Hors série - Numéro 2 - 2005 ISSN 1771 -1150

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sous la direction d'Évelyne Crégut-Bonnoure

AFEQ

Publié avec le concours de : Musée Requien, Ville d'Avignon ; Fondation Calvet ; Association des Amis du Musée Requien ; Conseil Général de Vaucluse ; Délégation Générale à la Langue Française et aux Langues de France

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International Journal of the French Quaternary Association

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« Actes Colloque international Avignon, 19-22 septembre 2000 »

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OSTEOLOGICAL INVESTIGATIONS ON SKELETON MATERIAL OF RHINOCEROSES (RHINOCEROTIDAE, MAMMALIA) FROM THE EARLY MIDDLE PLEISTOCENE LOCALITY OF MAUER NEAR HEIDELBERG (SW-Germany)

H. Dieter SCHREIBER*

ABSTRACT

The early Middle Pleistocene locality of Mauer near Heidelberg has yielded a rich and diverse faunal assemblage of fossil mammals. About a quarter of disarticulated finds belongs to material of rhinoceroses. In general complete and articulate skeletons of European Pleistocene rhinoceroses are rare. In this context the fossil remains of the nearly 20 m thick fluvial deposits of Mauer locality gives the opportunity to work on a large number of fossil remains of rhinoceroses which represent a relatively short geological time span.

By using morphological and metric characters of the skull, dentition and postcranial bones it is possible to assign the fossil remains from Mauer mainly to *Stephanorhinus hundsheimensis* (Toula, 1902). The variability of characters in comparision to other European Pleistocene rhinoceroses is also analysed. Additionally, it is possible to indentify the species *S. kirchbergensis* (Jäger, 1839) in Mauer in the case of some specimens of radius, II metacarpal, astragalus and III metatarsal. The present paper contains a selection of important examples (cranium, upper check teeth, radius, II metacarpal, astragalus, III metatarsal).

Key words: Rhinocerotidae, *Stephanorhinus hundsheimensis*, *Stephanorhinus kirchbergensis*, Mauer (Germany), early Middle Pleistocene, Osteology.

RÉSUMÉ

RECHERCHES OSTÉOLOGIQUES SUR LE SQUELETTE DES RHINOCÉROS (RHINOCEROTIDAE, MAMMALIA) DU GISEMENT PLÉISTOCÈNE MOYEN ANCIEN DE MAUER (HEIDELBERG, ALLEMAGNE)

Le gisement Pléistocène moyen de Mauer près de Heidelberg a livré un assemblage faunique riche en mammifères fossiles. Les rhinocéros représentent un quart des restes de la collection. En général, leurs squelettes complets et en connexion anatomique sont rares en Europe occidentale. Dans ce contexte, les restes des dépôts fluviatiles de Mauer, d'une épaisseur de 20 m représentant un temps géologique relativement bref, donnent l'occasion d'une analyse ostéologique sur une grande série d'ossements de rhinocéros fossiles.

L'étude des caractères anatomiques du crâne, de la dentition et du squelette post-crânien permet d'attribuer une grande partie de la collection à *Stephanorhinus hundsheimensis* (Toula, 1902). La variabilité des caractères est aussi comparée à celle des autres rhinocéros européens du Pléistocène. Quelques spécimens du radius, du métacarpien II, du talus et du métatarsien III sont attribuables à *S. kirchbergensis* (Jäger, 1839). Les données métriques des séries anatomiques les plus importantes sont aussi fournies (crâne, dentition supérieure, radius, métacarpien II, talus et métatarsien III).

Mots-clés : Rhinocerotidae, *Stephanorhinus hundsheimensis*, *Stephanorhinus kirchbergensis*, Mauer, Allemagne, base du Pléistocène moyen, ostéologie.

INTRODUCTION

The remains of the early Middle Pleistocene locality of Mauer near Heidelberg (SW-Germany) are usually disarticulated skeleton elements of fossil mammals. Nevertheless that quarry has yielded a rich and diverse faunal assemblage of fossil mammals (Koenigswald, 1997). About a quarter of the remains are material of rhinoceroses (Kraatz, 1992). At first this material of rhinoceroses was determined only by skulls and teeth (Wurm, 1912). Years ago some authors dealed additionally with the postcranial remains from Mauer (Guérin, 1980; Fortelius *et al.*, 1993).

