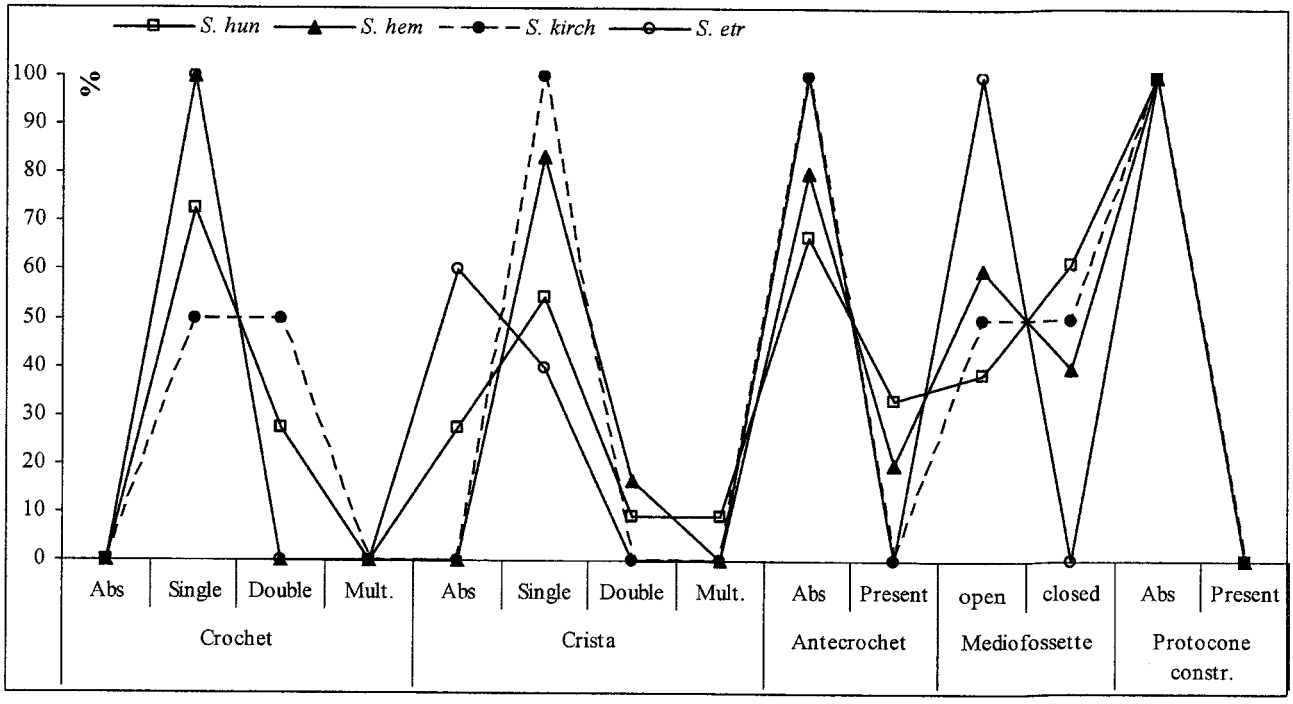

Fig. 3. Percentage distributions of qualitative character states for the upper P2 of the Pleistocene *Stephanorhinus.*

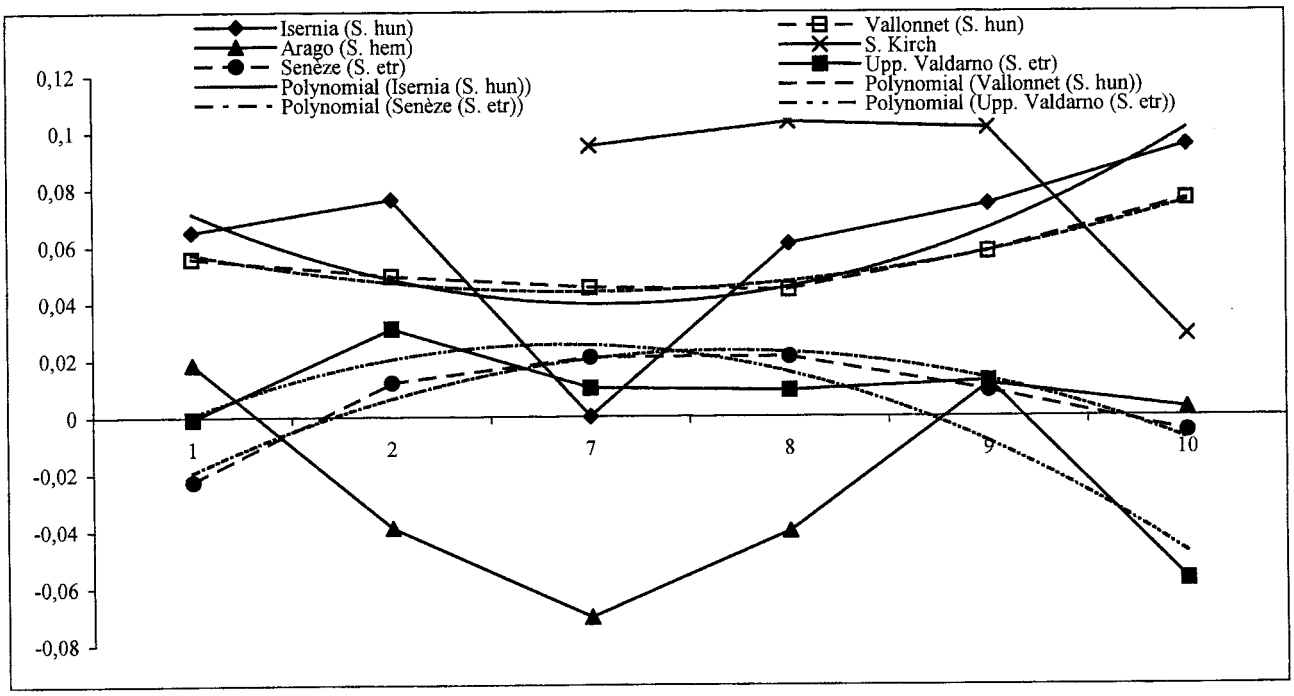

Fig. 4. Ratio diagram of the upper P2 of the Pleistocene *Stephanorhinus*. The referential is the present-day *Diceros bicornis*. *S. kirchbergensis* (data from FORTELIUS et al. 1993).

The vestibular and the distal cingulum are absent. The mesial and the lingual cingulum are always present, strong, continuous and horizontal. In this tooth, the Pleistocene species of *Stephanorhinus* have the same morphology of the cingulum.

The profile of the vestibular wall is regular. The paracone fold is slightly marked for *S. hundsheimensis*. In *S. etruscus* this presents a smoother and flatter profile than in *S. hundsheimensis*. Reliefs are more strongly marked at *S. hemitoechus*. *S. kirchbergensis* presents the same profile as the one of *S. hundsheimensis* for GUÉRIN (1980).

Simpson's diagram of the upper P2 (Fig. 4) shows the biometrical differences. *S. hundsheimensis* presents a more developed P2 than *S. etruscus*. This is very clear on the different lengths of this tooth, especially the lingual length that gives the upper P2 of *S. etruscus* a more triangular shape than the one of *S. hundsheimensis*. This is an archaic character of *S. hundsheimensis* that could be easily used to discriminate it from *S. etruscus*. The computation of a polynomial curve of tendency shows the differences: the curve of *S. hundsheimensis* has a slightly concave shape, whereas the shape of the curve of *S. etruscus* is distinctly convex, nearby to the reference. The only biometrical difference observed on this tooth within *S. hundsheimensis* is the mesial breadth (measurement n°7), which is more important on the upper P2 of the S. *hundsheimensis* from the early Middle Pleistocene. The upper P2 of *S. hundsheimensis* from the Early Pleistocene (Vallonnet cave) are therefore more symmetrical than those of the Middle Pleistocene (Isernia). The upper P2 of *S. hemitoechus* are the most reduced (Table 1) compared with the other species. That is particularly remarkable in the proportions. This reduction in size of the premolars and notably of the P2 is considered to be an evolved character of the species (VAN DER MADE 2000). The curve of *S. kirchbergensis* is derived from the data proposed by FORTELIUS et al. (1993). *S. kirchbergensis* presents specific proportions and the greatest size of the Pleistocene species. The hypsodonty index of this tooth is more important in the archaic forms than in more evolved forms. The hypsodonty index of the upper P2 is greater in the Vallonnet cave (Early Pleistocene) material than that from Isernia (early Middle Pleistocene), in the same way it is greater in the *S. hemitoechus* of Arago cave (Middle Pleistocene) than in that of the Observatory cave and of the Prince cave (Upper Pleistocene). Therefore, one can infer that a strong hypsodonty index on the P2 is an archaic character within the species.

Table 1. Measurements (in mm) of the upper P2.

P2/ Measurement n°		1	2	5	6	7	8	9	10
Senèze *(S. etr)*	MEAN (N=5)	28,12	35,01			33,85	36,24	27,99	21,18
	MIN	23,79	34,74	4,64		33,40	36,16	27,37	20,20
	MAX	30,20	35,28	20,23		34,30	36,31	28,40	23,25
Upper Valdarno *(S. etr)*	MEAN (N=2)	29,80	37,34			33,02	35,26	28,42	18,79
	MIN	29,58	36,57	18,43				28,21	
	MAX	30,01	38,11	20,50				28,63	
Cagnes sur mer *(S. hun)*	MEAN (N=2)	31,94	37,27		10,34	33,63	36,75	30,77	26,72
	MIN	31,26	36,90	25,50	9,66	32,85	36,54	30,73	26,72
	MAX	32,61	37,64	28,28	11,02	34,40	36,96	30,80	26,72
Vallonnet *(S. hun)*	MEAN (N=8)	33,68	38,16		10,46	35,82	38,26	31,32	25,56
	MIN	32,36	37,85	17,67	8,42	35,20	37,39	29,00	24,18
	MAX	35,16	38,75	38,73	13,18	36,56	39,12	33,98	26,89
Isernia *(S. hun)*	MEAN (N=17)	34,41	40,61		10,64	32,27	39,70	32,55	
	MIN	29,50	36,00	13,60	7,00	29,70	39,50		
	MAX	39,60	45,20	39,20	14,27	34,83	39,90		
Soleilhac *(S. hun)*	N=1	32,52	39,92	17,11		35,30	40,37	29,60	26,72
Arago *(S. hem)*	MEAN (N=18)	30,91	31,13		1,12	27,43	31,46	28,14	21,58
	MIN	29,23	28,11	0,00	0,25	22,22	25,19	24,12	18,23
	MAX	34,56	34,85	38,61	1,99	29,59	36,84	34,42	24,05
Orgnac 3 *(S. hem)*	MEAN (N=3)	32,38	35,73	20,38	6,87	35,16	35,26	31,22	22,58
	MIN	30,18	33,43	13,80		34,21	30,00	29,65	20,23
	MAX	35,43	38,22	29,90		36,11	40,51	32,79	24,93
Observatoire Cave *(S. hem)*	N=1	27,89	28,43	29,72	9,30	27,94	29,44	24,79	22,25
Prince Cave *(S. hem)*	MEAN (N=2)	30,68	33,33	30,24		34,75	32,72	27,55	22,88
	MIN	29,46	33,33	24,11		32,65	32,72	24,80	22,88
	MAX	31,90		36,37		36,85		30,29	
Prince Cave *(S. kirch)*	N=1	36,65	35,12	18,43			33,69	35,11	

Upper P3

(Figs. 5 and 6, Table 2)

The crochet is double on the majority of the upper P3 of *S. hundsheimensis* and single on the majority of the upper P3 of *S. hemitoechus* and *S. etruscus*. The crochet has always been observed to be multiple in *S. kirchbergensis*.

The crista is single or double in *S. hundsheimensis*. It is normally absent in *S. hemitoechus* (60 %) and *S. etruscus* (50 %) and always absent in *S. kirchbergensis*.

The antecrochet is rarely present in *S. hundsheimensis* (12,5 %). It is more present in *S. hemitoechus* (40 %). We never observed it in *S. kirchbergensis* or *S. etruscus*.

The mediofossette is open or closed in the same proportions in *S. hundsheimensis* and *S. hemitoechus*. It is always open in *S. kirchbergensis* and *S. etruscus*.

The angle between the crochet and the metacone is sharp to right-angled in *S. hundsheimensis* and *S. hemitoechus*. It is right-angled in *S. kirchbergensis* and *S. etruscus*.

The protocone constriction is only observable in *S. kirchbergensis*.

The vestibular and distal cingulum are absent in all the Pleistocene species. The mesial and lingual cingulum are present, strong, continuous and horizontal (*S. hemitoechus*) to slightly oblique (*S. hundsheimensis*).

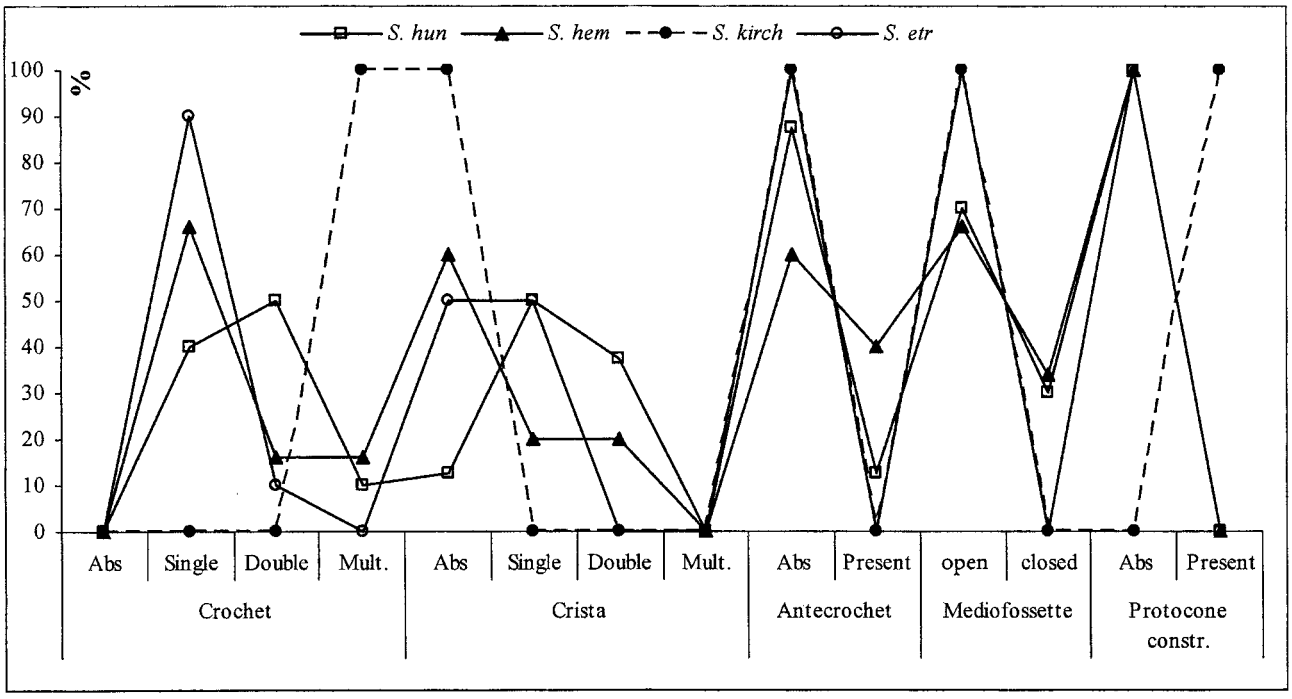

Fig. 5. Percentage distributions of qualitative character states for the upper P3 of the Pleistocene *Stephanorhinus*.

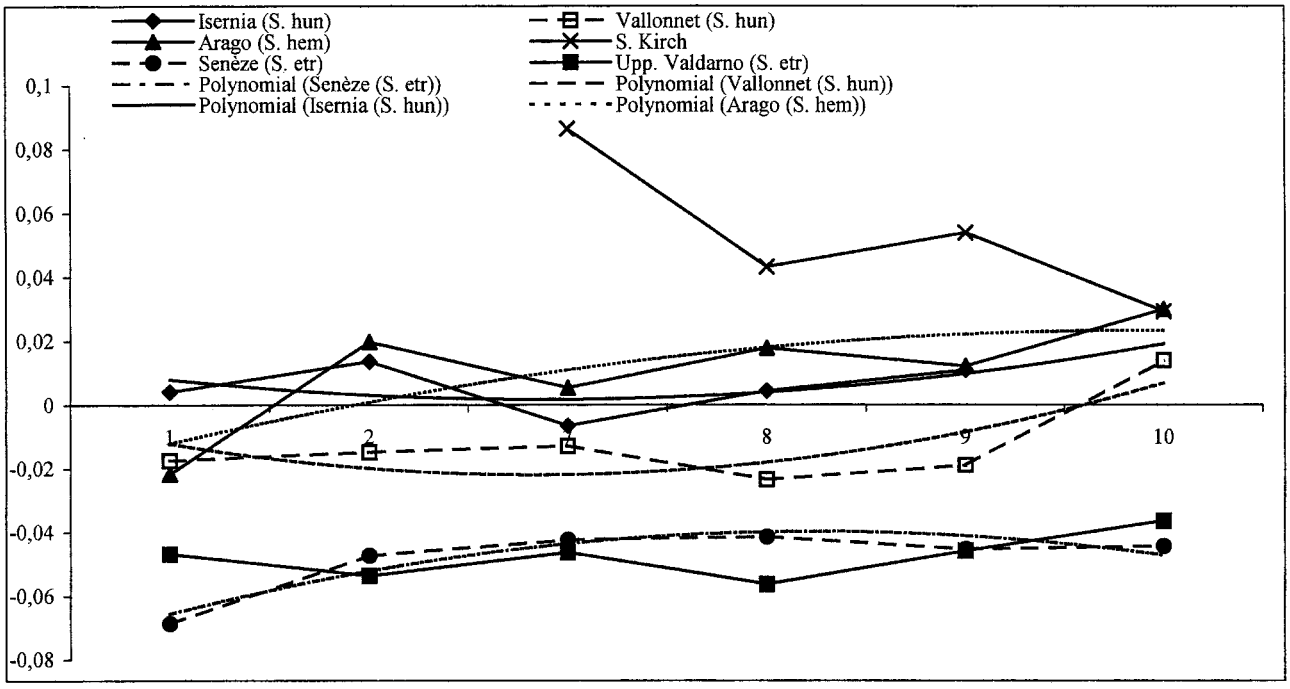

Fig. 6. Ratio diagram of the upper P3 of the Pleistocene *Stephanorhinus*. The referential is the present-day *Diceros bicornis*. *S. kirchbergensis* (data from FORTELIUS et al. 1993).

Table 2. Measurements (in mm) of the upper P3.

P3/ Measurement n°		1	2	5	6	7	8	9	10
Senèze *(S. etr)*	MEAN (N=4)	34,68	45,74			45,67	44,93	33,38	28,33
	MIN	34,27	45,15	13,04		45,12	44,60	32,60	27,20
	MAX	35,11	46,32	19,80		45,95	45,58	34,23	31,53
Upper Valdarno *(S. etr)*	N=1	36,47	45,07	22,33		45,26	43,42	33,34	28,86
Cagnes sur mer *(S. hun)*	MEAN (N=2)	39,77	47,84		14,12	48,08	44,22	35,90	30,55
	MIN	39,44	47,59	32,90	13,39	47,96	44,07	35,50	30,00
	MAX	40,09	48,08	35,00	14,85	48,20	44,37	36,30	31,09
Vallonnet *(S. hun)*	MEAN (N=12)	39,02	49,28		9,65	48,88	46,83	35,46	32,40
	MIN	36,30	47,83	15,11	8,23	47,88	44,25	33,28	30,44
	MAX	42,47	51,60	55,21	11,17	51,09	50,27	40,27	34,70
Isernia *(S. hun)*	MEAN (N=13)	41,00	52,62		14,92	49,93	49,59	37,99	
	MIN	34,93	49,72	19,00	12,66	48,44	48,47		
	MAX	45,00	55,40	46,90	17,17	51,42	50,72		
Soleilhac *(S. hun)*	MEAN (N=6)	42,22	52,84		13,61	52,32	51,25	37,66	33,42
	MIN	38,83	51,59	15,98	12,50	52,02	50,83	33,80	32,27
	MAX	44,23	54,09	28,17	14,73	52,63	51,67	40,03	34,10
Arago *(S. hem)*	MEAN (N=10)	38,64	53,37		12,92	50,97	51,49	38,10	33,62
	MIN	36,30	51,91	0,00	8,94		51,48	35,28	30,45
	MAX	41,06	54,82	54,89	17,67		51,50	39,94	37,29
Orgnac 3 *(S. hem)*	N=1	38,37	47,38	34,44		46,49	44,41	35,48	29,67
Mars Cave *(S. hem)*	N=1	43,43	47,00	51,94	16,37	48,16	42,47	39,63	32,85
Prince Cave *(S. hem)*	MEAN (N=3)	42,50	47,30		11,41	48,40	46,06	40,70	31,82
	MIN	40,80	46,00	35,66	9,90	48,33	44,39	39,16	31,03
	MAX	44,58	48,27	52,84	14,10	48,47	47,47	41,70	32,61
Prince Cave *(S. kirch)*	N=1	40,54	48,86	36,10	9,94	49,35		35,38	
Aldène *(S. kirch)*	N=1	42,95	49,15	44,02		51,64	50,23	38,22	35,41

The profiles of the vestibular wall are very different according to the species. The surface is waved and the paracone fold is thin and a little prominent in *S. hundsheimensis*. The shape is very irregular and the paracone fold is prominent in *S. hemitoechus*. The surface of the ectolophe is slightly convex, without a relief in *S. kirchbergensis* and its shape is similar in *S. etruscus*, although with a more developed paracone fold.

The biometrical data (Table 2) permits us to differentiate *S. kirchbergensis* from the other Pleistocene rhinoceros by the size and proportions.

S. hemitoechus, *S. hundsheimensis* and *S. etruscus* possess very similar upper P3, in absolute values. On the Simpson diagram (Fig. 6), the curve of *S. etruscus* is the lowest one. *S. hemitoechus* possesses a general size bigger than that of *S. etruscus/S. hundsheimensis*. To be able to differentiate these three different species, it is necessary to calculate the polynomial curve of tendency. *S. hundsheimensis* (Vallonnet and Isernia) presents a slightly concave curve. The polynomial curve of *S. etruscus* and *S. hemitoechus* presents a clear convex shape. *S. hundsheimensis* has a more developed upper P3 than *S. etruscus*, especially in its length. The hypsodonty index of this tooth is more important for the archaic forms than that of the more evolved forms, in the same way as on the P2. The hypsodonty index of the P3 is stronger in the Vallonnet (Early Pleistocene) material than that from Isernia (early Middle Pleistocene), as is the case for the Arago cave (Middle Pleistocene) material compared with that of the Observatoire cave and the Prince cave (Upper Pleistocene).

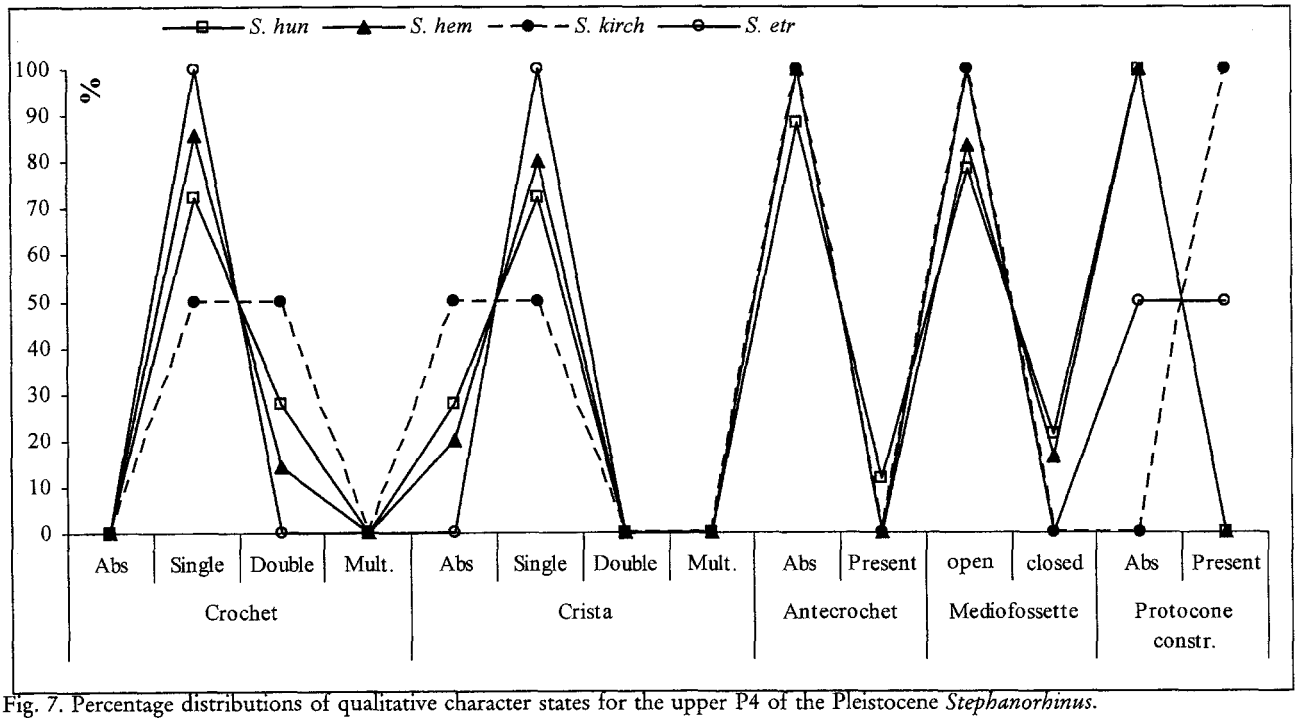

Fig. 7. Percentage distributions of qualitative character states for the upper P4 of the Pleistocene *Stephanorhinus*.

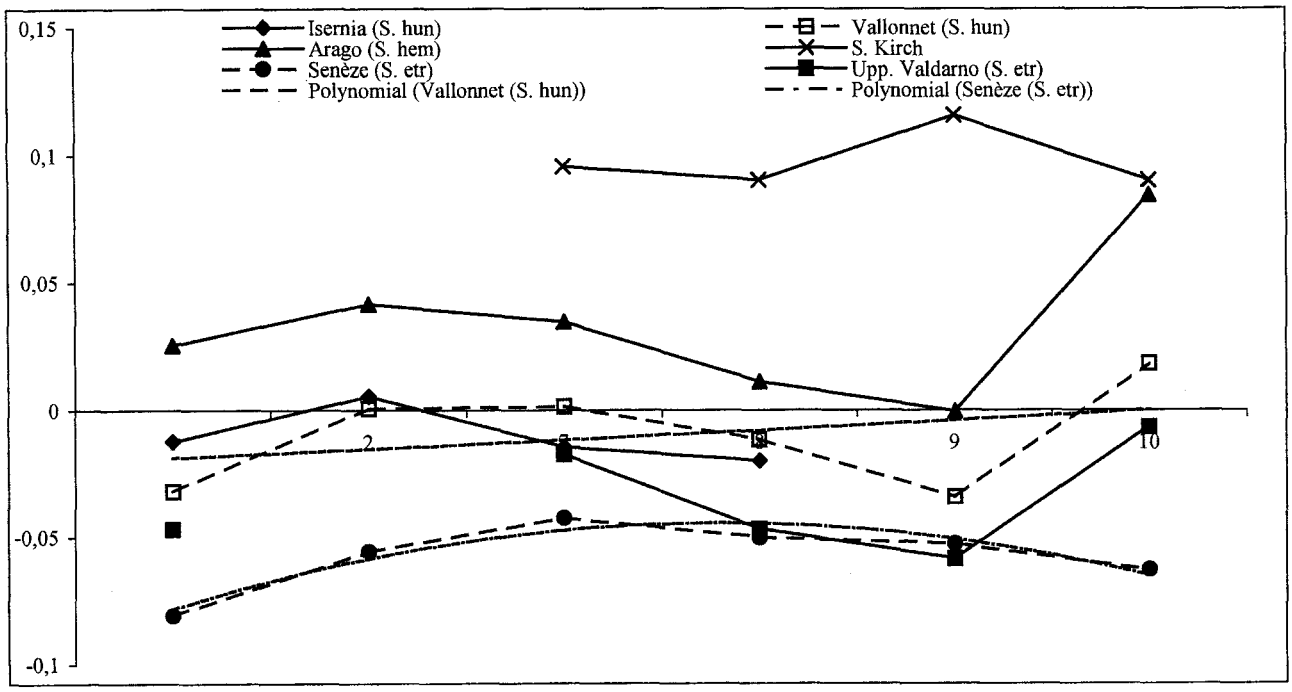

Fig. 8. Ratio diagram of the upper P4 of the Pleistocene *Stephanorhinus*. The referential is the present-day *Diceros bicornis*. *S. kirchbergensis* (data from FORTELIUS et al. 1993)

Table 3. Measurements (in mm) of the upper P4.

P4/ Measurement n°		1	2	5	6	7	8	9	10
Senèze *(S. etr)*	MEAN (N=4)	37,09	48,77			50,00	46,67	37,12	30,02
	MIN	35,00	48,12	14,09		48,92	45,59	34,80	29,30
	MAX	39,71	49,41	17,00		51,07	47,74	40,22	31,03
Upper Valdarno *(S. etr)*	N=1	40,10		25,09		52,96	47,03	36,63	34,18
Cagnes-sur-mer *(S. hun)*	MEAN (N=2)	39,07	49,59		14,41	50,47	44,96	38,98	31,50
	MIN	39,02	49,50	37,34	14,40	49,98	43,93	38,52	30,90
	MAX	39,11	49,67	38,94	14,42	50,96	45,98	39,43	32,10
Sainzelles *(S. hun)*	MEAN (N=2)	40,67							34,64
	MIN	40,41		32,10					34,54
	MAX	40,92		33,60					34,74
Vallonnet *(S. hun)*	MEAN (N=12)	41,50	55,50		11,89	55,31	50,99	38,72	36,17
	MIN	37,77	50,42	5,51	9,82	49,56	47,46	35,90	32,62
	MAX	43,89	60,26	42,22	13,30	60,08	53,20	42,85	39,90
Isernia *(S. hun)*	MEAN (N=17)	43,41	56,10		17,71	53,32	50,02		
	MIN	39,80	52,95	20,40	14,00	50,16	48,47		
	MAX	49,87	57,90	48,31	21,17	55,57	51,77		
Soleilhac *(S. hun)*	MEAN (N=3)	43,88	57,07		17,69	57,54	55,86	41,43	34,80
	MIN	42,72		16,79				40,76	
	MAX	45,04	57,07	25,90	17,69	57,54	55,86	42,09	34,80
Arago *(S. hem)*	MEAN (N)14)	47,37	60,97			59,71	53,75	41,85	42,14
	MIN	42,72	60,46	0,00		58,73	50,66	35,65	40,86
	MAX	52,53	61,48	61,13		60,68	56,13	46,16	43,31
Orgnac 3 *(S. hem)*	N=1	47,10	59,48	46,39					
Mars Cave *(S. hem)*	MEAN (N=2)	42,93	55,28				47,43	42,12	36,57
	MIN	42,91	55,28	65,86	15,20	54,72	47,33	41,85	36,57
	MAX	42,94		65,67			47,52	42,38	
Prince Cave *(S. hem)*	MEAN (N=3)	48,97	54,12		14,30	58,00	52,49	44,52	39,13
	MIN	43,16	54,12	43,12	9,25	53,19	46,66	39,69	35,81
	MAX	52,85	54,21	48,98	19,34	60,54	55,00	46,64	40,47
Prince Cave *(S. kirch)*	N=1	44,97	53,32	33,39		52,40	44,05		
Aldène *(S. kirch)*	N=1		55,81	50,89	16,61				

Upper P4

(Figs. 7 and 8, Table 3)

The crochet is always single on the P4 of *S. etruscus*. It is single or double in the other species but in different proportions (Fig. 7).

The crista is as often present as absent in *S. kirchbergensis*. It is normally absent in *S. hemitoechus* and *S. hundsheimensis*. It is always present in *S. etruscus*.

The antecrochet is only present on 11,8 % of the observation on the upper P4 of *S. hundsheimensis*. This internal fold is absent in *S. etruscus*, *S. hemitoechus* and *S. kirchbergensis*.

The mediofossette is closed in nearly 20 % of the observations in *S. hundsheimensis* and *S. hemitoechus*. It is always open in *S. etruscus* and *S. kirchbergensis*.

The angle between the crochet and the metacone is sharp to right-angled in *S. hundsheimensis* and *S. hemitoechus*. It is right-angled in *S. etruscus* and *S. kirchbergensis*.

The protocone constriction is always observable in *S. kirchbergensis* and can be present (50 %) on the upper P4 of *S. etruscus.*

The mesial cingulum can be absent in *S. hundsheimensis* and *S. hemitoechus*. The distal cingulum is absent in all the Pleistocene species. The lingual cingulum is absent in *S. kirchbergensis*, and may be present or absent in *S. hemitoechus*. Its absence becomes rare in *S. hundsheimensis* and in *S. etruscus.*

The profile of the vestibular wall is slightly convex with a paracone fold, lightly marked in *S. etruscus*. It becomes wavy with a thin and lightly prominent paracone fold in *S. hundsheimensis*. *S. kirchbergensis* has a general shape similar to this last species, without a paracone fold. *S. hemitoechus* presents a very wavy vestibular wall profile, the paracone fold is marked.

The proportions (Fig. 8) easily isolate *S. kirchbergensis*. On the Simpson diagram, *S. hemitoechus* has proportions wich are very close to *S. etruscus* and *S. hundsheimensis*, but it begins to differ with a larger size (Table 3). *S. hundsheimensis* and *S. etruscus* are very similar (even though the size of *S. etruscus* is slightly smaller, the proportions are very similar). Only their polynomial curves of tendency with an inverse shape can differentiate them. One can also note that the differences between the *S. hundsheimensis* of the Middle Pleistocene and the Early Pleistocene are imperceptible on the graphic representation.

The hypsodonty index of the upper P4 does not follow the same rule of that from one of the two first premolars. The indications are more important on the more recent forms. The hypsodonty index of *S. hundsheimensis* is more important in Isernia (early Middle Pleistocene) material than in that from the Vallonnet cave (Early Pleistocene). In the same way the hypsodonty index of the upper P4 of *S. hemitoechus* is greater at the end of the Middle Pleistocene (Mars cave) than in that of the Middle Pleistocene (Caune de l'Arago).

Upper M1

(Figs. 9 and 10, Table 4)

The crochet is variably single or double in *S. hemitoechus*, whereas it is always single in the other species.

The crista is very variable: absent, single or double.

The antecrochet is generally absent, and only present in (29,4 %) of *S. hundsheimensis* specimens.

The mediofossette is closed in 18,8 % of the upper M1 of *S. hundsheimensis*. It is always open in the other species.

The protocone constriction is present in *S. etruscus*, it can exist in *S. hemitoechus* (34 %) and becomes rare in *S. hundsheimensis* (13,1 %). It is absent in *S. kirchbergensis.*

The mesial cingulum is present in all the Pleistocene species, but can be absent in *S. hundsheimensis.*

The other cingula are absent, but *S. hundsheimensis* sometimes presents a lingual cingulum. The paracone fold is broad and lightly prominent in *S. hundsheimensis*, and is thinner in *S. etruscus* and very marked in *S. hemitoechus*. The profile of the vestibular wall of *S. kirchbergensis* is a succession of very light curling without a marked relief.

The biometrical data (Table 4) easily isolates *S. kirchbergensis* by its size and its proportions (Fig. 10). *S. hemitoechus* presents specific proportions and size. Its curve is close to the one of *S. hundsheimensis* from the Middle Pleistocene (Isernia). Their respective polynomial curves of tendency differentiate them: it is convex for *S. hemitoechus*, concave to sub-straight for *S. hundsheimensis* of the Middle Pleistocene. *S. hundsheimensis* of the Early Pleistocene and *S. etruscus* are always very similar. Their polynomial curve of tendency differentiates them: it is concave for *S. hundsheimensis* and convex for *S. etruscus*. The hypsodonty index cannot be calculated on the upper M1 of *S. hundsheimensis* of the Middle Pleistocene and on the upper M1 of *S. hemitoechus* of the Upper Pleistocene because of the advanced wear of this tooth. We therefore cannot discern on this tooth if it follows the rule observed on the P4.

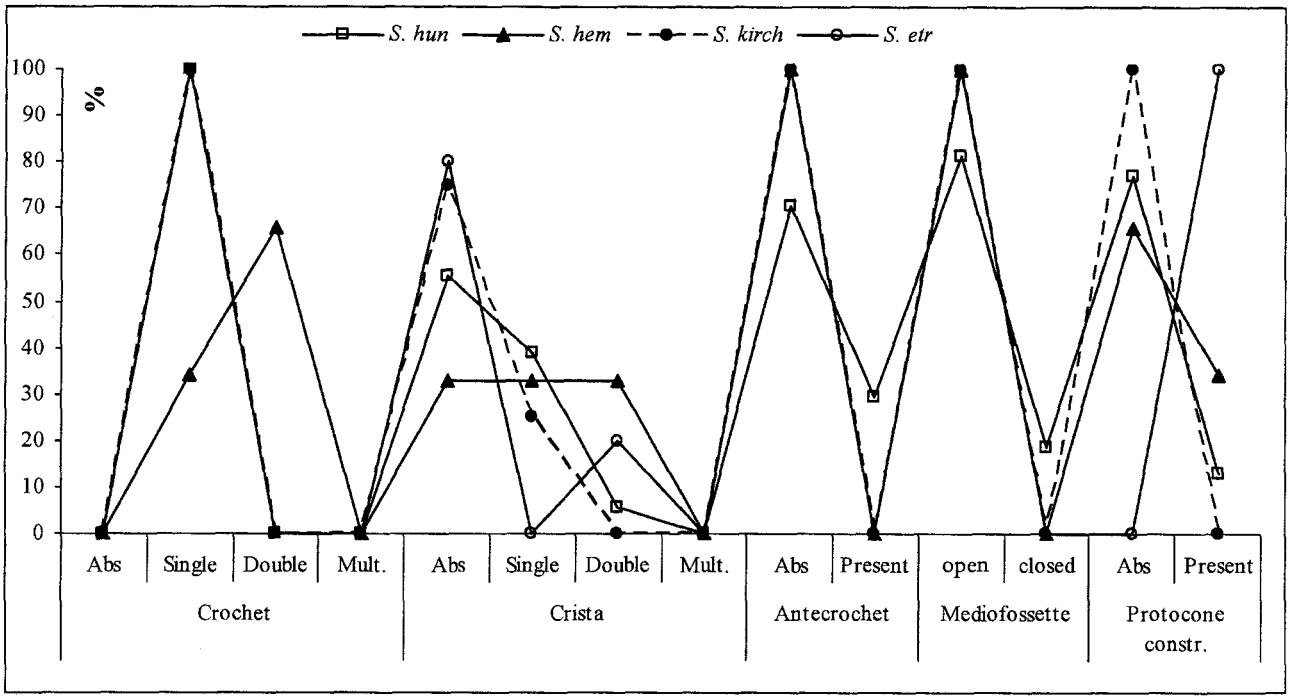

Fig. 9. Percentage distributions of qualitative character states for the upper M1 of the Pleistocene *Stephanorhinus*.

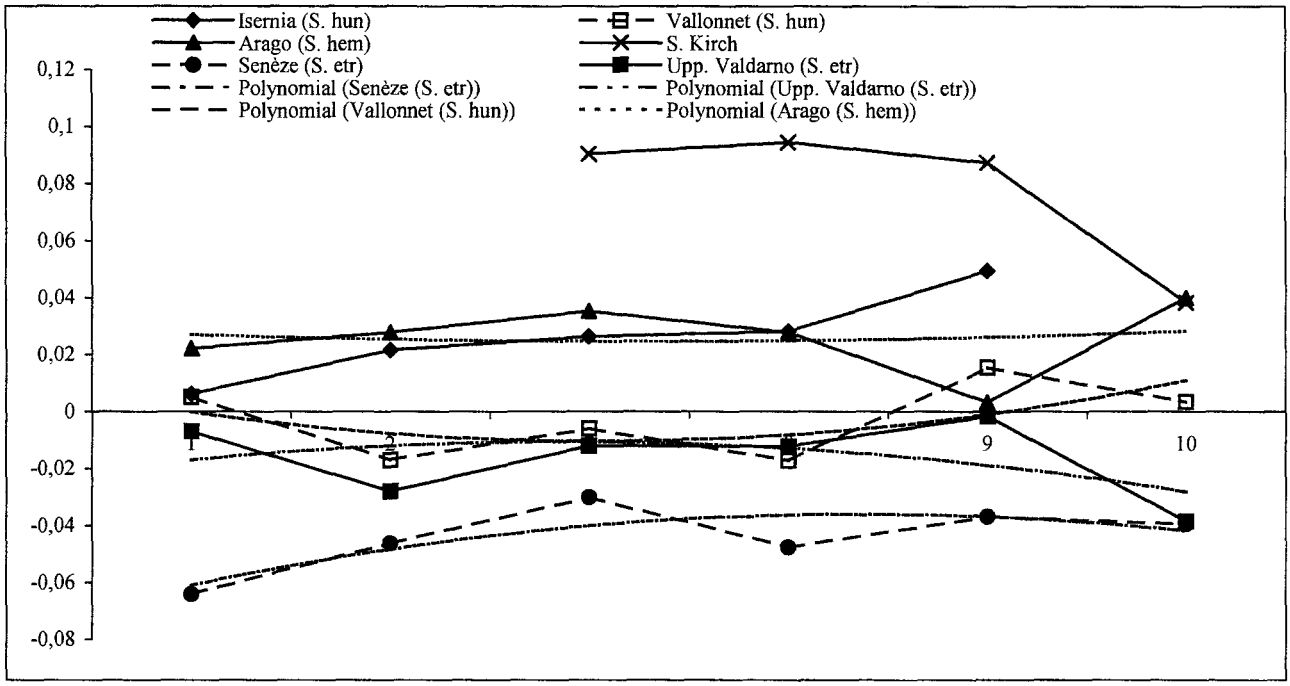

Fig. 10. Ratio diagram of the upper M1 of the Pleistocene *Stephanorhinus*. The referential is the present-day *Diceros bicornis*. *S. kirchbergensis* (data from FORTELIUS et al. 1993).