The fossil remains of rhinoceroses from Mauer make it possible to show that the postcranial skeleton elements can be used for sufficient results in the case of taxonomic classifications and for the faunal assemblage of a locality, too. The rich sample (more than 1020 specimens) of the nearly 20 m thick fluvial deposits of the Mauer locality gives the opportunity to work on a great number of fossil remains of rhinoceroses, which geologically represent a relative short periode of time.

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Manuscrit reçu le 07/02/2001, accepté le 25/03/2003

Rhinoceroses of the genera *Stephanorhinus* and *Coelodonta* occur in the European Pleistocene. The early representatives of both genera occur in Eurasia since the Pliocene. *Coelodonta* mainly expand its distribution area in the Late Pleistocene from Asia to W-Europe, while the Stephanorhines remained in Europe since the Pliocene. The taxonomic classification of the European Pleistocene Stephanorhines follows the topical opinion of Fortelius *et al.* (1993):

Family	Rhinocerotidae Gill, 1872
Subfamily	Rhinocerotinae Dollo, 1885
Genus	*Stephanorhinus* Kretzoi, 1942 *Brandtorhinus* Guérin, 1989
(Type-)Species	*Stephanorhinus etruscus* (Falconer, 1868) *Rhinoceros etruscus* Falconer, 1868 *Dicerorhinus* (*Brandtorhinus*) *etruscus etruscus* Guérin, 1980
Species	*Stephanorhinus hemitoechus* (Falconer, 1868) *Rhinoceros hemitoechus* Falconer, 1868
Species	*Stephanorhinus hundsheimensis* (Toula, 1902) *Rhinoceros hundsheimensis* Toula, 1902 *Rhinoceros etruscus heidelbergensis* Freudenberg, 1914 *Dicerorhinus handzellensis* Wang, 1928 *Dicerorhinus hemitoechus intermedicus* Cigala-Fulgosi, 1976 *Dicerorhinus* (*Brandtorhinus*) *etruscus brachycephalus* (Schroeder, 1903) in Guérin (1980)
Species	*Stephanorhinus kirchbergensis* (Jäger, 1839) *Rhinoceros kirchbergense* Jäger, 1839 *Rhinoceros merckii* Kaup, 1841.

The remains of rhinoceroses in Mauer are described by comparative morphological and metric investigations of skulls, teeth and postcranial material from Mauer and other localities, especially Hundsheim (Austria, type locality of *S. hundsheimensis*) and Mosbach (SW-Germany) in a diploma thesis by the author (Schreiber, 1999, unpublished). The investigations based on important papers from Toula (1902, 1906), Schroeder (1903), Wurm (1912), Freudenberg (1914), Wüst (1922), Borsuk-Bialynicka (1973), Guérin (1980), Prothero *et al.* (1986), Mazza (1988) and Fortelius *et al.* (1993). The variation in characters and sizes of the fossil remains could be estimated. The measurements which are used follow the standard methodology described by Von Den Driesch (1976) but based mainly on the measurements given by Guérin (1980) and Fortelius *et al.* (1993) for ease of comparison with the literature. In the present paper six skeleton elements are chosen as important examples with the most sufficient morphometric characters distinguishable at the moment.

DESCRIPTION

Cranium

Three nearly complete skulls are derived from Mauer (HMLD: Mau 85 (fig. 1), GPIH: M.298, M.350). These dolichocephalic skulls have a nasal and a frontal hornbase rugosity and a partial ossified nasal septum. An anterior dentition is lacking. The skulls show the typical feature of *Stephanorhinus* described by Fortelius *et al.* (1993).

The important characters on the Cranium to separate the species of *Stephanorhinus* are the positions of the posterior rim of the nasal incision and the anterior rim of the orbit in relation to the tooth row. Another character is the degree of the caudal elongation of the Crista lambdoidalis. These characters will be proved vertically to a 'reference level' (RL) which is nearly parallel to the palatinum region and defined by the crown bases of the mesial P2 and the distal M3 (fig. 1).