Table 4. Measurements (in mm) of the upper M1.

M1/ Measurement n°		1	2	5	6	7	8	9	10
Senèze *(S. etr)*	MEAN (N=3)	43,63	51,28			52,04	46,48	41,03	35,80
	MIN	41,90	50,51	9,84		51,45	46,47	40,05	35,40
	MAX	45,34	52,05	14,53		52,62	46,49	41,84	36,47
Upper Valdarno *(S. etr)*	MEAN (N=5)	49,10	53,48	34,59	17,31	54,26	50,43	44,54	35,79
	MIN	44,92	51,15	19,32	15,45	50,58	47,90	39,38	33,77
	MAX	53,26	56,95	55,82	19,30	58,03	52,97	49,64	38,12
Cagnes-sur-mer *(S. hun)*	MEAN (N=2)	44,54	51,95		18,53	56,10	53,13	41,47	35,11
	MIN	44,26	51,62	36,43	17,56	55,60	52,80	41,00	35,02
	MAX	44,81	52,28	37,08	19,49	56,59	53,46	41,93	35,20
Sainzelles *(S. hun)*	MEAN (N=3)				18,53				36,23
	MIN			28,80	17,76	55,82			35,76
	MAX				19,22				36,84
Vallonnet *(S. hun)*	MEAN (N=20)	50,48	54,85		16,60	55,02	49,86	46,32	39,41
	MIN	46,98	51,56	16,21	12,68	52,15	44,88	43,05	37,08
	MAX	54,80	58,50	55,62	20,34	58,36	53,14	52,54	44,17
Isernia *(S. hun)*	MEAN (N=16)	50,62	59,93		20,31	59,27	55,34	50,09	
	MIN	46,70	57,00	5,15	19,57	58,00	54,31		
	MAX	53,00	61,92	52,40	21,04	60,53	56,36		
Soleilhac *(S. hun)*	N=1	50,77		25,30	18,43			47,10	38,52
Arago *(S. hem)*	MEAN (N=12)	52,50	60,80		18,49	60,50	55,30	43,90	42,87
	MIN	49,88	58,77	0,00	16,55	57,47	50,28	40,14	
	MAX	55,45	62,82	62,77	20,43	64,76	61,54	50,59	
Orgnac 3 *(S. hem)*	MEAN (N=2)	51,90	60,05	51,43	17,15	59,16	52,05	48,53	36,90
	MIN	51,00	57,10	38,28	13,70	55,03	50,10	47,31	34,30
	MAX	52,80	63,00	64,58	20,60	63,29	54,00	49,75	39,50
Prince Cave *(S. kirch)*	N=1	54,27	55,92	46,18	16,22	55,68	48,05	51,17	41,74
Aldène *(S. kirch)*	N=1	62,89	65,48	51,89		66,27		58,50	49,30

Upper M2

(Figs. 11 and 12, Table 5)

The crochet is always single (Fig. 11). A few rare specimens of *S. hundsheimensis* present a double crochet (5,3 %).

The crista is absent on most of the upper M2 of *S. hundsheimensis* (55,6 %) and *S. etruscus* (80 %), otherwise it is respectively single or double. When it is present (40 %) it is always single in *S. hemitoechus* and always exists in *S. kirchbergensis.*

The antecrochet is absent in *S. etruscus*, it can be observed in *S. hundsheimensis* (26,7 %); it becomes very frequent in *S. hemitoechus* (40 %) and always exists on the upper M2 of *S. kirchbergensis.*

The protocone constriction is present in *S. etruscus*; it becomes less frequent in *S. hundsheimensis* (45,5 %) and rare in *S. hemitoechus* (16 %). It does not exist in *S. kirchbergensis.*

The mesial cingulum is present in all the Pleistocene species. The distal cingulum is absent; it can, occasionally to be observed in *S. hundsheimensis.* The lingual cingulum is normally absent; it persists on the upper M2 of *S. hundsheimensis.* The vestibular cingulum is absent.

The protocone fold of the upper M2 is broad and lightly prominent in *S. etruscus*, it becomes prominent in *S. hundsheimensis* and very prominent in *S. hemitoechus.* The profile of the vestibular wall of *S. kirchbergensis* presents light curling without distinct relief.

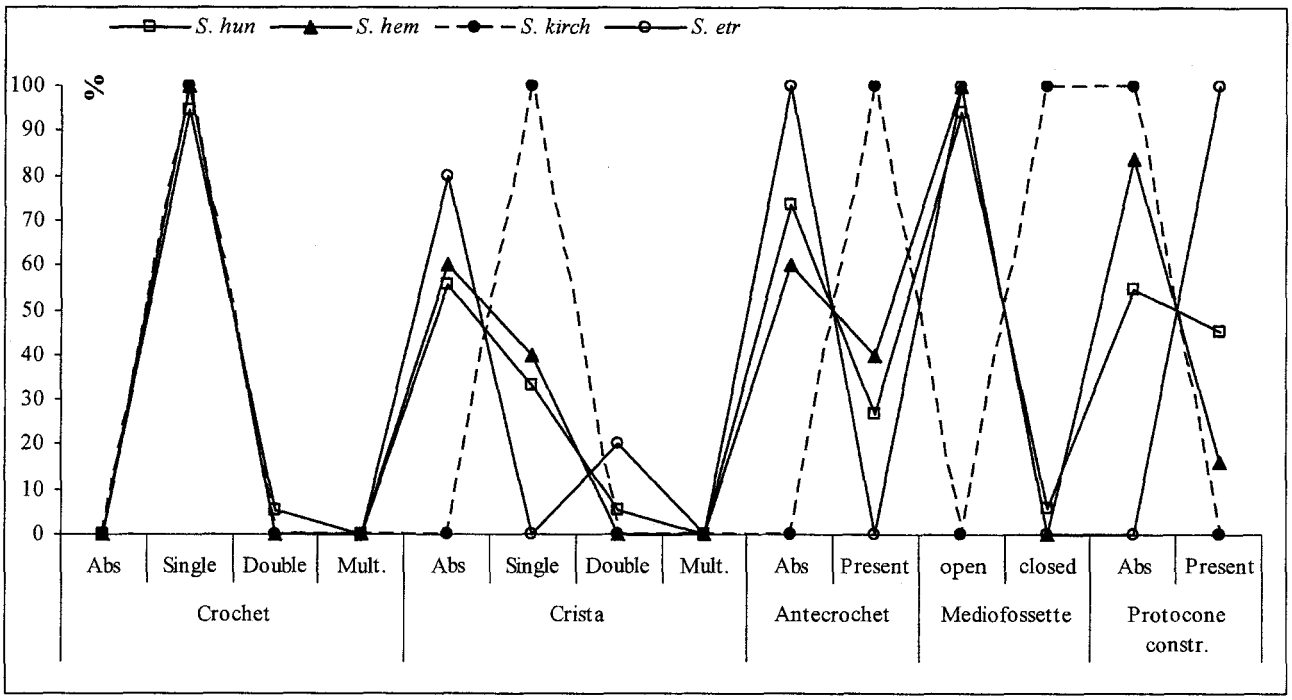

Fig. 11. Percentage distributions of qualitative character states for the upper M2 of the Pleistocene *Stephanorhinus*.

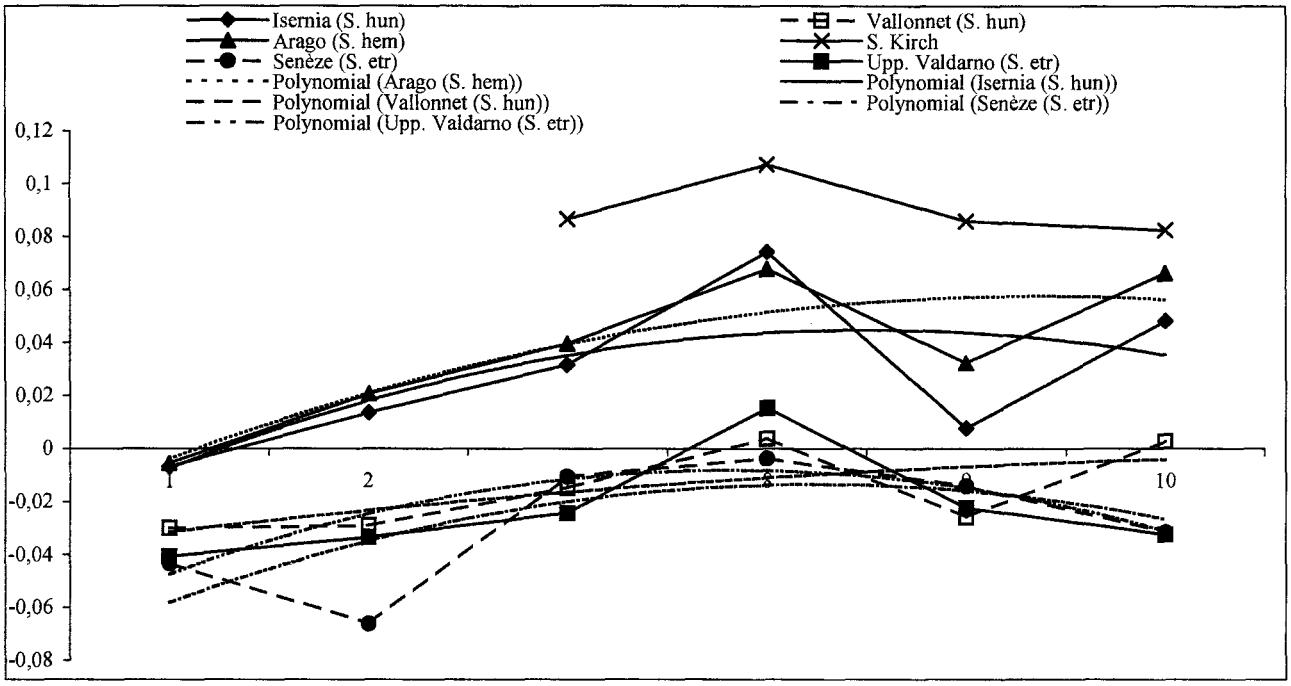

Fig. 12. Ratio diagram of the upper M2 of the Pleistocene *Stephanorhinus*. The referential is the present-day *Diceros bicornis*. *S. kirchbergensis* (data from FORTELIUS et al. 1993).

Table 5. Measurements (in mm) of the upper M2.

M2/ Measurement n°		1	2	5	6	7	8	9	10
Senèze *(S. etr)*	MEAN (N=4)	49,97				55,79	48,02	47,69	40,91
	MIN	48,45		16,76		54,80	47,77	46,00	37,50
	MAX	51,94		24,40		56,77	48,26	49,93	45,20
Upper Valdarno *(S. etr)*	MEAN (N=2)	50,53	56,09		15,84	55,37	51,39	47,35	38,92
	MIN	49,60	52,43	27,47		51,98	50,98	45,33	38,91
	MAX	51,46	59,74	44,74		58,75	51,80	49,37	38,92
Cagnes-sur-mer *(S. hun)*	MEAN (N=2)	50,10	54,41		18,47	52,23	45,78	48,78	38,94
	MIN	49,80	54,40	41,08	17,92	52,20	45,55	48,26	38,38
	MAX	50,40	54,42	43,00	19,01	52,26	46,00	49,30	39,50
Sainzelles *(S. hun)*	N=1	50,90	56,99	35,83	20,01	56,46		48,96	44,98
Vallonnet *(S. hun)*	MEAN (N=18)	51,78	56,65		15,18	56,59	50,05	46,98	42,20
	MIN	46,83	53,97	7,53	10,26	53,67	46,22	43,78	40,35
	MAX	55,30	60,12	53,58	17,00	60,44	52,80	50,91	44,38
Isernia *(S. hun)*	MEAN (N=8)	54,64	62,50		21,93	62,98	58,86		
	MIN	53,00	60,60	20,80	18,75	62,25	54,76		
	MAX	56,35	67,40	44,00	25,10	63,70	62,95		
Soleilhac *(S. hun)*	N=1	57,47	61,26	35,27	18,00	60,45	58,20	50,76	46,86
Arago *(S. hem)*	MEAN (N=13)	54,80	63,55		23,06	64,16	58,00	53,72	48,85
	MIN	50,92	60,81	10,20	18,72	60,33	52,73	49,80	45,21
	MAX	57,23	66,92	61,71	26,71	67,86	62,67	58,18	52,97
Orgnac 3 *(S. hem)*	N=1	58,67		61,97					
Mars Cave *(S. hem)*	N=1	58,17	62,37	64,96	16,30	61,13	51,08	57,53	43,45
Prince Cave *(S. hem)*	N=1	60,03		52,07	17,63			55,14	
Prince Cave *(S. kirch)*	N=1	61,33	63,56	49,17	20,12	62,06	52,77	57,04	46,39

The upper M2 of *S. hemitoechus* and *S. kirchbergensis* differentiate themselves distinctly by their proportions (Fig. 12) and their size. *S. hundsheimensis* of the Early Pleistocene and *S. etruscus* remain similar, but their polynomial curves of tendency are different, nearly right for the first named and extensively convex for the second. *S. hundsheimensis* of the Middle Pleistocene and *S. hemitoechus* are inseparable in the Simpson diagram. The absolute values of the biometrical measurements space out the different species according to their size (Table 5). The hypsodonty index of the M2 from *S. hemitoechus* is greater at the end of the Middle Pleistocene (Mars cave) than that of the Middle Pleistocene (Caune de l'Arago). This observation is not possible in Middle Pleistocene forms of *S. hundsheimensis* owing to advanced wear of the studied teeth.

Upper M3

(Figs. 13 and 14, Table 6)

The crochet is always single on the upper M3 of the Pleistocene rhinoceroses.

The crista is single on most of the upper M3 of *S. hundsheimensis* and *S. kirchbergensis*, but it can be also absent. It is normally absent in *S. etruscus* (75 %). It is always absent on the upper M3 of *S. hemitoechus.*

On the upper M3 of *S. kirchbergensis* and *S. hemitoechus*, the frequency of the presence of the antecrochet is important, whereas in the other two species this internal fold is more occasional.

The mediofossette is always open in *S. etruscus*, but it is unusually closed in *S. hundsheimensis* (15,4 %). It is closed on most of the upper M3 of *S. kirchbergensis* (66 %) and of *S. hemitoechus* (80 %).

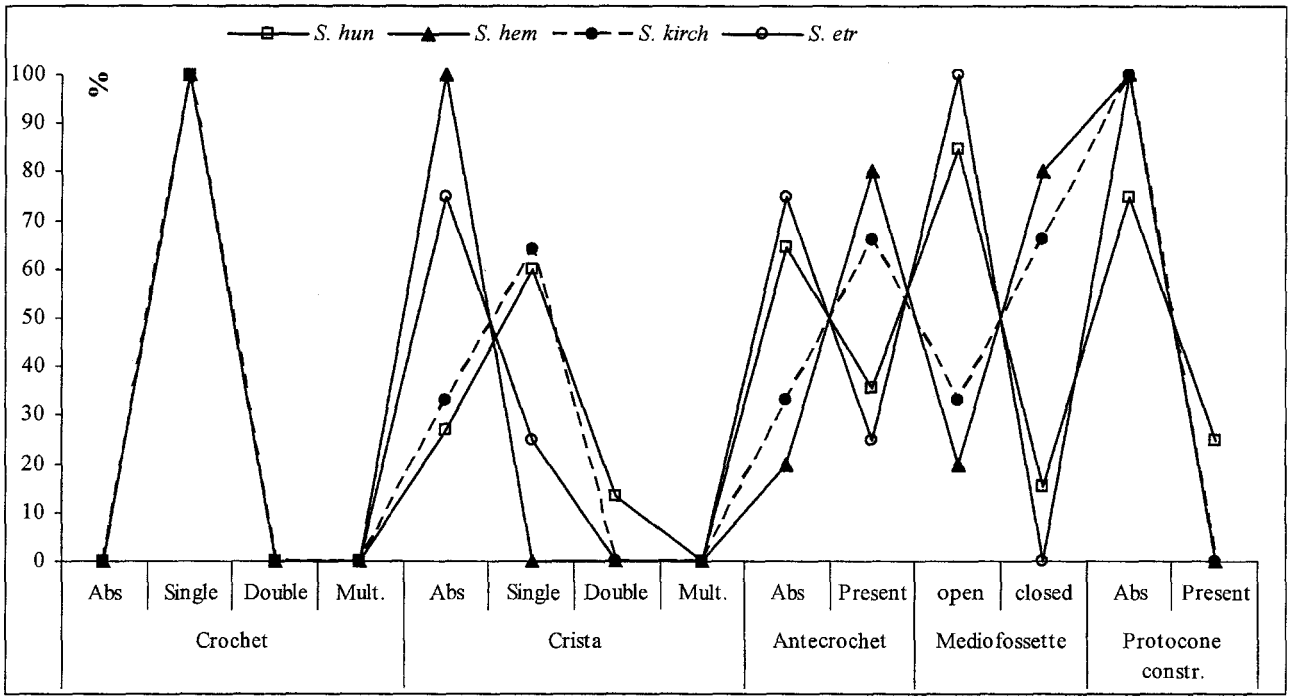

Fig. 13. Percentage distributions of qualitative character states for the upper M3 of the Pleistocene *Stephanorhinus*.

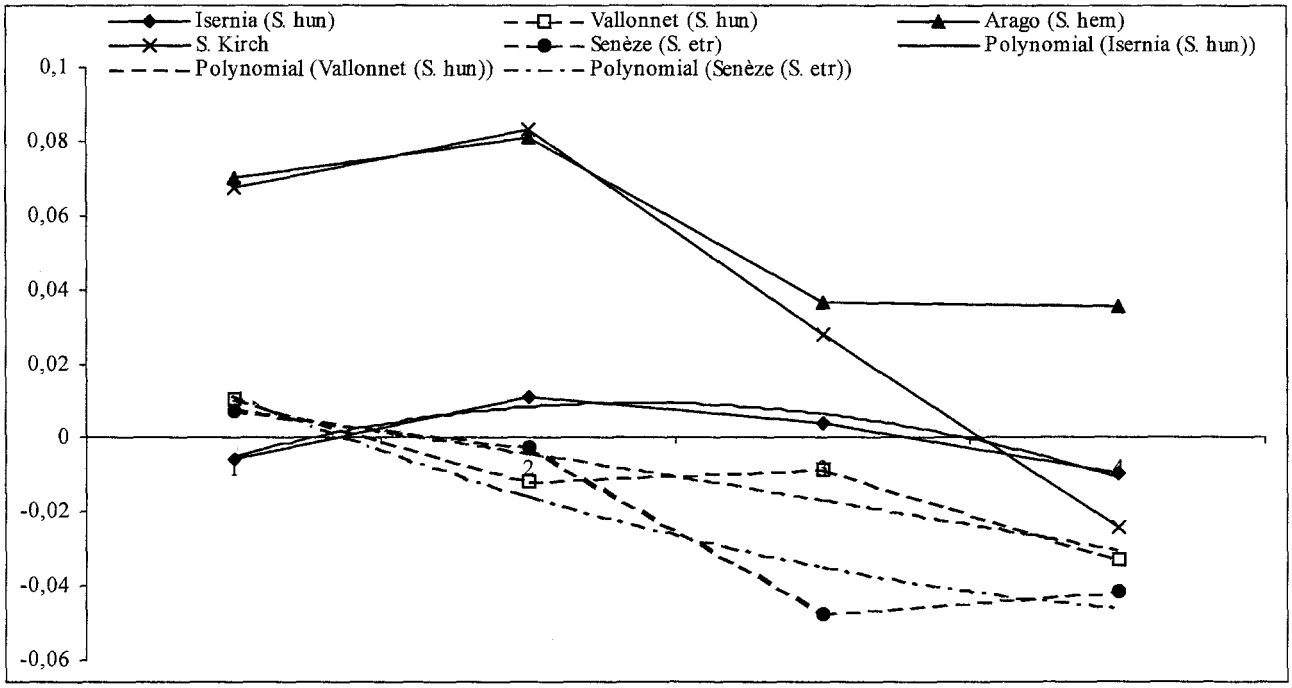

Fig. 14. Ratio diagram of the upper M3 of the Pleistocene *Stephanorhinus*. The referential is the present-day *Diceros bicornis*. *S. kirchbergensis* (data from FORTELIUS et al. 1993).

Table 6. Measurements (in mm) of the upper M3.

M3/ Measurement n°		L ana	L abs	l ana	l abs	H
Senèze *(S. etr)*	MEAN (N=4)	51,84	54,41	43,17	47,72	
	MIN	49,48	53,84	42,85	47,61	27,30
	MAX	52,90	55,79	43,85	47,82	30,40
Cagnes-sur-Mer *(S. hun)*	MEAN (N=2)	49,55	52,87	46,56	45,38	
	MIN	48,53	51,71	45,13	44,51	44,00
	MAX	50,56	54,03	47,98	46,25	44,12
Sainzelles *(S. hun)*	MEAN (N=2)	49,35	53,54	45,71	51,23	
	MIN	49,35	53,54	45,23	50,01	38,80
	MAX			46,18	52,45	40,24
Vallonnet *(S. hun)*	MEAN (N=7)	52,24	53,27	47,20	48,70	
	MIN	49,98	50,68	39,09	43,62	25,32
	MAX	54,94	55,39	49,84	51,78	42,92
Tour de Grimaldi *(S. hun)*	N=1			45,71	46,89	39,86
Isernia *(S. hun)*	MEAN (N=11)	50,32	56,14	48,58	51,34	
	MIN	45,50	52,40	44,57	46,45	19,30
	MAX	55,20	60,40	56,40	58,10	51,40
Soleilhac *(S. hun)*	MEAN (N=2)	50,90	53,42	50,04	44,17	
	MIN	50,90	53,42	46,83	43,87	28,11
	MAX			53,25	44,47	34,27
Arago *(S. hem)*	MEAN (N=15)	59,94	65,92	52,41	56,98	32,09
	MIN	52,83	58,67	46,10	48,77	5,43
	MAX	65,82	73,20	59,17	63,84	57,47
Barma Grande *(S. hem)*	MEAN (N=3)			47,22		
	MIN			46,57		31,70
	MAX			47,86		42,00
Prince Cave *(S. kirch)*	MEAN (N=5)	59,59	66,27	51,37	49,68	
	MIN	55,86	60,05	47,24	46,69	44,69
	MAX	63,60	73,49	52,92	52,41	65,32

The angle between the crochet and the metacone is variable in *S. hundsheimensis* and *S. hemitoechus*. It is obtuse to right-angled in *S. kirchbergensis* and always right-angled in *S. etruscus*.

The protocone constriction is absent on the M3, it can only be seen rarely in *S. hundsheimensis*. The mesial cingulum is always present. The other cingula are absent or can be replaced by stylii. The paracone fold of the M3 is broad and prominent in *S. hundsheimensis* and *S. hemitoechus*, it is thinner in *S. etruscus* and slightly marked in *S. kirchbergensis*.

S. hemitoechus and *S. kirchbergensis* present some different proportions (Fig. 14). The first one possesses a developed upper M3, whereas the second possesses a rather narrower M3. *S. etruscus* and *S. hundsheimensis* always have a similar shape to their respective curve. One can note a difference in the two breadths (measurements 3 and 4) distinctly greater in *S. hundsheimensis*. These breadths are the inflection point of the curve of tendency of *S. etruscus*, slightly concave. The curve of tendency of the *S. hundsheimensis* is straight or convex. The absolute dimensions (Table 6) isolate the M3 of *S. hemitoechus* by their size. *S. kirchbergensis* possesses an intermediate position between *S. hundsheimensis* and *S. hemitoechus*. The curve of *S. hundsheimensis* is close to the curve of *S. etruscus*. The hypsodonty index of the M3 of *S. hundsheimensis* is greater at the beginning of the Middle Pleistocene (Isernia) than in the Early Pleistocene (Vallonnet cave). This result was not confirmed in *S. hemitoechus* due to the advanced wear of the teeth.

Upper D1

(Fig. 15, Table 7)

The crochet is normally single on the upper D1 of the Pleistocene rhinoceroses. It is occasionally double or multiple in *S. hundsheimensis*. It can be absent in *S. etruscus.*

The crista can be double in *S. hundsheimensis* and *S. etruscus*, absent in *S. hemitoechus.*

The antecrochet is absent on the upper D1 of *S. hemitoechus*, it can be observed in *S. hundsheimensis*, it is more rare in *S. etruscus.*

The mediofossette is open or closed without any marked tendency.

The angle between the crochet and the metacone is right-angled in *S. etruscus* and *S. hemitoechus*; it can be, in the same proportions, obtuse in *S. hundsheimensis*. The protocone constriction is absent on the upper D1 of the Pleistocene rhinoceroses.

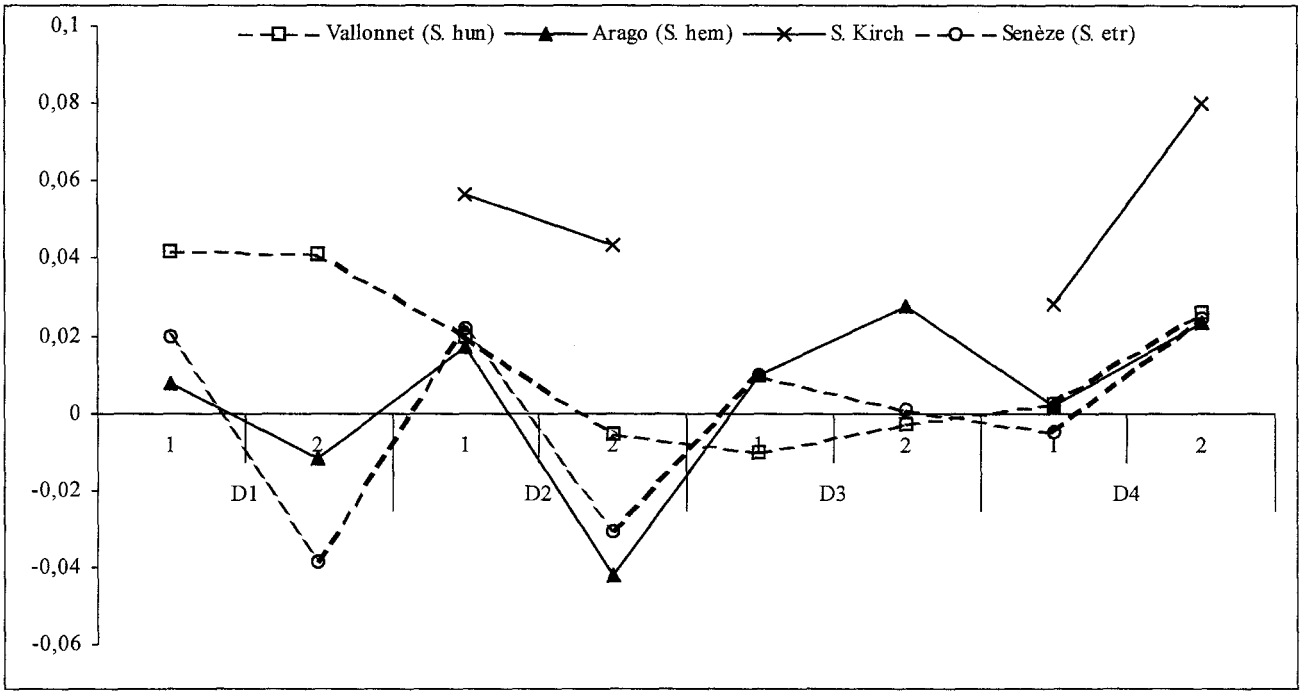

Fig. 15. Ratio diagram of the upper milk teeth of the Pleistocene *Stephanorhinus*. The referential is the present-day *Diceros bicornis*.

Table 7. Measurements (in mm) of the upper D1.

D1/ Measurement n°		1	2	5	6	8	9	10
Senèze *(S. etr)*	MEAN (N=2)	24,60	19,87					
	MIN	23,76	18,58	11,00				
	MAX	25,44	21,16	13,21				
Upper Valdarno *(S. etr)*	MEAN (N=3)	26,96	23,12	22,27		23,46	27,32	17,84
	MIN	26,43	21,58	21,84		21,67	25,31	15,54
	MAX	27,48	24,83	22,57		25,79	28,96	20,13
Vallonnet *(S. hun)*	MEAN (N=14)	25,88	23,87		6,71	23,88	23,87	18,85
	MIN	22,84	20,90	11,93	4,09	20,96	21,50	17,50
	MAX	31,35	27,29	21,14	8,61	27,12	26,75	20,64
Arago *(S. hem)*	MEAN (N=9)	23,92	21,12		21,30	19,73	19,10	18,31
	MIN	19,70	18,45	14,77				18,21
	MAX	28,79	22,34	22,85				18,40

The biometrical data bring the upper D1 of *S. hemitoechus* closer in proportions and in size to that of *S. etruscus*. *S. hundsheimensis* has some large D1s, compared with these last two species, and its characteristic proportions are specific (Fig. 15).

Upper D2

(Fig. 15, Table 8)

The crochet is normally single. It is more variable in *S. hundsheimensis* where it can take all the different shapes.

The crista is always single. It can only be double on the upper D2 of *S. hundsheimensis* and *S. etruscus*.

The antecrochet is absent, it can be observed in *S. hundsheimensis*.

The mediofossette is closed; it is unusually open in *S. hemitoechus*.

The angle crochet/metacone is very variable in *S. hemitoechus*, it is obtuse in *S. kirchbergensis* and right-angled in *S. etruscus*. *S. hundsheimensis* presents an intermediate angle between these two last.

Biometrical data (Table 8) and proportions (Fig. 15) isolate *S. kirchbergensis*. The three other rhinoceros species present very similar proportions. However, the upper D2 of *S. hundsheimensis* are slightly larger.

Upper D3

(Fig. 15, Table 9)

The crochet is single or double in *S. hundsheimensis* and more often single in *S. etruscus*. It can be unusually multiple in *S. hemitoechus*.

The crista is mostly present on the upper D3 of *S. hemitoechus*, it is variably present or absent in *S. etruscus* and *S. hundsheimensis*.

The antecrochet is normally absent on the upper D3 of the Pleistocene rhinoceroses, but can be observed in *S. etruscus*.

The mediofossette is more often closed in *S. hemitoechus* and *S. hundsheimensis*. It is open in a more constant way in *S. etruscus*.

The angle between the crochet and the metacone is variable.

The protocone constriction can be observed in *S. etruscus* and *S. hundsheimensis*. It is more rare in *S. hemitoechus*.

The biometrical data (Table 9) do not show a clear differentiation between the Pleistocene rhinoceroses on this tooth. The curves of the Simpson diagram (Fig. 15) are very close, and the differences in proportions are indiscernible for this tooth.

Table 8. Measurements (in mm) of the upper D2.

D2/Measurement n°		1	2	5	7	8	9	10
Senèze (*S. etr*)	MEAN (N=2)	35,02	33,18			31,58	32,89	30,34
	MIN	35,02	33,18	12,72		31,50	32,42	29,62
	MAX			16,60		31,66	33,36	31,05
Upper Valdarno (*S. etr*)	MEAN (N=4)	37,28	34,60	24,77	34,57	35,25	36,82	27,34
	MIN	36,35	31,86	23,06	32,50	33,51	35,45	25,31
	MAX	38,05	36,81	26,48	36,80	36,73	38,90	29,15
Vallonnet (*S. hun*)	MEAN (N=5)	34,86	35,15		32,13	35,37	32,08	29,35
	MIN	33,18	34,35	16,34	30,72	34,93	30,65	28,30
	MAX	37,03	36,63	21,32	33,19	36,1	35,62	30,48
Arago (*S. hem*)	MEAN (N=9)	34,62	32,32					
	MIN	31,72	29,68	17,23				
	MAX	37,63	34,20	28,59				
Orgnac 3 (*S. hem*)	N=1	36,23	32,02	29,42				
Aldène (*S. kirch*)	N=1	37,92	39,33	20,55	16,38	35,18	38,50	36,48

Table 9. Measurements (in mm) of the upper D3.

D3/Measurement n°		1	2	5	6	7	8	9	10
Senèze (*S. etr*)	MEAN (N=2)	40,80	40,30			40,49	32,90	36,35	
	MIN	40,80	40,30	17,43		40,49	32,90	36,15	26,77
	MAX			21,60				36,55	
Upper Valdarno (*S. etr*)	MEAN (N=4)	42,22	40,10	29,04	12,97	41,51	38,79	38,79	29,97
	MIN	40,45	38,41	17,28	12,66	40,55	35,28	34,55	26,81
	MAX	44,30	41,86	34,16	13,26	43,53	40,23	41,42	31,93
Vallonnet (*S. hun*)	MEAN (N=11)	38,99	39,96		14,04	38,92	39,23	35,94	32,83
	MIN	34,63	36,32	16,00	12,20	33,20	36,15	33,45	31,12
	MAX	44,33	44,51	30,02	15,61	44,91	41,88	38,19	34,41
Soleilhac (*S. hun*)	N=1				12,56				30,60
Arago (*S. hem*)	MEAN (N=13)	40,82	42,43						
	MIN	31,59	37,43	13,91					
	MAX	48,10	45,44	36,24					
Observatoire Cave (*S. hem*)	N=1				12,13				29,75

Upper D4

(Fig. 15, Table 10)

The crochet is always single.

The crista is absent on the upper D4 of *S. hundsheimensis*. It can be present in *S. etruscus, S. hemitoechus* and *S. kirchbergensis.*

The antecrochet is absent in all the species.

The mediofossette is open; it is closed only in *S. hemitoechus.*

The protocone constriction is present in all the species of Pleistocene rhinoceros.

The biometrical data (Table 10) allows us to isolate *S. kirchbergensis*, by its proportions (Fig. 15) and its size. *S. hemitoechus, S. etruscus* and *S. hundsheimensis* present identical dimensions and proportions, which make it impossible to differentiate these three species on the upper D4.

Table 10. Measurements (in mm) of the upper D4.

D4/Measurement n°		1	2	5	6	7	8	9	10
Senèze (*S. etr*)	MEAN (N=2)	48,31	49,07			46,83	39,15	43,78	36,06
	MIN	47,90	49,07	45,79		46,83	38,57	43,62	36,06
	MAX	48,72		45,81			39,73	43,93	
Upper Valdarno (*S. etr*)	MEAN (N=4)	48,52	45,23		14,07	45,14	42,91	43,95	34,45
	MIN	48,19	45,23	22,16	12,59	44,05	42,91	43,21	34,21
	MAX	48,88	45,23	36,49	15,55	46,23	42,91	44,68	34,69
Vallonnet (*S. hun*)	MEAN (N=13)	45,76	46,19		15,16	46,04	41,47	43,04	36,70
	MIN	41,41	44,25	20,78	14,30	43,06	39,20	40,46	35,83
	MAX	50,57	48,62	40,15	17,36	49,95	43,09	48,66	39,83
Arago (*S. hem*)	MEAN (N=8)	45,61	45,89						
	MIN	44,44	45,51	25,24					
	MAX	46,52	46,26	40,46					
Prince Cave (*S. kirch*)	N=1	48,53		35,25	16,85			42,26	

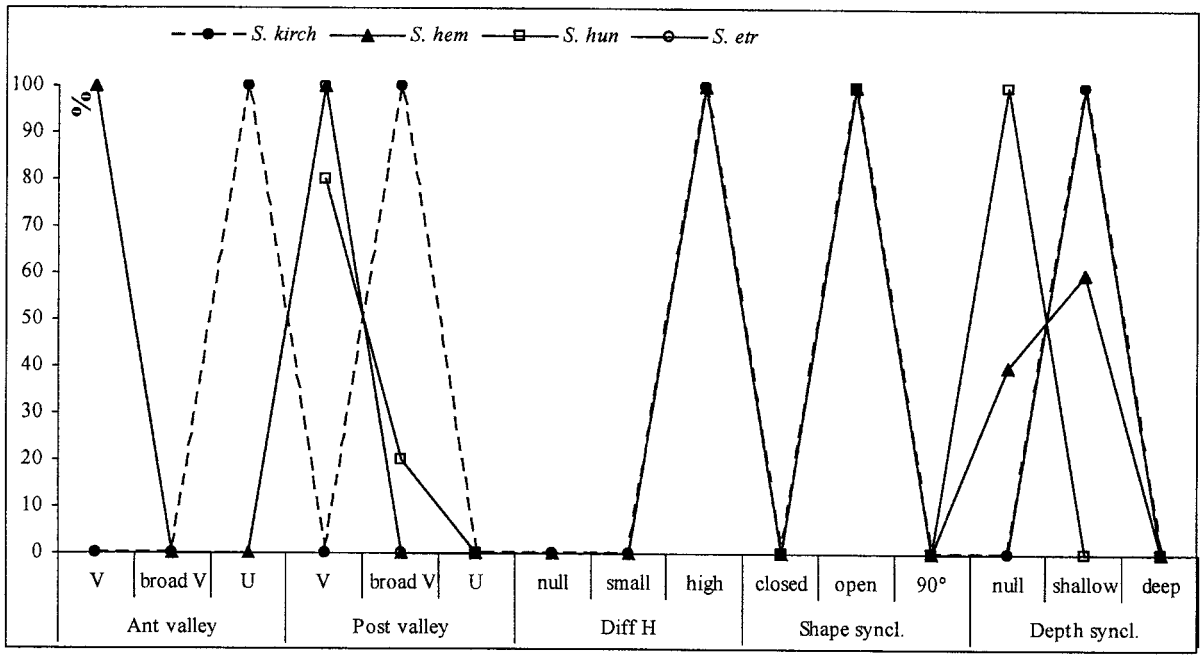

Fig. 16. Percentage distributions of qualitative character states for the lower P2 of the Pleistocene *Stephanorhinus*.

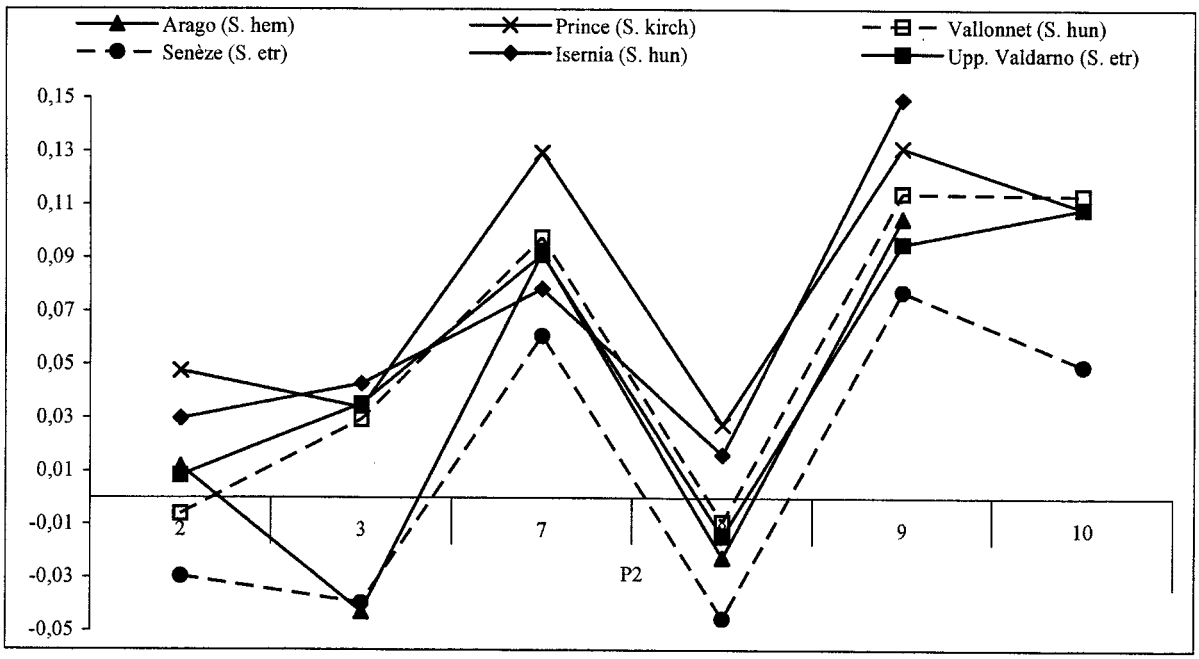

Fig. 17. Ratio diagram of the lower P2 of the Pleistocene *Stephanorhinus*. The referential is the present-day *Diceros bicornis*.

Table 11. Measurements (in mm) of the lower P2.