The Cranium Mau 85 (fig. 1) shows a weak caudaly elongated Crista lambdoidalis. The posterior rim of the nasal incision is situated above P4 and the anterior rim of the orbit reaching back above M2. The Crania M.298 and M.350 have the same conditions as mentioned before. Just M.350 has more posteriorly shifted positions

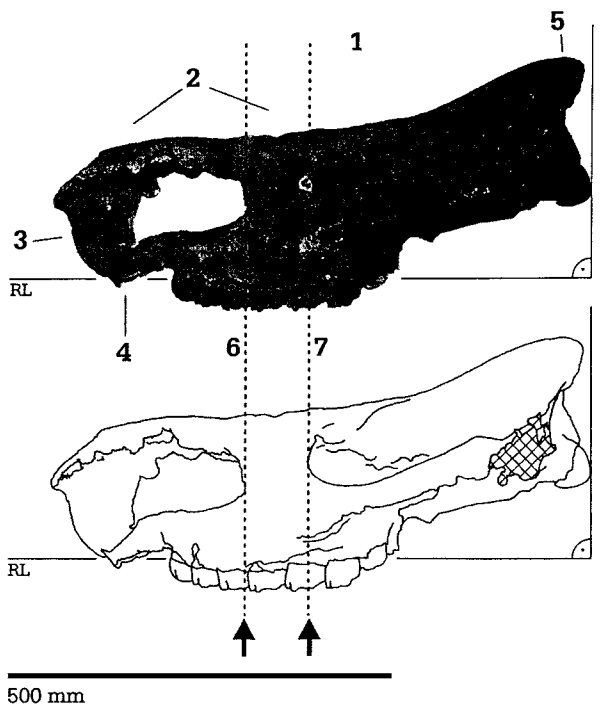

Figure 1: Characters on the Cranium of *Stephanorhinus hundsheimensis* (Toula, 1902), Mauer, Mau 85, HLMD, lateral, sin (photography and drawing). 1- dolichocephalic shape of cranium; 2- nasal and frontal horn; 3- partial, anterior ossified nasal septum; 4- lack of anterior dentition (completely reduced); 5- weak caudaly elongated *Crista lambdoidalis*; 6- nasal incision above P4/M1; 7- orbit above M2 (RL – reference level).

Figure 1 : Caractères crâniens de *Stephanorhinus hundsheimensis* (Toula, 1902), Mauer, Mau 85, lateral, gauche, HLMD (photographie et dessin). 1- contour dolichocephalique du crâne ; 2- corne nasale et frontale ; 3- cloison nasale partiellement ossifiée antérieurement ; 4- denture antérieure réduite ; 5- *Crista lambdoidalis* moins élargie caudalement ; 6- échancrure nasale au-dessus de P4/M1 ; 7- orbite au-dessus de M2 (RL – plan de référence).

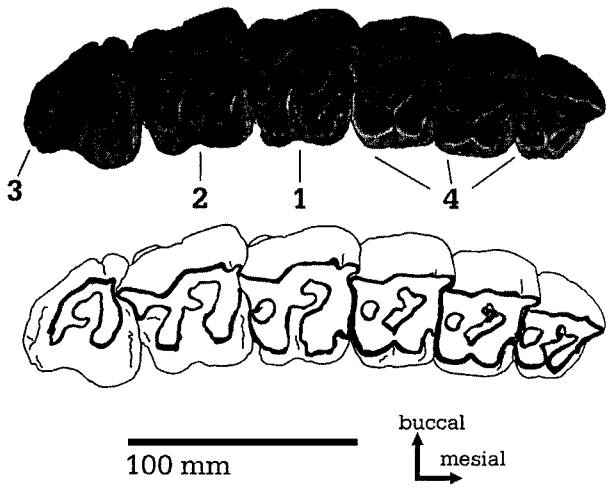

Figure 2: Characters on upper cheek theeth of the Cranium of *S. hundsheimensis* (Toula, 1902), Mauer, Mau 85, HLMD, P2 to M3, dex (photography und drawing). 1- Median valley in cross section on M1 wide and V-shaped, 2- Median valley on M2 wide and U-shaped, 3- transvers lophs lingually not inflated, 4- no lingodistal cingulum on the premolars.
Figure 2 : Caractères de la dentition supérieure du crâne de *S. hundsheimensis* (Toula, 1902), Mauer, Mau 85, HLMD, P2 à M3, spécimen droit (photographie et dessin). 1- vallée mediane large et en V sur M1 ; 2- vallée mediane large et en U sur M2 ; 3- lophes transversaux sans renflement lingual ; 4- absence de cingulum linguo-distal sur les prémolaires.