P/2 Measurement n°		2	3	5	6	7	8	9	10	11	12
Senèze *(S. etr)*	MEAN (N=3)	17,94	14,56			26,46	17,57	25,98	23,71		
	MIN	17,54	14,07			25,70	17,43	25,54	22,87	19,56	19,71
	MAX	18,60	15,42			27,26	17,80	26,49	24,55	19,56	22,40
Upper Valdarno *(S. etr)*	MEAN (N=4)	19,22	17,52			28,80	18,75	27,12	27,17		
	MIN	17,58	16,73			27,16	17,80	26,07	25,10	13,17	13,60
	MAX	19,88	18,30			30,43	19,69	28,16	29,23	26,17	28,96
Ceyssaguet *(S. hun)*	N=1		17,74	17,74		29,60		30,60		18,47	23,30
Vallonnet *(S. hun)*	MEAN (N=6)	18,59	17,28	15,69		29,22	18,98	28,33	27,48		
	MIN	18,34	16,28			27,41	18,88	26,80	26,84	10,63	11,96
	MAX	18,84	18,15			32,29	19,08	30,49	28,12	24,53	34,70
Tour de Grimaldi *(S. hun)*	N=1	20,71	17,10	13,11		28,61	20,90	29,04	26,79	21,57	
Soleilhac *(S. hun)*	N=1	22,41	17,13	18,01		29,95	22,93	30,92	27,09	23,10	24,48
Isernia *(S. hun)*	MEAN (N=4)	20,18	17,82			27,95	20,12	30,72		24,55	
	MIN					25,20	19,50				21,20
	MAX					30,40	21,00				29,80
Arago *(S. hem)*	MEAN (N=16)	19,37	14,63	12,12	18,30	28,82	18,40	27,72			
	MIN	17,82	12,99		17,82	24,64	15,32	24,16		14,28	16,54
	MAX	21,59	16,97		18,77	32,28	21,44	30,51		26,07	31,40
Orgnac 3 *(S. hem)*	N=1					29,12	15,03				11,22
Cavillon *(S. hem)*	N=1	19,32	16,03			27,37	19,48	27,16	24,64	13,06	16,33
Prince Cave *(S. kirch)*	MEAN (N=3)	21,03	17,45	14,38		31,44	20,64	29,45	27,17		
	MIN	20,59	16,06	12,79	19,84	30,12	20,06	29,20	26,45	25,52	32,98
	MAX	21,58	18,38	16,41		32,13	21,38	29,67	27,62	33,53	37,60

Lower P2

(Figs. 16 and 17, Table 11)

A slightly marked anterior valley is observable on the lower P2 of *S. hemitoechus* (V-shaped) and *S. kirchbergensis* (U-shaped).

The posterior valley is V-shaped in *S. etruscus* and *S. hemitoechus*. This morphology is also common in *S. hundsheimensis*, but this species can also possess a broad V-shaped posterior valley (20 %). In *S. kirchbergensis*, the posterior valley is always broadly V-shaped.

The difference in height between the bottoms of the valleys is important in the two species that possess an anterior valley.

The mesial cingulum is absent on the lower P2 of the *Stephanorhinus* of the Pleistocene. The distal cingulum has only been observed in *S. hemitoechus*. The vestibular cingulum is absent in *S. etruscus* and *S. hemitoechus*. Its presence is possible in *S. hundsheimensis*; it is more often observable in *S. kirchbergensis*. The lingual cingulum has been observed only on the lower P2 of *S. kirchbergensis*.

The vestibular syncline is always open, its depth is weak to null on all the lower P2 of the Pleistocene *Stephanorhinus*.

The Simpson diagram (Fig. 17) shows that the curves of the lower P2 of the different species are relatively similar. *S. kirchbergensis* presents the larger lower P2 after *S. hundsheimensis*. *S. hemitoechus* possesses a reduced P2, slightly larger (Table 11) than that of *S. etruscus*. For each species, the development of the lower P2 is similar to that of the upper P2.

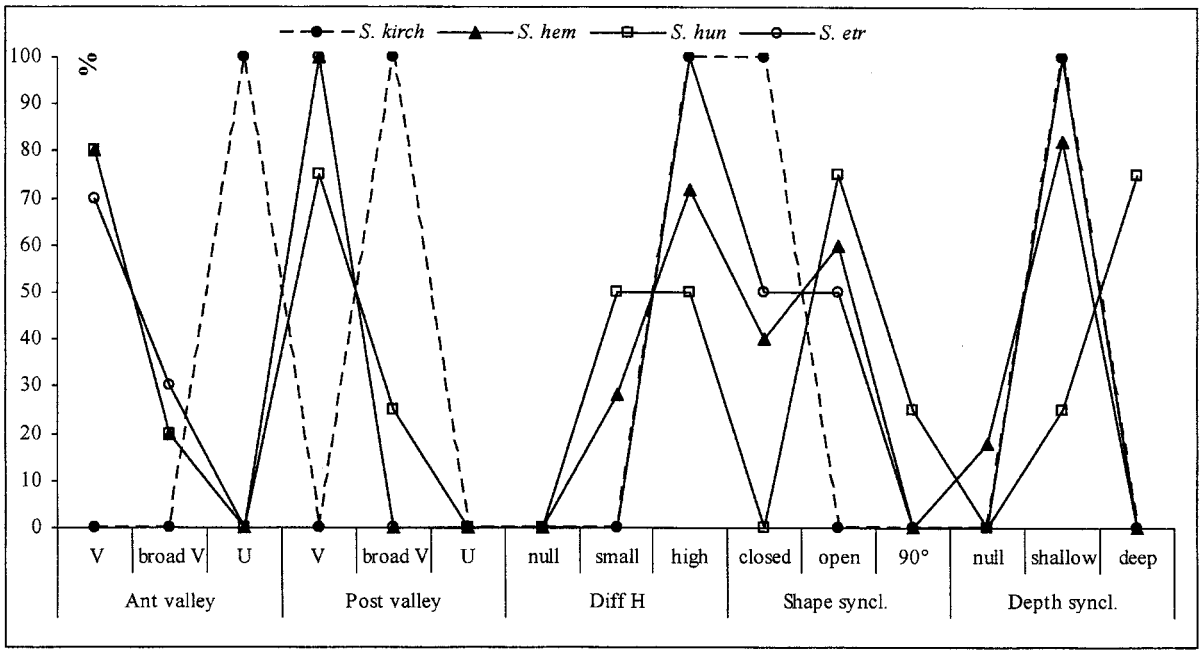

Fig. 18. Percentage distributions of qualitative character states for the lower P3 of the Pleistocene *Stephanorhinus*.

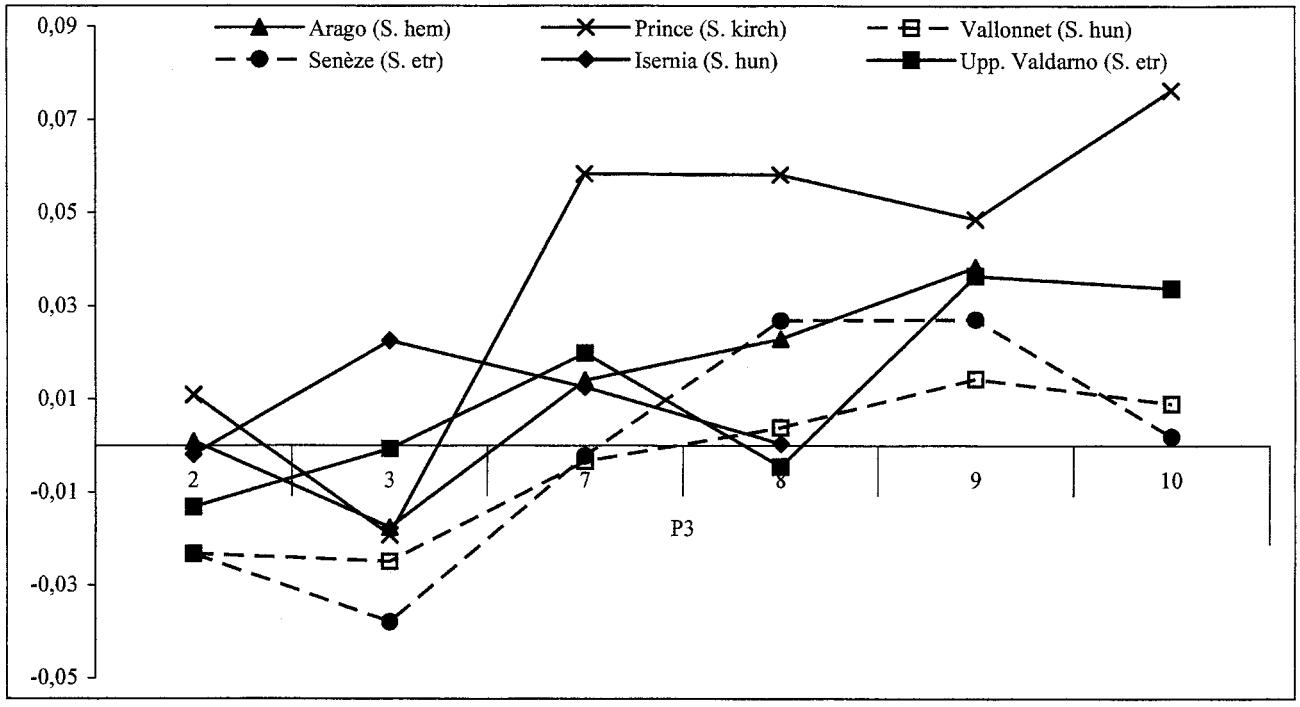

Fig. 19. Ratio diagram of the lower P3 of the Pleistocene *Stephanorhinus*. The referential is the present-day *Diceros bicornis*.

Table 12. Measurements (in mm) of the lower P3.

P/3 Measurement n°		2	3	5	6	7	8	9	10	11	12
Senèze *(S. etr)*	MEAN (N=4)	24,86	21,67	12,86	19,34	33,57	26,22	34,14	31,00		
	MIN	23,08	18,86	11,88		31,29	25,00	31,95	28,53	16,02	18,37
	MAX	27,74	27,11	14,40		38,65	28,68	37,87	35,38	21,72	28,33
Upper Valdarno *(S. etr)*	MEAN (N=11)	25,44	23,61	14,79	19,25	35,32	24,39	34,89	33,36	23,22	26,50
	MIN	22,60	21,35	13,59	18,60	32,39	20,29	33,07	29,59	14,69	13,65
	MAX	28,93	25,23	16,65	20,39	39,67	26,35	36,91	36,66	31,41	33,42
Ceyssaguet *(S. hun)*	N=1	26,71	23,88	13,90		34,47	26,56	33,62	32,70	17,61	19,37
Vallonnet *(S. hun)*	MEAN (N=12)	24,86	22,33	14,57	18,77	33,48	24,87	33,15	31,51		
	MIN	23,59	21,15	11,91	16,36	31,22	23,28	31,58	30,09	10,00	9,66
	MAX	26,51	24,16	16,30	21,86	35,63	26,30	35,25	33,41	32,44	45,91
Soleilhac *(S. hun)*	MEAN (N=2)	28,55	23,73	11,57		36,32	27,88	35,93	34,96		
	MIN	27,02	23,70	10,00	13,85	35,76	26,70	35,71	34,37	18,70	20,04
	MAX	30,09	23,75	13,15		36,88	29,07	36,16	35,56	18,81	26,30
Isernia *(S. hun)*	MEAN (N=10)	26,11	24,91	13,23	17,44	34,73	24,67				
	MIN					32,70	22,00			9,74	14,00
	MAX					37,50	28,40			26,69	35,15
Arago *(S. hem)*	MEAN (N=14)	26,28	22,71	15,37	19,92	34,85	25,99	35,03			
	MIN	24,80	21,73	12,09	17,36	31,63	24,79	30,29		9,92	13,79
	MAX	28,29	26,77	19,45	23,75	36,81	28,32	37,88		39,79	49,56
Mars Cave *(S. hem)*	N=1	23,73	19,22	11,51	16,59	36,02	21,14	32,52	30,59	28,34	40,70
Cavillon Cave *(S. hem)*	MEAN (N=2)	25,04	20,30			35,15	24,79	35,33	31,83		
	MIN					32,60		32,76		13,55	15,70
	MAX					37,69		37,89			16,61
Prince Cave *(S. kirch)*	MEAN (N=2)	26,89	22,63	12,56	23,74	38,59	28,18	35,87	36,80		
	MIN	26,67	22,31	10,94	23,04	38,50	27,70	35,77	36,78	29,58	37,18
	MAX	27,11	22,94	13,77	24,43	38,68	28,65	35,97	36,81	31,52	37,71
Aldène *(S. kirch)*	N=1	26,83	24,88			40,04	28,33	40,04	37,87	17,34	16,96

Lower P3

(Figs. 18 and 19, Table 12)

The anterior valley is more often V-shaped (70 %) than broad V-shaped (30 %) in *S. etruscus*. The broad V-shaped morphology is a lot less frequent in *S. hundsheimensis* and *S. hemitoechus* (20 %). *S. kirchbergensis* possesses a U-shaped anterior valley.

The morphology of the posterior valley is similar to the one of the anterior valley in *S. hundsheimensis*. *S. hemitoechus* and *S. etruscus* always possess a V-shaped posterior valley. It is always broad V-shaped in *S. kirchbergensis*.

The difference in height between the bottom of the valleys is small in *S. hundsheimensis* (measurement n°5/6 = 0,72 to 0,77) and *S. hemitoechus*. It is more important in *S. kirchbergensis* (5/6 = 0,52) and *S. etruscus* (5/6 = 0,65).

The mesial cingulum is absent on the lower P3 of *S. kirchbergensis*. It is rare in *S. hemitoechus*, and more frequent in *S. hundsheimensis* and *S. etruscus*. The distal cingulum is absent on the lower P3 of *S. kirchbergensis*. It is rare in *S. etruscus* and more frequent in *S. hundsheimensis* and *S. hemitoechus*. The lingual cingulum is absent on the lower P3 of *S. kirchbergensis*, *S. etruscus* and *S. hemitoechus*. Its presence is possible in *S. hundsheimensis*. The

vestibular cingulum is absent on the lower P3 of *S. etruscus* and *S. hemitoechus*. Its presence is possible in *S. hundsheimensis*. It is more frequent in *S. kirchbergensis*.

The morphology of the vestibular syncline is non constant in *S. hemitoechus* and shows a similar shape within the three other species. Its depth is always shallow in all the species.

The Simpson diagram (Fig. 19) differentiates *S. kirchbergensis*, in which the size and the proportions of the lower P3 are considerably more important, from the other Pleistocene *Stephanorhinus*. *S. hemitoechus* presents a more reduced P3 than this last species but slightly larger than that of *S. hundsheimensis* and *S. etruscus*. The polynomial curve of tendency of *S. hemitoechus* is distinctly concave. It is straight for *S. hundsheimensis* and slightly convex for *S. etruscus*. It is not possible to discriminate these last two species based only on the dimensions (Table 12). The hypsodonty index of the lower P3 of *S. hemitoechus* follows the same rule as that of the upper P3. This index is more important in the Middle Pleistocene forms (Caune de l'Arago) than that of the Mars cave from the end of the Middle Pleistocene. It can also be verified on the lower P3 of *S. hundsheimensis*, and is more hypsodont in the rhinoceros of the Vallonnet cave from the Early Pleistocene than that from Isernia at the beginning of the Middle Pleistocene. The hypsodonty index is distinctly greater in *S. hemitoechus* than in *S. hundsheimensis*, itself more hypsodont than *S. kirchbergensis*.

Lower P4

(Figs. 20 and 21, Table 13)

The anterior valley is V-shaped on the lower P4 of *S. hundsheimensis* and *S. hemitoechus*. It is as often V-shaped as broad V-shaped in *S. etruscus*. It is always U-shaped in *S. kirchbergensis*.

The posterior valley is V-shaped in *S. hemitoechus* and *S. etruscus*. It is also the dominant morphology in *S. hundsheimensis*, although a broad V-shaped is also commonly observed (20 %). The posterior valley is broad V-shaped in *S. kirchbergensis*.

The difference of height between the bottoms of the valleys is variable in *S. hemitoechus*. The ratio (Measurement n°5/6) is very different in *S. hemitoechus* according to which forms of the species is considered. The small-sized forms (Terra Amata and Orgnac 3) have a low ratio (Measurement n°5/6); the larger forms (Caune de l'Arago and the *S. hemitoechus* from the Upper Pleistocene) show a higher ratio. It is strong in *S. kirchbergensis* (5/6 = 0,64), low in *S. etruscus* (5/6 = 0,97). The ratio 5/6 varies between 0,78 and 0,87 in *S. hundsheimensis*. The evolved forms of the Middle Pleistocene (Isernia and Soleilhac) show a low ratio, but the small *S. hundsheimensis* of the Early Pleistocene, (Vallonnet, Ceyssaguet) have an high ratio.

The mesial cingulum is rare in *S. hemitoechus*, distinctly more frequent in *S. etruscus, S. hundsheimensis* and *S. kirchbergensis*. The distal cingulum is absent on the lower P4 of *S. hemitoechus*. Its presence is possible in *S. etruscus, S. hundsheimensis* and *S. kirchbergensis*. The vestibular cingulum is absent on the lower P4 of *S. hemitoechus*. Its presence is possible in *S. hundsheimensis* and *S. kirchbergensis*; very rare in *S. etruscus*. The lingual cingulum is absent in *S. hemitoechus*. Its presence is possible in *S. hundsheimensis* and *S. kirchbergensis*; rare in *S. etruscus*.

The vestibular syncline is closed and straight in *S. hundsheimensis* and *S. kirchbergensis*. It is more often closed than open in *S. etruscus* and normally open in *S. hemitoechus*. The depth of the syncline is variable in *S. hundsheimensis* and *S. hemitoechus*. It is shallow in *S. etruscus* and deep in *S. kirchbergensis*.

The Simpson diagram (Fig. 21) discriminates *S. kirchbergensis* distinctively by its proportions and by its size (Table 13). *S. hemitoechus* is smaller than *S. kirchbergensis*, but larger than *S. hundsheimensis* and *S. etruscus*. Only the polynomial curves of tendency permit us to differentiate *S. hundsheimensis* and *S. etruscus*. It is distinctly concave for *S. hundsheimensis* and convex for *S. etruscus*. The hypsodonty index is greater for the lower P4 of *S. hemitoechus* than that of *S. hundsheimensis*. *S. kirchbergensis* is the more brachyodont species.

Lower M1

(Figs. 22 and 23, Table 14)

The anterior valley is V-shaped in *S. hundsheimensis* and *S. hemitoechus*. It can be broad V shaped (40 %) or U-shaped (30 %) in *S. etruscus*. It is exclusively U-shaped in *S. kirchbergensis*.

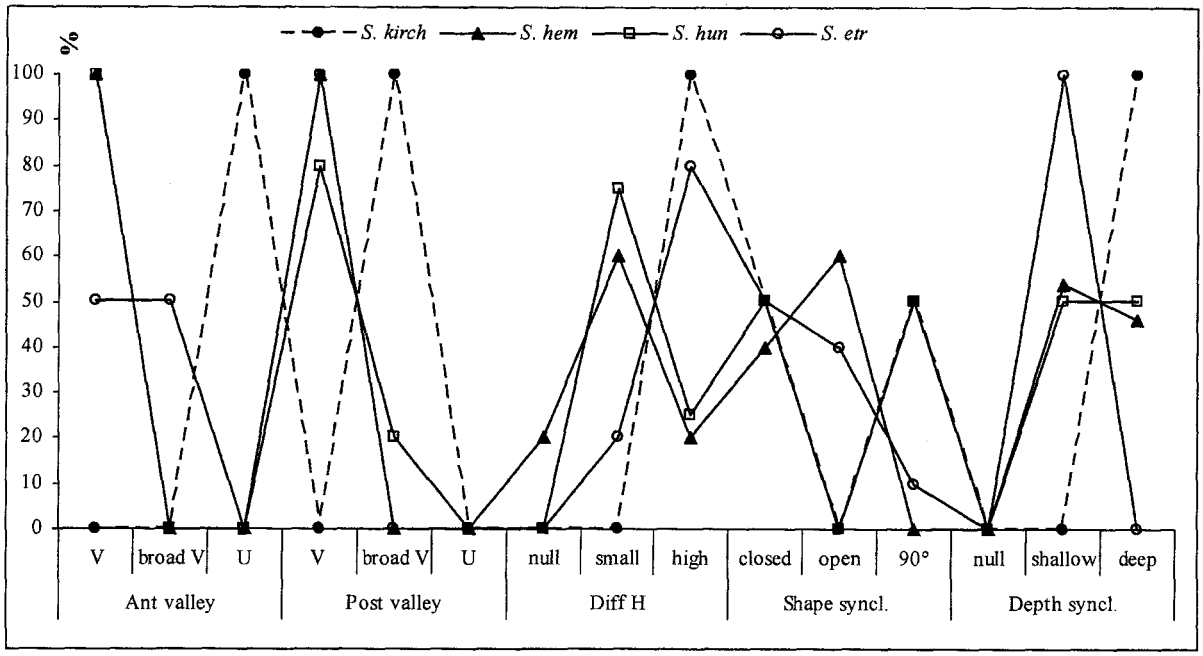

Fig. 20. Percentage distributions of qualitative character states for the lower P4 of the Pleistocene *Stephanorhinus*.

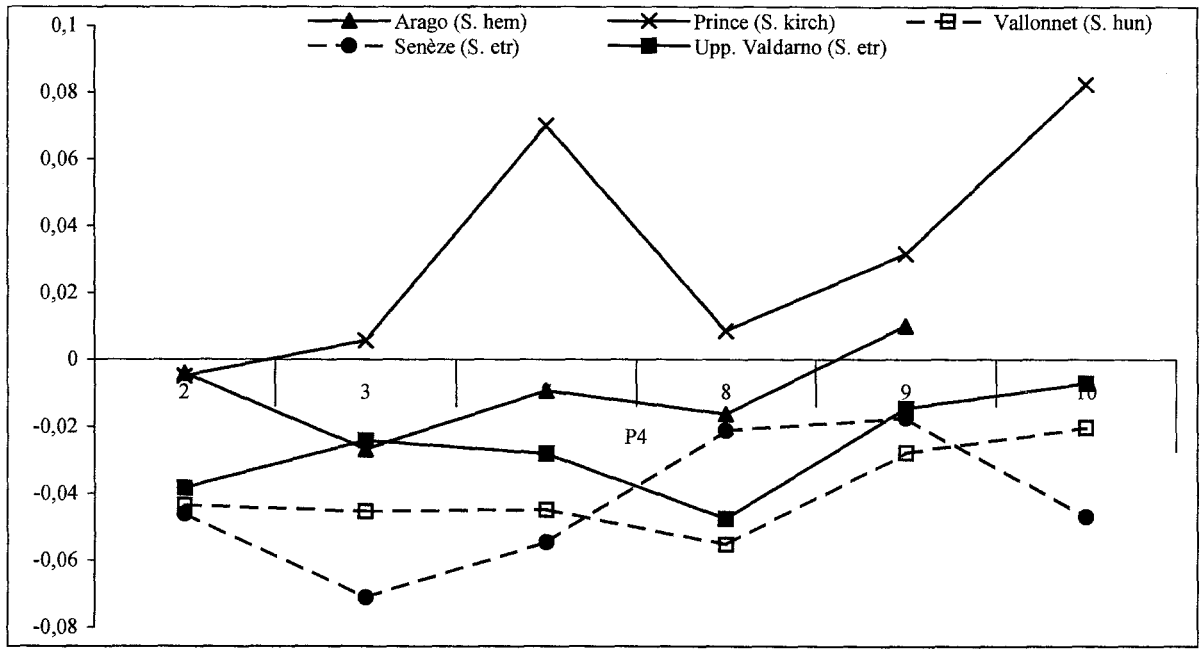

Fig. 21. Ratio diagram of the lower P4 of the Pleistocene *Stephanorhinus*. The referential is the present-day *Diceros bicornis*.

Table 13. Measurements (in mm) of the lower P4.

P/4 Measurement n°		2	3	5	6	7	8	9	10	11	12
Senèze *(S. etr)*	MEAN (N=3)	27,92	24,04	12,38	13,31	34,87	29,99	37,17	32,03		
	MIN	27,57	23,45	12,36	12,83	35,05	29,30	35,75	31,51	16,01	20,36
	MAX	28,30	25,20	12,39	13,80	34,40	30,68	38,58	32,54	16,06	23,50
Upper Valdarno *(S. etr)*	MEAN (N=17)	28,43	26,78	15,56	19,64	37,06	28,23	37,41	35,12	22,09	25,01
	MIN	24,92	23,19	13,14	17,32	34,69	24,26	33,21	31,56	13,98	13,35
	MAX	31,13	29,93	17,18	21,15	39,63	31,51	40,26	37,75	32,84	42,58
Ceyssaguet *(S. hun)*	N=1	30,09				34,87		38,01		16,60	18,19
Vallonnet *(S. hun)*	MEAN (N=13)	28,09	25,51	14,68	16,90	35,65	27,73	36,29	34,05		
	MIN	26,84	23,14	13,08	14,37	33,96	26,36	34,25	30,55	10,57	12,20
	MAX	30,66	28,37	16,22	18,75	37,00	29,96	38,24	36,30	28,10	44,29
Tour de Grimaldi *(S. hun)*	N=1	26,93	23,28			37,44	26,28	36,30	33,65	12,87	16,25
Soleilhac *(S. hun)*	N=1	30,75	25,23			38,41	30,20	37,99	37,28	18,60	28,79
Isernia *(S. hun)*	MEAN (N=7)	32,25	26,86	15,07	19,23	38,26	27,06				
	MIN	27,98				36,70	21,20			11,68	12,85
	MAX	38,72				40,23	32,65			29,03	40,65
Arago *(S. hem)*	MEAN (N=17)	30,76	26,62	15,90	18,30	38,70	30,33	39,60			
	MIN	27,9	24,85	14,84	15,33	35,08	28,43	35,70		11,32	11,68
	MAX	32,46	29,53	18,63	22,67	41,97	31,83	43,93		34,50	47,79
Terra Amata *(S. hem)*	N=1	25,52	21,72	12,58	20,16	33,58	25,64			22,92	28,17
Mars Cave*(S. hem)*	N=1	26,90	24,91			38,75		36,67	33,50	32,53	44,62
Cavillon Cave *(S. hem)*	N=1	29,39				37,54	30,13	35,76		13,73	18,10
Prince Cave *(S. kirch)*	MEAN (N=4)	30,70	28,69	13,86	21,73	46,44	32,12	41,61	43,14		
	MIN	29,47	26,19	11,87	18,97	44,07	32,05	38,77	39,52	35,09	37,18
	MAX	31,89	31,02	14,84	24,66	49,67	32,18	45,97	50,09	38,97	44,32
Aldène *(S. kirch)*	MEAN (N=2)	29,64		11,29			29,82	43,64			
	MIN	27,77		10,24			28,13	42,42		26,42	32,25
	MAX	31,51		12,34			31,51	44,86		37,00	43,85

The posterior valley presents the same morphology than that of the anterior valley in *S. etruscus*. It is normally V-shaped, but possibly broad V-shaped (20%) in *S. hundsheimensis*. It is V-shaped, rarely broad V-shaped (9%) in *S. hemitoechus*. The lower M1 of *S. kirchbergensis* has a posterior valley broad V-shaped.

The difference between the bottoms of the valleys is small in *S. hundsheimensis* (measurement n°5/6 = 0,63 to 1,1) and *S. hemitoechus* (5/6 = 0,82 to 0,85). It is always greater in *S. kirchbergensis* (5/6 = 0,52).

The mesial cingulum is absent in *S. kirchbergensis*. It is present in *S. hundsheimensis*, its frequency is less important in *S. hemitoechus* and *S. etruscus*. The distal cingulum is absent in *S. kirchbergensis* and rare in *S. etruscus*. It is present in *S. hundsheimensis*, its frequency is less important in *S. hemitoechus*. The lingual cingulum is absent in the lower M1 of *S. kirchbergensis* and *S. hundsheimensis*. It is rare in *S. etruscus* and *S. hemitoechus*. The vestibular cingulum exists more or less in all the species with a variable frequency. It is more absent in *S. etruscus*.

The vestibular syncline is closed or open, in the same proportion, in *S. etruscus*. It is as often closed as right-angled in *S. kirchbergensis*. It is rather open in *S. hundsheimensis* and *S. hemitoechus*. The depth of the syncline is normally important in *S. hundsheimensis* and *S. kirchbergensis*. It is less important in *S. hemitoechus* and *S. etruscus*.

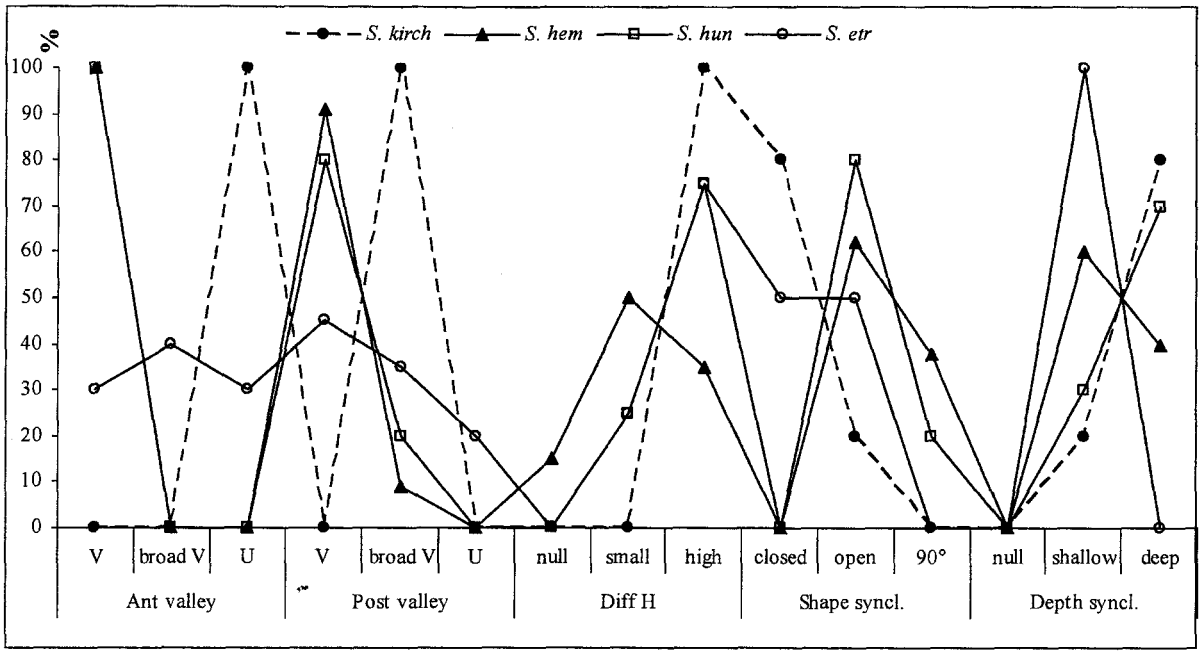

Fig. 22. Percentage distributions of qualitative character states for the lower M1 of the Pleistocene *Stephanorhinus*.

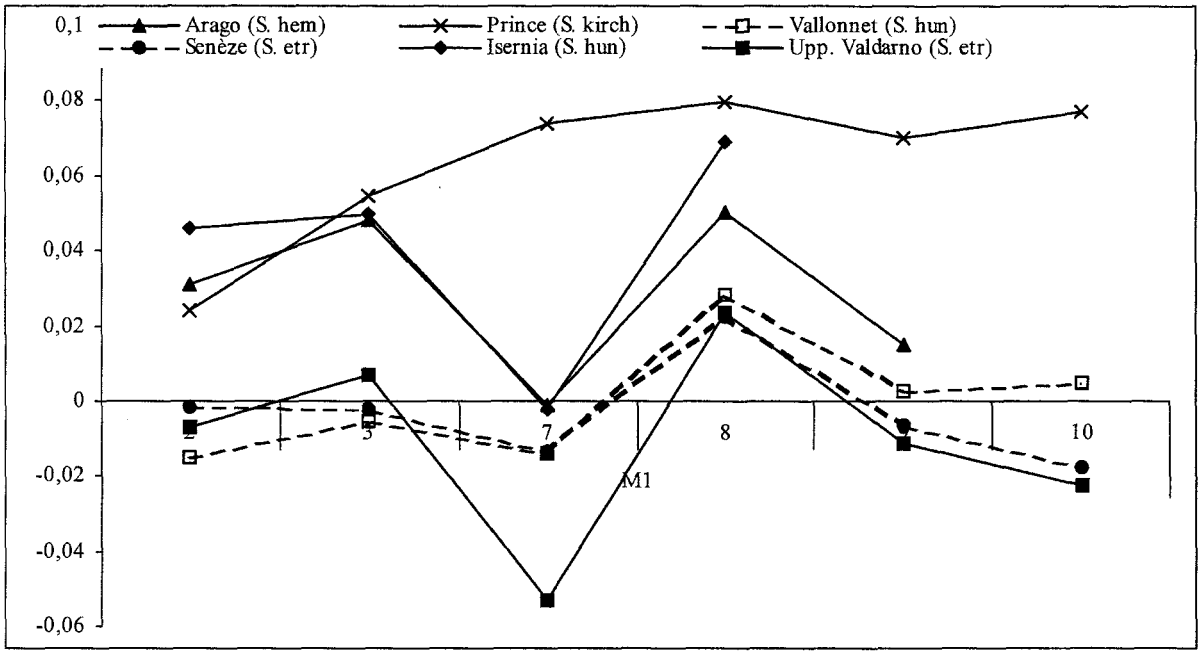

Fig. 23. Ratio diagram of the lower M1 of the Pleistocene *Stephanorhinus*. The referential is the present-day *Diceros bicornis*.

Table 14. Measurements (in mm) of the lower M1.

M/1 Measurement n°		2	3	5	6	7	8	9	10	11	12
Sénèze *(S. etr)*	MEAN (N=7)	29,39	27,24	10,32	14,23	42,45	28,26	39,95	37,92		
	MIN	26,60	24,96	8,90		40,80	25,46	38,89	36,17	12,79	14,24
	MAX	31,65	28,43	11,27		45,30	30,46	41,31	40,02	28,61	37,28
Upper Valdarno *(S. etr)*	MEAN (N=22)	29,03	27,83	14,12	20,45	38,77	28,36	39,48	37,51	18,96	20,27
	MIN	25,76	24,30	9,69	15,89	35,13	26,00	34,93	25,89	8,50	10,18
	MAX	34,09	32,81	16,58	26,60	43,73	33,12	43,16	41,81	33,73	38,45
Ceyssaguet *(S. hun)*	N=1	27,44	27,77	9,67	8,75	40,94	28,57	41,05	42,35	20,30	20,30
Vallonnet *(S. hun)*	MEAN (N=14)	28,52	27,06	12,94	14,66	42,42	28,66	40,76	39,95		
	MIN	25,73	24,33	8,69	11,08	38,28	25,58	37,77	36,49	7,79	11,71
	MAX	31,22	29,36	17,81	18,50	47,35	31,20	43,90	43,62	34,24	51,40
Soleilhac *(S. hun)*	N=1	30,56	27,46	9,86	15,61	42,33	30,00	40,71	40,31	20,80	26,70
Isernia *(S. hun)*	MEAN (N=22)	32,82	30,72	12,58	17,14	43,60	31,45				
	MIN	29,49	29,25	11,81	14,88	40,12	28,00			11,78	12,00
	MAX	38,27	31,40	13,83	20,15	48,00	38,64			26,05	34,86
Arago *(S. hem)*	MEAN (N=26)	31,69	30,58	13,07	15,31	43,66	30,78	43,15		13,08	20,30
	MIN	28,83	27,03	11,41	13,67	40,43	26,36	39,58		0,00	5,28
	MAX	35,78	34,04	14,72	16,95	47,88	33,48	46,52		27,94	63,17
T. Amata *(S. hem)*	N=1	28,86	25,47			39,85	28,32	37,63	34,44	13,93	21,90
Orgnac 3 *(S. hem)*	N=1	27,88	24,39	14,40	17,30	40,30	27,78	37,86	35,00	34,57	45,63
Mars Cave *(S. hem)*	N=1	28,47	26,64			46,55		43,60	40,50	26,34	40,10
Prince Cave *(S. hem)*	MEAN (N=4)	28,93	28,64			47,95	29,43	44,62	42,49	20,77	29,95
	MIN	28,14	27,18			41,60	27,95	40,44	36,90	16,93	21,36
	MAX	30,53	30,14			51,70	30,84	46,97	46,40	25,30	41,41
Prince Cave *(S. kirch)*	MEAN (N=5)	31,18	31,03	10,60	20,24	51,91	32,26	47,65	47,15		
	MIN	29,29	29,88	8,95	7,23	48,77	30,48	43,70	43,71	24,46	30,46
	MAX	32,88	34,62	13,50	26,78	54,79	33,90	51,55	53,29	29,73	39,60

The Simpson diagram (Fig. 23) differentiates *S. kirchbergensis* from the other species by its greater size (Table 14) and by its specific proportions. *S. hemitoechus* has a more reduced lower M1. The most important distinction between *S. hundsheimensis* and *S. etruscus* is found on the mesial and distal breadth (measurements n°2 and 3). *S. hundsheimensis* and *S. etruscus* present very similar curves that prevent all discriminations based only on the dimensions. However, the vestibular and lingual lengths (measurements n° 9 and 10) are more important in *S. hundsheimensis*. The hypsodonty index is more important on the lower M1 of *S. hemitoechus* than that of the *S. hundsheimensis*. *S. kirchbergensis* is the more brachyodont species.

Lower M2

(Figs. 24 and 25, Table 15)

The anterior valley is V-shaped, broad V-shaped or U-shaped in *S. etruscus* (50 % – 35 % – 15 %), *S. hundsheimensis* (60 % – 15 % – 25 %) and *S. hemitoechus* (91 % – 9 % – 0 %) but in different proportions. The U-shaped morphology dominates in *S. kirchbergensis* (60 %).

The posterior valley is V-shaped, broad V-shaped or U-shaped in *S. etruscus* (35 % – 55 % – 10 %) and *S.*

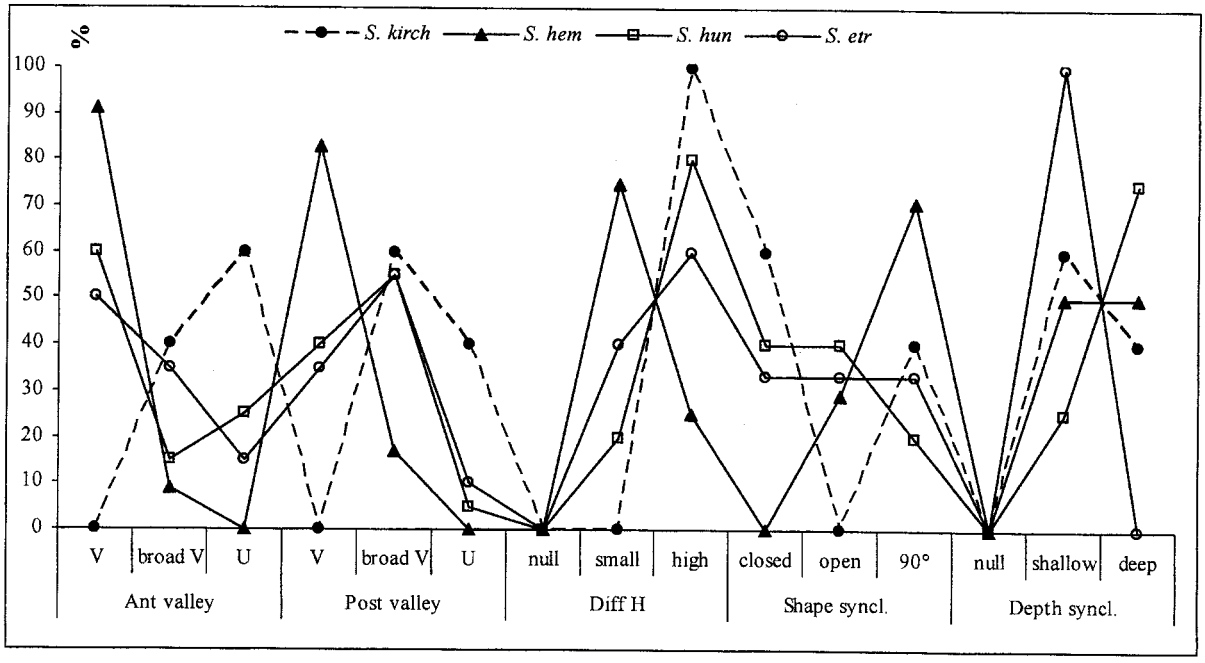

Fig. 24. Percentage distributions of qualitative character states for the lower M2 of the Pleistocene *Stephanorhinus*.

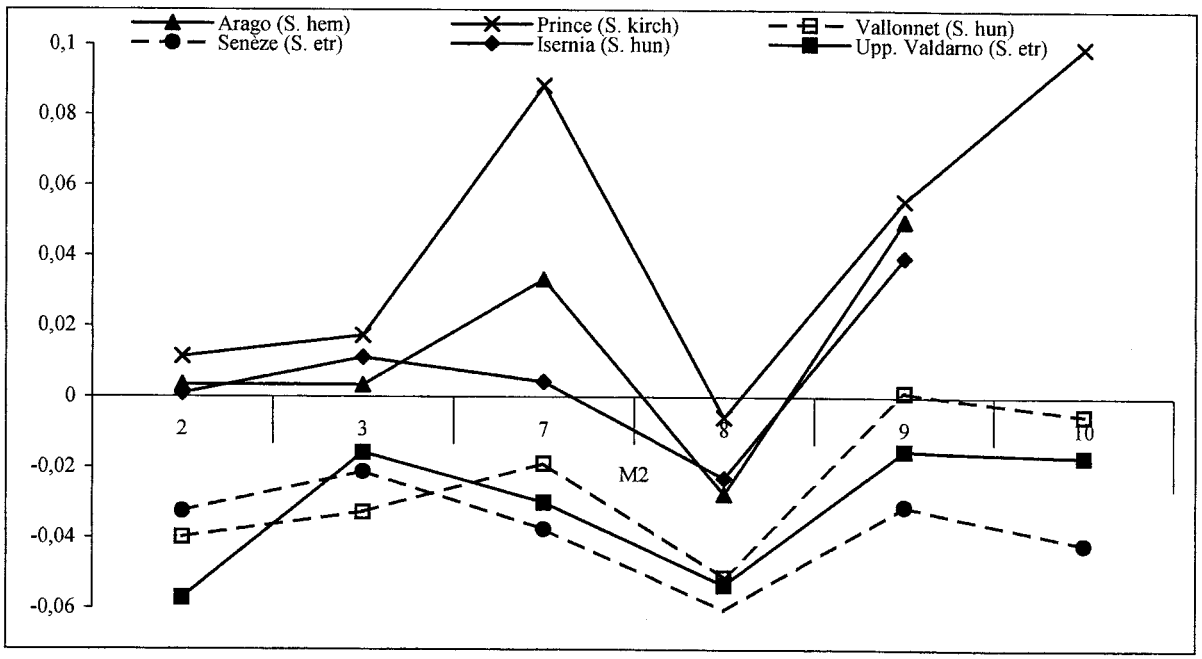

Fig. 25. Ratio diagram of the lower M2 of the Pleistocene *Stephanorhinus*. The referential is the present-day *Diceros bicornis*.