Cranium	1.	2.	4.	8.	9.	22.
Mauer: *S. hundsheimensis* (TOULA, 1902)						
M.350	~ 710	~ 740	~ 95	~ 185	~ 320	-
M.298	-	~ 690	-	-	-	~ 225
Mau 85	710,5	~730	85	265	320	245
Hundsheim: *S. hundsheimensis* (TOULA, 1902); * TOULA (1906)						
1H	-	-	-	206	312	250*
S. etruscus (FALCONER, 1868)						
N	13	11	19	4	14	12
μ	615,31	620,64	105,47	187,25	287,68	230,71
min	530	530	90	162	253,5	220
max	648	655	123	200	324	245
S. hundsheimensis (TOULA, 1902)						
N	12	9	12	6	7	16
μ	706,17	691,56	99,5	216,58	315,57	243,91
min	640	605	81	172	270	226
max	750	760	122	263	340	263,5
S. kirchbergensis (JÄGER, 1839)						
N	3	2	4	3	4	5
μ	708	735	112,5	227,33	342,75	272,6
min	634	730	89	216	297	266
max	780	740	133	246	380	289,5

Table 1: Assemblage of measurements of the skulls from Mauer and statistical parameters for *S. etruscus*, *S. hundsheimensis* and *S. kirchbergensis* based on Guérin (1980). Abbreviations of dimensions: 1- skull length from occipital condyle to tip of nasals, 2- skull length from Crista lambdoidalis to the tip of nasals, 4- distance from anterior rim of orbit to posterior rim of nasal incision, 8- greatest skull width over orbits, 9- greatest skull width over zygomatic arches, 22- buccal length of upper check teeth (P2-M3).
Tableau 1 : Dimensions des crânes de Mauer et paramètres statistiques de *S. etruscus*, *S. hundsheimensis* et *S. kirchbergensis* d'après C. Guérin (1980). Abréviations des mesures: 1- distance occipito-nasale, 2- distance nasal-chignon, 4- distance échancrure nasale-orbite, 8- largeur aux processus post-orbitaires, 9- largeur maximale aux arcades zygomatiques, 22- longueur buccale de la rangée dentaire.

of the nasal incision (above P4/M1) and the orbit (above M2/M3).

In comparison the skull from the type-specimen of Hundsheim (NMW) has the similar conditions. The nasal incision is above P4/M1 and the orbita reaches above M2 (Toula, 1902, Taf. 2, fig.2). The specimens from Mosbach of *S. hundsheimensis* shows the positions of the nasal incision and the orbita above P4-M1 and M2-M2/M3 (NMM: 1958/764, 1956/963, 1977/13, 1945/172). Their Crista lambdoidalis is caudaly weak elongated. Two specimens of *S. kirchbergensis* from Mosbach have the positions above P3-P4 and M1/M2-M2, with a hardly caudaly elongated Crista lambdoidalis (NMM: 1956/62, 1996/113). The conditions in the skull of *S. kirchbergensis* from Daxlanden (SMNK: Qp/650) with the positions above P3 and M1/M2 are quite similar to the skulls of the same species from Mosbach.

The positions of nasal incision and the orbita are given for *S. etruscus* above P4 and M2, for *S. hundsheimensis* above P4/M1 and M2, and for *S. kirchbergensis* above P3-P4 and M1 by Guérin (1980) and Fortelius *et al.* (1993). The posterior rim of nasal incision in relation to the tooth row is more retracted in *S. hundsheimensis* than in *S. etruscus*, especially in *S. kirchbergensis*. In *S. hundsheimensis* the position of the anterior rim of the orbita is situated slightly more backwards than in *S. etruscus* and *S. kirchbergensis* but there is a larger variability. The caudal elongation of the Crista lambdoidalis is in *S. kirchbergensis* distinctly weaker than in *S. etruscus* and *S. hundsheimensis*.