Table 15. Measurements (in mm) of the lower M2.

M/2 Measurement n°		2	3	5	6	7	8	9	10	11	12
Senèze *(S. etr)*	MEAN (N=3)	29,67	29,31	9,31		42,59	28,99	40,63	39,53		
	MIN	29,50	29,00	8,93		41,60	28,45	40,10	39,11	13,60	18,61
	MAX	29,83	29,62	9,68		43,18	29,52	41,30	39,94	15,18	22,00
Upper Valdarno *(S. etr)*	MEAN (N=20)	28,03	29,68	11,56	17,37	43,34	29,46	42,14	41,86	21,15	25,66
	MIN	24,41	26,69	8,74	12,55	40,35	28,08	39,64	38,90	13,26	14,00
	MAX	30,93	33,79	16,12	24,65	45,98	32,41	46,02	45,17	30,02	35,28
Ceyssaguet *(S. hun)*	N=1	30,65	30,22	10,86			30,00	40,25	41,87	16,10	22,65
Vallonnet *(S. hun)*	MEAN (N=14)	29,17	28,54	11,32	14,94	44,46	29,61	43,77	43,01		
	MIN	26,17	26,13	9,13	13,00	40,19	26,04	41,52	40,68	13,38	9,98
	MAX	32,80	31,60	14,26	16,33	47,23	32,33	45,39	44,60	34,61	48,89
Durfort *(S. hun)*	N=1	29,77	29,63	9,85		44,18	29,74	43,22	42,12	15,95	18,56
Soleilhac *(S. hun)*	N=1	30,48	29,27	12,86	15,67	46,44	30,56	41,61	43,74	24,40	27,82
Isernia *(S. hun)*	MEAN (N=20)	32,04	31,57	9,65	13,51	46,90	31,60	47,81			
	MIN	29,32	29,91	5,29	11,06	41,30	29,40			12,09	11,30
	MAX	38,56	34,36	12,30	15,04	50,14	36,60			34,00	36,42
Arago *(S. hem)*	MEAN (N=33)	32,23	31,01	12,34	16,76	50,14	31,27	49,84			
	MIN	27,41	23,43	7,73	11,85	46,17	25,81	46,33		2,50	4,33
	MAX	37,93	34,53	15,43	19,84	53,22	35,53	53,69		48,63	60,29
Terra Amata *(S. hem)*	N=1	27,96	26,55	12,09	17,71	46,07	28,70	43,35	44,20	23,77	24,96
Orgnac 3 *(S. hem)*	MEAN (N=2)	25,55		8,60		45,02	26,12	45,83	47,41		
	MIN	23,36								41,00	50,50
	MAX	27,45									56,84
Mars Cave *(S. hem)*	N=1	30,47	28,69	10,26	14,41	53,50	30,48	44,65	47,58	34,10	45,97
Prince Cave *(S. hem)*	N=1	31,05	31,71	13,98	16,90	51,20		48,90	51,12		
Prince Cave *(S. kirch)*	MEAN (N=5)	32,82	32,03	11,82	17,03	56,91	32,88	49,63	54,70		
	MIN	31,88	31,40	11,02	13,08	52,25	32,17	47,22	50,55	28,20	31,03
	MAX	33,97	32,69	13,57	22,14	61,74	33,77	52,16	58,87	39,60	47,32

hundsheimensis (40% – 55% – 5%), more often broad V-shaped (60%) than U-shaped (40%) in *S. kirchbergensis*, while the V-shaped morphology dominates in *S. hemitoechus* (83%).

The difference in height between the bottoms of the valleys is normally important in *S. etruscus* and *S. kirchbergensis* (5/6 = 0,69). It is smaller in *S. hemitoechus* (5/6 = 0,68 to 0,82) and *S. hundsheimensis* (5/6 = 0,74 to 0,82).

The mesial cingulum is absent in *S. kirchbergensis*. It is as often present as absent in *S. etruscus* and *S. hemitoechus*. It is normally present in *S. hundsheimensis*. The distal cingulum is as often present as absent in *S. etruscus* and *S. hemitoechus*. It is normally present in *S. hundsheimensis*. It can be observed in *S. kirchbergensis*. The lingual cingulum is absent on the M2 of the Pleistocene *Stephanorhinus*, and only *S. etruscus* possesses it in some cases. The vestibular cingulum is observed with a greater or lesser frequency in all the species.

The morphology of the vestibular syncline is variable in *S. etruscus, S. hundsheimensis* and *S. hemitoechus*. It is closed to right – angled in *S. kirchbergensis*. Its depth is shallow in *S. etruscus*. It is variable in *S. hemitoechus* and *S. kirchbergensis*. It is normally important in *S. hundsheimensis*.

The Simpson diagram (Fig. 25) of the lower M2 presents the same features as that of the lower M1. *S. kirchbergensis* differentiates itself distinctly. *S. hemitoechus* is intermediate between *S. kirchbergensis* and *S.*

hundsheimensis/S. etruscus. These last two species are still very close. One can note a small difference in the level of the different lengths (measurements n°7, 9 and 10). The hypsodonty index is greater on the M2 of *S. hemitoechus* than that of *S. hundsheimensis*. *S. kirchbergensis* is the more brachyodont species.

Lower M3

(Figs. 26 and 27, Table 16)

The anterior valley is normally broad V-shaped (75 %) in *S. etruscus*. *S. kirchbergensis* presents a U-shaped posterior valley (60 %). The lower M3 of *S. hundsheimensis* is V-shaped or broad V-shaped in the same proportions, it is commonly V-shaped (89 %) in *S. hemitoechus*.

The posterior valley is broad V-shaped (75 %) in *S. etruscus*, U-shaped in *S. hundsheimensis* (70 %) and *S. kirchbergensis* (80 %). It is as often V-shaped (54 %) as broad V-shaped (46 %) in *S. hemitoechus*.

The difference of height between the bottoms of the valleys is normally small in *S. hemitoechus* (5/6 = 0,74 to 0,96). It is strong in *S. etruscus* (5/6 = 0,63) and *S. kirchbergensis*. It is more variable in *S. hundsheimensis* (5/6 = 0,62 to 0,64 in the advanced forms and 5/6 = 0,77 to 0,87 in the Early Pleistocene forms).

The mesial and distal cingula are present on all the lower M3 of the Pleistocene species with a variable frequency. The lingual cingulum is absent in the Pleistocene *Stephanorhinus*, only *S. etruscus* possesses it. The vestibular cingulum has not been observed in *S. hundsheimensis* and is rare in *S. hemitoechus*. It is sometimes observed in *S. etruscus* and *S. kirchbergensis*. The vestibular syncline possesses a variable morphology in *S. etruscus* and *S. hundsheimensis*, but in different proportion. It is closed to right-angled in *S. hemitoechus*. It forms an orthogonal angle in *S. kirchbergensis*. The depth of the vestibular syncline is shallow to deep in *S. etruscus* and *S. hemitoechus*. It is deep in the two other species.

The Simpson diagram (Fig. 27) of the lower M3 presents the same features as that of the two first molars. The curve of *S. hemitoechus* is close to the one of *S. kirchbergensis*, but it remains below it. *S. hundsheimensis* and *S. etruscus* are still quite close. The most important difference between these two species is the different lengths (measurements n°7, 9 and 10, Table 16).

Lower D1

(Fig. 28, Table 17)

No particular morphological character can be observed on this tooth. Dimensions (Table 17) and proportions (Fig. 28) D1 of the lower D2 of *S. hundsheimensis* are specific. This tooth is distinctly bigger than that of *S. hemitoechus* and *S. etruscus*. It represents an archaic character retained on this milk tooth. These last two species present some similar curves.

Lower D2

(Fig. 28, Table 18)

The posterior valley is broad V-shaped or U-shaped in *S. hundsheimensis*. It is V-shaped in *S. hemitoechus*.

The mesial, vestibular and lingual cingula have never been observed on this tooth. Only *S. hundsheimensis* possesses a light distal cingulum.

For all the Pleistocene species, the vestibular syncline is extensively open; its depth is always very shallow.

The Simpson diagram (Fig. 28) clearly differentiates *S. hundsheimensis* from the other species. Its D2 are more developed. *S. hemitoechus* shows a reduced D2. *S. etruscus* and *S. kirchbergensis* possess a comparable size and proportion of their lower D2.

Lower D3

(Fig. 28, Table 19)

The anterior valley is V-shaped on the lower D3 of *S. hundsheimensis*, *S. etruscus* and *S. hemitoechus*, it can also be broad V-shaped. It is U-shaped in *S. kirchbergensis*.

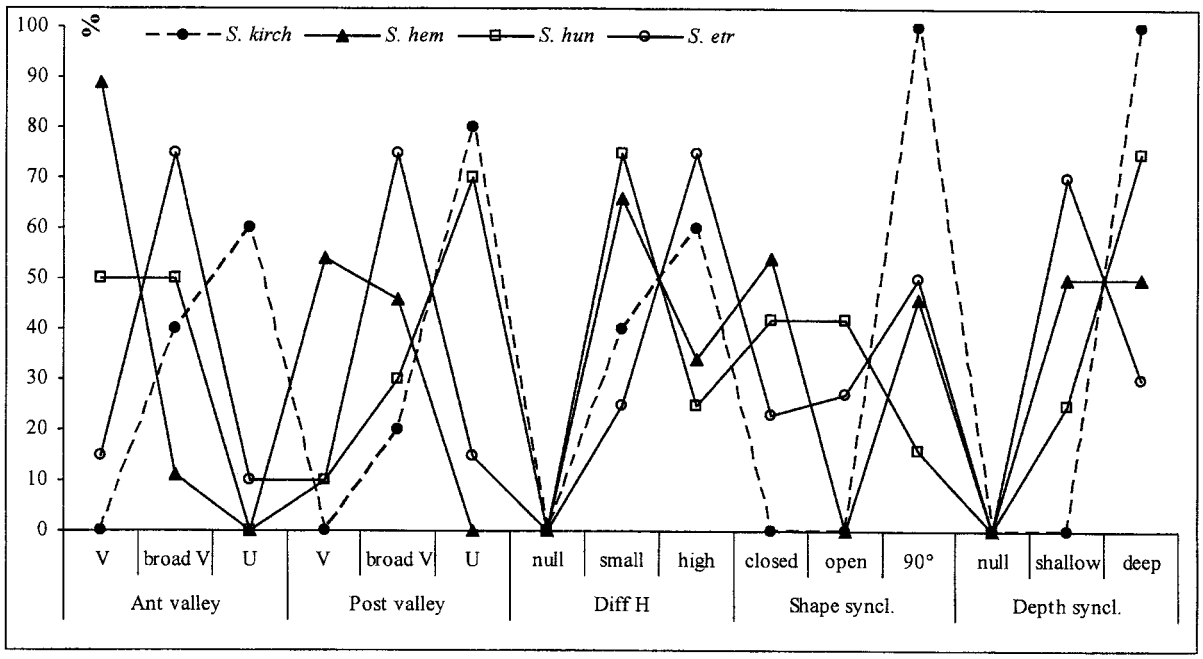

Fig. 26. Percentage distributions of qualitative character states for the lower M3 of the Pleistocene *Stephanorhinus*.

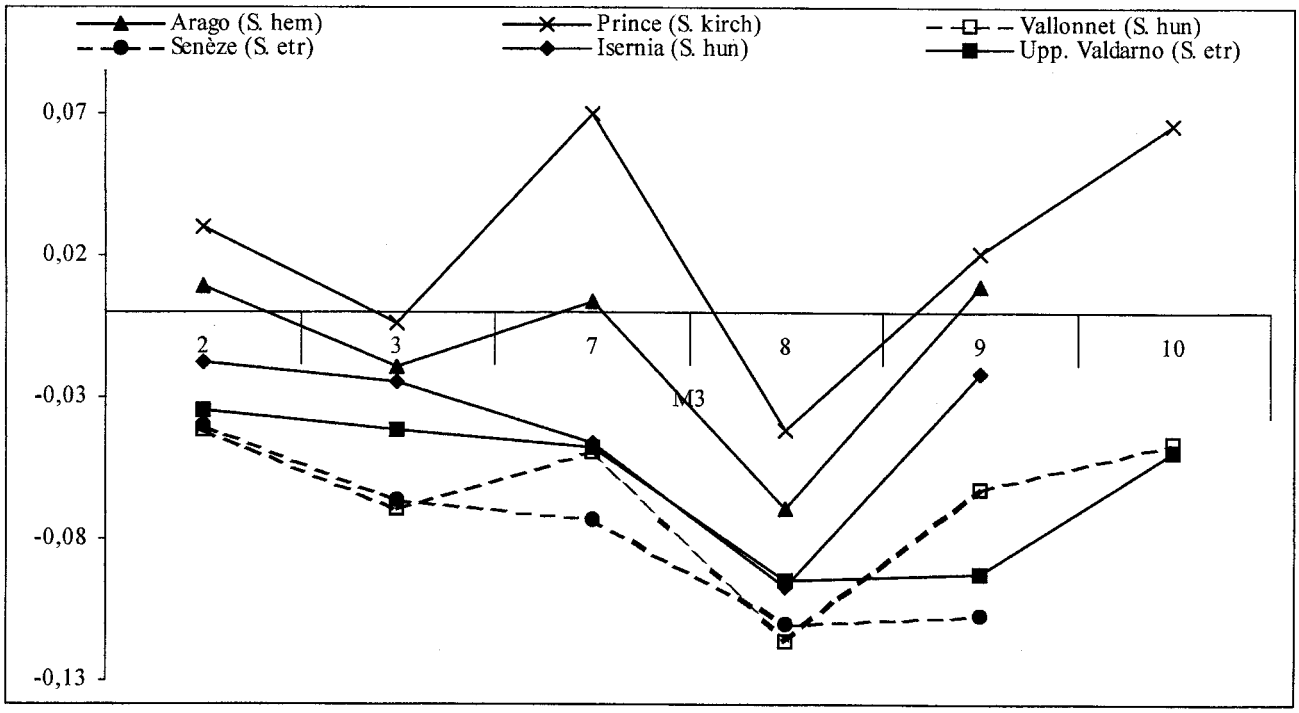

Fig. 27. Ratio diagram of the lower M3 of the Pleistocene *Stephanorhinus*. The referential is the present-day *Diceros bicornis*.

Table 16. Measurements (in mm) of the lower M3.

M/3 Measurement n°		2	3	5	6	7	8	9	10	11	12
Senèze *(S. etr)*	MEAN (N=3)	27,16	27,31	7,06	11,19	42,91	28,16	39,48	40,45		
	MIN	27,00	26,71	6,62	11,09	42,64	27,57	36,92	40,05	14,54	22,45
	MAX	27,32	27,90	7,50	11,30	43,18	28,74	42,40	40,85	19,02	24,34
Upper Valdarno *(S. etr)*	MEAN (N=19)	27,50	28,89	7,70	12,33	45,54	29,16	40,84	44,17		
	MIN	24,85	26,06	0,00	9,00	41,08	26,00	36,71	39,87	15,40	16,30
	MAX	30,63	32,19	12,93	16,51	48,36	33,44	43,95	47,48	35,00	43,15
Ceyssaguet *(S. hun)*	N=1		27,51		12,25			41,59		17,56	24,26
Vallonnet *(S. hun)*	MEAN (N=6)	27,07	27,09	7,35	8,46	45,32	27,77	43,80	44,44		
	MIN	24,36	26,57	7,00	7,80	45,11	26,49	43,00	43,96	13,00	11,10
	MAX	29,11	28,41	7,70	9,00	45,66	28,47	44,60	45,30	33,10	41,57
Tour de Grimaldi *(S. hun)*	N=1	26,69	26,80	7,62	9,95	43,66	27,56	43,23	45,98	32,93	39,33
Durfort *(S. hun)*	N=1	29,10	28,83	6,43	10,10	49,05	30,07	44,40	45,90	21,30	24,20
Soleilhac *(S. hun)*	N=1	32,29	29,73	6,95	10,80	46,31	29,47	44,66	46,99	23,80	26,90
Isernia *(S. hun)*	MEAN (N=15)	28,57	30,02	6,13	9,83	45,67	29,02	48,12			
	MIN	26,16	28,92	4,70	8,83	40,80	27,30	46,57		12,06	7,10
	MAX	30,11	31,96	8,18	10,90	51,60	31,30	49,60		30,57	38,50
Arago *(S. hem)*	MEAN (N=19)	30,42	30,40	9,12	10,61	51,22	30,89	53,27			
	MIN	27,05	26,49	5,15	7,48	46,78	27,08	46,22		14,16	13,43
	MAX	32,37	34,08	12,10	14,27	55,12	33,67	59,66		38,96	53,60
Terra Amata *(S. hem)*	N=1	27,44	27,33	9,55	12,82		27,59	41,02		25,20	30,13
Orgnac 3 *(S. hem)*	N=1	29,44	31,19	10,23	13,09	47,92	31,40	46,60	46,80	35,56	47,80
Prince Cave *(S. hem)*	N=1	29,59	31,51	14,41	15,00		32,30	47,75	43,25	32,39	34,94
Prince Cave *(S. kirch)*	MEAN (N=5)	31,88	31,49	11,60	16,64	59,68	32,97	53,02	57,59		
	MIN	26,21	29,53	9,22	12,22	55,00	30,56	48,00	51,94	31,08	36,36
	MAX	38,18	32,69	17,24	23,39	61,74	36,97	57,62	60,05	48,24	64,73

The posterior valley is broad V-shaped in *S. etruscus* and *S. kirchbergensis*. It is as often V-shaped as broad V-shaped in *S. hundsheimensis*. The V-shaped morphology is less frequent in *S. hemitoechus*.

The differences of height between the bottom of the valleys is small in *S. hundsheimensis* (5/6 = 0,92). It is more important in *S. kirchbergensis* (5/6 = 0,64) and *S. etruscus* (5/6 = 0,62) and average in *S. hemitoechus* (5/6 = 0,67 to 0,79).

The mesial, vestibular and lingual cingulum are absent on the lower D3 of the Pleistocene *Stephanorhinus*. The distal cingulum can be observed in *S. etruscus* and *S. hundsheimensis*. It is more frequent in *S. hundsheimensis*. Only *S. kirchbergensis* presents a closed vestibular syncline. The other species have an opened syncline. The depth of this syncline is deep in *S. kirchbergensis*. It is shallow in the other species.

The Simpson diagram (Fig. 28) clearly differentiates *S. kirchbergensis*, by its large size (Table 19) and its proportions. The other species have similar dimensions and proportions.

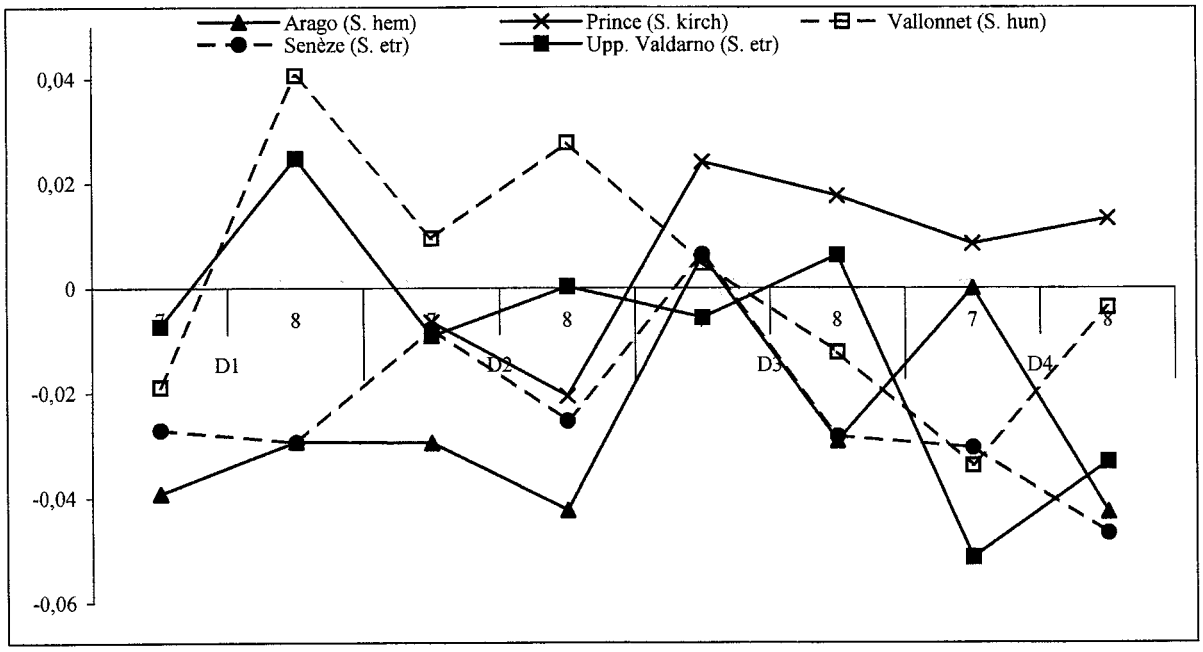

Fig. 28. Ratio diagram of the lower milk teeth of the Pleistocene *Stephanorhinus*. The referential is the present-day *Diceros bicornis*.

Table 17. Measurements (in mm) of the lower D1.

D/1 Measurement n°		2	3	7	8	9	10	11	12
Senèze *(S. etr)*	N=1			17,52	9,55				15,28
Upper Valdarno *(S. etr)*	MEAN (N=3)	17,82	13,91	29,82	16,61	28,09	27,81	17,83	20,76
	MIN	17,48	13,26	28,73	15,94	26,29	25,61	16,83	19,68
	MAX	18,26	14,28	30,86	16,98	29,93	29,23	18,78	22,12
Upper Valdarno *(S. etr)*	MEAN (N=2)	10,57	9,21	18,34	10,82	17,12	16,57	16,64	16,02
	MIN	10,53	8,82	18,17	10,67	16,50	16,54	14,14	15,65
	MAX	10,60	9,60	18,51	10,97	17,74	16,60	19,14	16,39
Vallonnet *(S. hun)*	MEAN (N=7)	11,20	9,19	17,86	11,22	16,04	15,63		
	MIN	10,33	8,84	16,60	10,48	15,33	14,20		11,81
	MAX	12,44	9,96	20,46	12,44	17,00	17,58		16,60
Isernia *(S. hun)*	N=1			19,20	13,80				16,70
Arago *(S. hem)*	MEAN (N=6)			17,04	9,55			14,39	12,87
	MIN			15,12	8,18			11,58	10,83
	MAX			20,50	10,63			17,16	17,16
Orgnac 3 *(S. hem)*	N=1			17,91	8,64				10,80
Mars Cave (*S. hem*)	N=1			24,31	12,93			17,36	18,00

Table 18. Measurements (in mm) of the lower D2.

D/2 Measurement n°		2	3	5	7	8	9	10	11	12
Senèze *(S. etr)*	MEAN (N=3)	15,15	11,82		29,91	15,66	28,36	28,46		
	MIN				29,28	15,10	27,46	26,52	13,36	14,33
	MAX				30,55	16,62	29,07	30,41		17,33
Upper Valdarno *(S. etr)*	MEAN (N=4)	21,56	19,49	8,35	38,45	21,66	38,36	36,98	18,10	21,58
	MIN	20,94	19,01	6,44	37,90	21,66	36,53	35,55	17,90	20,23
	MAX	21,98	19,80	10,00	39,00	21,66	40,18	38,40	18,32	23,40
Vallonnet *(S. hun)*	MEAN (N=9)	17,49	14,34		31,12	17,69	30,59	29,54		
	MIN	15,74	13,35	14,89	28,50	15,46	27,85	26,81	12,96	14,89
	MAX	18,58	15,28	20,58	32,87	18,95	32,75	31,97	16,49	23,95
Arago *(S. hem)*	MEAN (N=9)				28,45	15,06				
	MIN				27,17	14,19				8,24
	MAX				30,67	16,06				24,51
Orgnac 3 *(S. hem)*	N=1				25,70	13,80				16,40
Mars Cave *(S. hem)*	N=1	21,26	16,59	10,89	33,36	21,00	32,06	31,69	18,66	23,58
Observatoire Cave *(S. hem)*	N=1	14,31	12,43	11,06	29,37	14,74	25,73	27,87	19,76	25,23
Prince Cave *(S. kirch)*	N=1	15,93	13,75		28,67	16,17	27,99	25,14	13,92	17,09
Grotte des Enfants *(S. kirch)*	N=1	16,80	11,56		30,00	15,83	26,35	27,15	17,06	23,22

Table 19. Measurements (in mm) of the lower D3.

D/3 Measurement n°		2	3	5	6	7	8	9	10	11	12
Senèze *(S. etr)*	MEAN (N=3)	20,05	18,52	7,71	12,35	39,53		40,44	39,31		
	MIN					38,53			38,45	14,17	15,90
	MAX					40,72			40,00		17,33
Upper Valdarno *(S. etr)*	MEAN (N=3)	23,15	22,92	9,10	12,34	38,47	22,70	36,92	38,01	23,65	26,85
	MIN	22,76	22,51	8,98	11,91	37,82	22,70	36,44	37,91	22,27	25,69
	MAX	23,53	23,75	9,22	13,17	39,11	22,70	37,40	38,10	25,02	28,16
Vallonnet *(S. hun)*	MEAN (N=9)	21,53	19,75	8,29	8,98	39,38	20,76	40,41	39,39		
	MIN	20,53	19,11	7,02	9,14	38,15	19,20	38,70	37,19	11,34	11,23
	MAX	22,79	20,65	9,16	13,50	41,70	21,41	43,00	41,11	20,46	28,41
Arago *(S. hem)*	MEAN (N=13)	20,80	19,19	8,09	12,12	39,51	19,96	34,76			
	MIN	19,56	18,70	4,16	10,62	37,09	19,24	21,48		12,96	14,26
	MAX	23,10	19,96	12,00	13,73	43,02	21,47	40,34		28,26	37,40
Observatoire Cave *(S. hem)*	N=1		19,45		14,43					25,56	
Prince Cave *(S. kirch)*	MEAN (N=2)	21,41	10,57	9,44	10,73	38,31	21,76	34,89	35,69		
	MIN	21,34	19,30			37,73	21,12	32,90	33,25	12,98	18,53
	MAX	21,47	19,84			38,88	22,40	36,87	38,12	31,81	38,23
Grotte des Enfants *(S. kirch)*	N=1	21,78	20,73	9,02	14,14	41,17	22,23	40,69	40,87	22,21	25,68

Lower D4

(Fig. 28, Table 20)

The anterior valley is V-shaped in *S. etruscus*. It is V-shaped or broad V-shaped in *S. hemitoechus*. The broad V-shaped valleys are rare in *S. hundsheimensis*. The anterior valley of the lower D4 of *S. kirchbergensis* is U-shaped.

The posterior valley is broad V-shaped in *S. etruscus* and *S. kirchbergensis*. It can also be V-shaped in *S. hemitoechus*; this morphology is rare in *S. hundsheimensis*.

The differences of height between the bottom of the valleys is large in *S. etruscus* (5/6 = 0,60) and *S. kirchbergensis* (5/6 = 0,61 to 0,64). It is small in *S. hemitoechus* (5/6 = 0,82 to 0,87) and *S. hundsheimensis* (5/6 = 0,92).

The mesial cingulum is absent in *S. etruscus*. It is present in the other species with a variable frequency. The distal cingulum is absent in *S. kirchbergensis*. It can be observed in the other species. The lingual and vestibular cingula have never been observed on this tooth.

The vestibular syncline is obtuse in *S. hundsheimensis*. It is obtuse to right-angled in *S. etruscus* and always right-angled in *S. hemitoechus*. It is sharp in *S. kirchbergensis*. Its depth is shallow in *S. hundsheimensis*. It is strong on the lower D4 of the other Pleistocene species.

The Simpson diagram (Fig. 28) clearly differentiates *S. kirchbergensis* by it dimensions and proportions. The lower D4 of *S. hundsheimensis* have a similar length to that of *S. etruscus*, but clearly broader. *S. hemitoechus* follows an inverse rule, longer than that of *S. etruscus*, the breadth of its lower D4 is comparable to this last species.

Table 20. Measurements (in mm) of the lower D4.

D/4 Measurement n°		2	3	5	6	7	8	9	10	11	12
Senèze *(S. etr)*	MEAN (N=3)	22,08	20,56	6,29	10,41	40,36		38,90	37,96		
	MIN					39,50			36,49	16,37	21,79
	MAX					41,84			39,19		23,43
Upper Valdarno *(S. etr)*	MEAN (N=3)	23,15	22,92	9,10	12,34	38,47	22,70	36,92	38,01	23,65	26,85
	MIN	22,76	22,51	8,98	11,91	37,82		36,44	37,91	22,27	25,69
	MAX	23,53	23,75	9,22	13,17	39,11		37,40	38,10	25,02	28,16
Vallonnet *(S. hun)*	MEAN (N=7)	24,30	22,04	10,47	11,34	40,05	24,29	39,46	39,77		
	MIN	23,20	20,81	9,09	9,09	38,10	23,42	37,56	38,46	13,97	19,20
	MAX	25,84	23,51	13,44	13,44	41,99	25,46	42,51	41,63	27,30	35,70
Isernia *(S. hun)*	MEAN (N=3)					41,17	24,50				
	MIN					40,00					23,41
	MAX					42,39					29,60
Arago *(S. hem)*	MEAN (N=11)	23,97	21,85	9,40	11,53	43,31	22,21	43,74			
	MIN	22,29	20,43	7,83	9,65	40,23	20,03	40,37		12,12	11,70
	MAX	25,52	24,49	11,95	13,93	46,84	25,47	46,37		28,87	42,00
Prince Cave *(S. kirch)*	N=1	24,65	23,96	7,70	12,70	41,74	24,53	40,50	39,30	23,04	28,34
Grotte des Enfants *(S. kirch)*	N=1	23,26	23,33	7,86	12,12	44,15	25,26	37,25	39,40	27,68	34,18

Conclusions

Detailed study of the upper and lower teeth of the four different species of *Stephanorhinus* from Mediterranean Europe and the Massif Central permits a morphological and biometrical discrimination, despite the fact that the morphological characters of the teeth of the species are similar.

The quantification of the qualitative data gives us further information on the specific characters of fossil rhinoceroses from Mediterranean Europe: the morphological characters are described. Some are specific to the four species (upper teeth: shape of the crochet, crista, antecrochet, mediofossette, paracone fold and protocone constriction – lower teeth: shape of the valleys, difference in height of the bottom of the valleys, shape of the vestibular syncline). These characters have quite constant frequencies within each species. Cingula are more variable in any given species but their presence or absence seems to be characteristic. However, the angle between the crochet and the metacone on the upper teeth and the depth of the vestibular syncline on the lower teeth are too variable to be taken into account in the further studies.

The teeth of the Pleistocene species of the genus *Stephanorhinus* are characterised as following:

- *Stephanorhinus etruscus* possesses upper premolars with a single crochet, a crista absent or present, no antecrochet and an open mediofossette. The protocone constriction is never observed. The mesial and lingual cingula are the only cingula existing on these teeth. The paracone fold is not very prominent. The crochet is always single on the upper molars, while the crista is often absent. The antecrochet is observed on the third upper molar. The mediofossette is open and the mesial cingulum is the only cingulum. The protocone constriction is present on the two first upper molars. The paracone fold is still not very prominent. The upper milk teeth possess a single crochet, the crista is only absent on the D4. The antecrochet is rare and the mediofossette is equally open or closed. The protocone constriction is observed on the D2, D3 and D4. The lower premolars show a V-shaped or broad V-shaped anterior valley, while the posterior valley is only V-shaped. A light vestibular cingulum can be present. The anterior and posterior valleys of the upper molars are broad V-shaped or U-shaped. A light vestibular cingulum can also be present. The milk teeth possess a V-shaped anterior valley and a broad V-shaped posterior valley. The distal cingulum is present.
- *Stephanorhinus hundsheimensis* possesses a single or double crochet on the upper premolars. The crista is often present, the antecrochet could be observed. The mediofossette is equally open or closed. The mesial and lingual cingulum are always present, the protocone constriction is absent. The paracone fold is thin and slightly prominent. The upper molars show a single crochet, a crista equally present or absent and a rare antecrochet. The mediofossette is open. The mesial cingulum is always observed while the lingual cingulum is less frequent. The protocone constriction is rare; the paracone fold is wide and prominent. The crochet is simple on the upper milk teeth, the crista is rare only on the D4; the antecrochet is not frequent. The mediofossette is normally closed on the three first upper milk teeth and open on the last one. The protocone constriction exists on the upper D3 and D4. The anterior valley of the lower premolar is V-shaped, the posterior valley can also be eventually broad V-shaped. The four cingula have been observed on these teeth. The molars possess a V-shaped or broad V-shaped anterior valley while the posterior valley is broad V-shaped and U-shaped (lower M3). The mesial and distal cingula are normally present. The lower milk teeth show a V-shaped anterior valley and a broad V-shaped posterior valley. A distal and a mesial cingulum can be observed on the lower D3 and D4.
- The upper premolars of *Stephanorhinus hemitoechus* possesses, in majority of the cases a single crochet. The crista is present on the upper P2. The antecrochet is rare, the mediofossette is open. The protocone constriction is not observed, whereas the mesial and lingual cingula are. The paracone fold is prominent on the ectolophe. The upper molars show a single crochet and a rare crista. The antecrochet and the protocone constriction are also rare. The mesial cingulum is the only cingulum observable. The paracone fold is very prominent. The upper milk teeth show a single crochet, a crista equally present or absent, no antecrochet, a closed mediofossette and a protocone constriction on the upper D4. The lower premolars possess an anterior and a posterior valley V-shaped. The mesial and distal cingula are not frequently present. The anterior and posterior valley of the lower molars are V-shaped, a broad V-shaped morphology is also possible on the posterior valley. The lingual cingulum is the only cingulum which has never been observed on these teeth. The anterior valleys of the lower milk teeth of this species are V-shaped whereas the posterior valleys are broad V-shaped. The mesial and distal cingulum could be observed.

– The crochet on the upper premolars of *Stephanorhinus kirchbergensis* is frequently multiple. The crista and the antecrochet are normally absent, the mediofossette is open. The protocone constriction and the mesial cingulum are observed on the upper premolars. The paracone fold is very little prominent or absent. The crochet and the crista are single on the upper molars. The antecrochet exists on the upper M2 and M3. The protocone constriction is absent, the mesial cingulum is present. The ectolophe of the upper molars are lightly wavy without any well distinguishable paracône fold. The anterior valleys of the lower teeth are U-shaped. The posterior valley is broad V-shaped on the lower premolars and U-shaped on the lower molars. All the cingula show a variable frequency on the lower premolars, whereas the mesial, distal and vestibular cingula are more often present on the lower molars. The valleys of the lower milk teeth show the same morphology as that of the definitive teeth, and they do not possess any cingulum.

Biometrical data confirms the morphological results by the size and the proportions on each tooth of each species. The developed and hypsodont P2-P3 segment and the relatively reduced M3 of *S. hundsheimensis* and *S. kirchbergensis* give to these two species an archaic character compared with the more brachyodont and reduced P2-P3 segment and the relatively more developed M3 of *S. etruscus* and *S. hemitoechus*. This characteristic is also true within the evolution of *S. hundsheimensis* and *S. hemitoechus*. This is an evolutionary character useful for biochronology and also with phylogenic implications. The 'archaic' or 'small form' *S. hundsheimensis* seems to have a closer relation to the Early Villafranchian *S. jeanvireti* (FORTELIUS et al., 1993; LACOMBAT 2004–2005) than to the more evolved *S. etruscus*. In the same way, the qualitative and quantitative data of *S. hemitoechus* brings it closer to *S. etruscus* than *S. hundsheimensis*. The archaic and large *S. kirchbergensis* does not have a close relationship with the three other species. Its Asian origin (CHOW 1979, GUÉRIN 1980, FORTELIUS et al. 1993, CERDENO 1997 and VAN DER MADE 2000) suggests an alternative lineage of the genus *Stephanorhinus*.

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References

CERDENO, E. (1997): Diversity and evolutionary trends of the family Rhinocerotidae (Perissodactyla). – Paleogeogr. Paleoclimat. Paleoecol., **141:** 13–34.

CHOW, B. (1979): The fossil rhinocerotides of Locality 1, Choukoutien. – Vert. Pal. Asiatica, 17(3): 236–258.

FALCONER, H. (1868): Palaeontological memoirs and notes, vol. II Mastodon, elephant, rhinoceros, ossiferous caves, primeval man and his cotemporaries. – 675 p., R. Hardwicke ed., London.

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, tav V., 1-16: 63–155, Pisa.

GROVES, C.-P. (1983): Phylogeny of the living species of rhinoceros. – Z. zool. Systematik u. Evolutionsforsch, **21:** 293–313.

GUERIN, C. (1980): Les rhinocéros (Mammalia, Perissodactyla) du Miocène terminal au Pléistocène supérieur en Europe occidentale. Comparaison avec les espèces actuelles. – Docum. laborat. géol. Lyon, **79** (1, 2, 3), 1185p.

HEISSIG, K. (1981): Probleme bei der cladistischen Analyse einer Gruppe mit wenigen eindeutigen apomorphen Rhinocerotidae. – Paläont. Z., **55:** 117–123.

–,– (1989): The Rhinocerotidae. – In: PROTHERO, D.R. & SCHOCH, R.M. (Eds.): The evolution of perissodactyls. – Oxford University Press, New York.

KAHLKE, H-D. (1965): Die Rhinoceotiden-Reste aus den Tonen von Voigtstdet in Thüringen. – Paläont. Abh., A **2** (2/3): 451–520.

–,– (1969): Die Rhinoceotiden-Reste aus den Kiesen von Süssenborn bei Weimar. – Paläont. Abh., A 3 (3/4): 667–709.

–,– (1975): Die Rhinoceotiden-Reste aus den Travertinen von Weimar-Ehringsdorf. – Paläont. Abh., A **23:** 337–398.

–,– (1977): Die Rhinoceotiden-Reste aus den Travertinen von Taubach. – Quartärpaläont., **2:** 305–359.

KRETZOÏ, M. (1942): Bemerkungen zum System der nachliozänen Nashorn-Gattungen. – Foldt. Kozl., **72:** 309–323.

LACOMBAT, F. (2003): Etude des rhinocéros du Pléistocène de l'Europe méditerranéenne et du Massif Central. Paléontologie, phylogénie et biostratigraphie. – 511 p., Thèse de Doctorat du Muséum National d'Histoire Naturelle. (inéd.)

–,– (eds) (2004–2005): Les grands mammifères fossiles du Velay. Les collections paléontologiques du Plio-Pléistocène du Musée Crozatier, Le Puy-en-Velay. – Ann. Amis Musée Crozatier, **13-14**: 208 p.

–,– (2005): Les rhinocéros fossiles des sites préhistoriques de l'Europe méditerranéenne et du Massif Central. Paléontologie et implications biochronologiques. – BAR Internat. Ser. **1419**: 175 p.

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

OSBORN, H.F. (1900): Phylogeny of the rhinoceroses of Europe. – Bull. Amer. Mus. Nat. Hist., **13:** 229–267, New York.

PROTHERO, D. R., GUERIN, C. & MANNING, E. (1989): The history of the rhinocerotoidae. – In: PROTHERO & SCHOCH (Eds.): The perissodactyls symposium (IV Theriological congress of Edmonton, Alberta, 1985). – Oxford University Press.

PROTHERO, D.R., MANNING, E. & HANSON, C.B. (1986): The phylogeny of Rhinocerotoidae. – Zool. J. Linnean Soc., **87:** 341–366.

SCHROEDER, H. (1903): Die Wirbelthier-Fauna des Mosbacher Sandes. 1. Gattung Rhinoceros. – Abh. kgl. Preuss. Geol. Landesanst., N.F., **18**: 143p.

–,– (1906): *Rhinoceros mercki* Jäger von Heggen im Sauerlande. – Kgl. Geol. Landesanst. Bergakad., **4:** 215–241, Berlin.

SIMPSON, G.G. (1941): Large Pleistocene Felines of North America. – Amer. Mus. Novit., **1136:** 1–27.

TOULA, F. (1902): Das Nashorn von Hundsheim. *Rhinoceros* (*Ceratorhinus* Osborn) *hundsheimensis* nov. form. – Abh. K.K. Geol. Reichsanst., **19** (1): 1–92.

–,– (1906): Das Gebiss und Reste der Nasenbeine von *Rhinoceros* (*Ceratorhinus* Osborn) *hundsheimensis*. – Abh. K.K. Geol. Reichsanst., **20** (2): 37p.

VAN DER MADE, J. (2000): A preliminary note on the rhinos from Bilzingsleben. – Praehistoria Thuringica **4**: 41–64.