The skulls from Mauer have quite similar dimensions in the length and breadth (1., 2., 8., tabl. 1) like *S. hundsheimensis*. The skull from Hundsheim are on the same degrees, too. *S. etruscus* is smaller and *S. kirchbergensis* has usually higher values, especially in the length of the upper tooth row (22). The three crania from Mauer are assigned to *S. hundsheimensis* (Toula, 1902).

Upper cheek teeth

In general, all upper check teeth from Mauer were brachydont. Their occlusal surface is ectolophodont and they lack coronal cement, corresponding to an less rough enamel.

A wide Median valley between protocone and hypocone exists on the molars M1 and M2 from Mauer (Wurm, 1912). The same conditions are also mentioned in material from Mosbach and Hundsheim by Wurm. The tooth rows of the three crania (Mau 85 (fig. 2), M.298, M.350) and the fragmented tooth rows from Mauer (SMNK: M.395, M.776, M.780, M.2232.3,7-9, M.1737/1738/1745, M.2233, M.2234, HLMD: Mau 132) have M1 with a wide Median valley, V-shaped and sometimes U-shaped in cross section. The Median valley of M2 is wide and mainly U-shaped. Additionaly, these tooth rows have no lingual inflated transverse lophs. A great number of isolated M1 and M2 (N = 67) supplements the feature that the Median valley of M1 is mainly wide and V-shaped with a high percentage of U-shaped Median valleys (37% of all M1 in Mauer). The M2 have wide and U-shaped median valleys.

On the other hand M1 and M2 of *S. etruscus* and *S. kirchbergensis* show a narrow Median valley (Wurm, 1912; Mazza, 1988). Similarly, Schroeder (1903) speaks about these morphological differences. He decribes the features on the Median valleys of the tooth rows, assigned to *S. kirchbergensis* from serveral localities, as V-shaped (Schroeder, 1903; Taf. 5; Taf. 7, Fig. 2; Taf. 9, Fig. 2 a-b; Taf. 14, Fig. 1 a-b). Other figures in this paper also show tooth rows from the Mosbach locality with the conditions of *S. hundsheimensis* but they are assigned to ‚*etruscus*' (Schroeder, 1903; Taf. 4; Taf. 6, Fig.1; Taf. 10). Generally the premolars always have a narrow V-shaped Median valley. On M3 the conditions of the Median valley are variable.

The material from Mauer clarifies the variability of the M1 and M2 morphology and makes it possible to modify the description of the dental characters. The M1 of *S. hundsheimensis* have a wide Median valley which is predominantly V-shaped in cross section but very often U-shaped and rarely narrow. The Median valley of M2 is wide and U-shaped, rarely V-shaped. On the other hand *S. etruscus* und *S. kirchbergensis* show a narrow and V-shaped Median valley on M1 and M2. On M2 the Median valley could be slightly widened.

Additionally, the lingual inflated transverse lophs in the whole tooth row (Fortelius *et al.*, 1993) could be used to determine *S. kirchbergensis*. The disto-lingual portion of the lingual cingulum on the premolars (Mazza, 1988) characterize *S. etruscus*.

The sizes of the teeth (esp. MBB) of Mauer and Hundsheim are quite similar and in the same degrees like *S. hundsheimensis* (tabl. 2). The teeth of *S. etruscus* are some degrees smaller and the teeth of *S. kirchbergensis* are some degrees larger. The teeth of Mauer especially the teeth of the skulls are assigned to *S. hundsheimensis* (Toula, 1902).

Radius

On the distal epiphysis of the radii from Mauer (SMNK: M.477, M.480, M.838, M.1730 (fig. 3, a)) and Hundsheim (NMW: Holotype-specimens, Toula 1902, 1909II.540, 1909II.541, IPW: C38, C50, R') there is palmarly a slightly developed transverse groove, as named for *S. hundsheimensis* by Guérin (1980). They have also a similar size (tabl. 3). In *S. etruscus* this groove is weak (Mazza, 1988).

P2	BBL	MBB	P3	BBL	MBB	P4	BBL	MBB	M1	BBL	MBB	M2	BBL	MBB	M3	BBL	MBB
Mauer (upper check teeth): *S. hundsheimensis* (TOULA, 1902)																	
N	17	17	N	21	20	N	14	14	N	15	15	N	11	12	N	9	9
μ	33,71	38	μ	36,14	50,7	μ	40,29	55,43	μ	44,93	56,77	μ	50,23	57,75	μ	52,5	52,11
min	30	33	min	32	46	min	37	52	min	41	52	min	47,5	56	min	38	48,5
max	39,5	42	max	40	57	max	43	58	max	49	61	max	53	61	max	58,5	55
σ	1,969	2,995	σ	2,032	2,807	σ	1,816	1,616	σ	2,520	2,078	σ	1,862	1,545	σ	6,205	2,219
v	5,842	7,881	v	5,622	5,536	v	4,507	2,915	v	5,609	3,660	v	3,708	2,675	v	11,819	4,258
Med	34	38	Med	37	50,75	Med	40	55,75	Med	45	57	Med	50	57,5	Med	54	52
Mauer (isolated upper check teeth): *S. hundsheimensis* (TOULA, 1902)																	
N	13	12	N	25	24	N	13	12	N	19	17	N	19	18	N	21	20
μ	33,58	37,63	μ	38,04	50,08	μ	39,77	54,79	μ	47,74	56,82	μ	49,61	58,44	μ	53,67	53,15
min	31	34	min	33	40	min	37	50	min	41	51	min	46	55	min	49	48
max	38,5	45	max	43	55	max	44	60,5	max	52	62	max	53	62	max	59	58
σ	2,308	3,068	σ	2,746	2,962	σ	2,176	3,011	σ	3,066	3,428	σ	2,059	2,064	σ	2,497	2,183
v	6,874	8,155	v	7,218	5,915	v	5,471	5,495	v	6,422	6,032	v	4,150	3,532	v	4,652	4,107
Med	33	37,5	Med	38	50,5	Med	40	55	Med	48,5	58	Med	50	58	Med	54	53
Hundsheim: *S. hundsheimensis* (TOULA, 1902)																	
N	2	2	N	2	2	N	2	2	N	1	1	N	4	4	N	4	3
μ	-	-	μ	-	-	μ	-	-	μ	-	-	μ	53,25	62,25	μ	55,88	-
min	34	36	min	40	52,8	min	42,7	56,5	min	58,4	57,1	min	51	58	min	54,5	53,5
max	36,9	41,9	max	41,3	53	max	44	57	max	58,4	57,1	max	55	66	max	57	58
S. etruscus (FALCONER, 1868)																	
N	10	19	N	10	19	N	9	18	N	10	18	N	9	18	N	10	16
μ	32	38,11	μ	38,35	48,66	μ	39,89	54,69	μ	48	55,61	μ	49,89	57,25	μ	53,2	51,91
min	29	32	min	35	42	min	37	45	min	41	48	min	45,5	48	min	47	46
max	35	42,5	max	41	54	max	42,5	63	max	50,5	60,5	max	57	65,5	max	59	56,5
S. hundsheimensis (TOULA, 1902)																	
N	15	16	N	15	16	N	16	18	N	15	16	N	16	19	N	12	15
μ	34,5	38,59	μ	40,93	50,03	μ	43,09	54,69	μ	49,9	57,44	μ	53,88	59,42	μ	55,71	53,07
min	28,5	33	min	35	45	min	39	50	min	44	51	min	47	52	min	50,5	46
max	37,5	44	max	46	57,5	max	48,5	59	max	57,5	63	max	63	67	max	66	60
S. kirchbergensis (JÄGER, 1839)																	
N	4	7	N	4	7	N	5	5	N	4	7	N	4	6	N	-	-
μ	47,13	57,29	μ	51,88	63,64	μ	58,3	67,2	μ	64,75	67,57	μ	63,88	63,42	μ	-	-
min	45,5	50	min	50	56	min	52	60	min	61,5	62	min	63	59,5	min	-	-
max	49	63	max	53	69,5	max	63,5	71,5	max	67	72,5	max	65	68,5	max	-	-

Table 2: Assemblage of measurements and statistical parameters of the upper check teeth from Mauer and statistical parameters for *S. etruscus*, *S. hundsheimensis* and *S. kirchbergensis* based on Guérin (1980). Abbreviations of dimensions: BBL = buccal length, MBB = mesial width.

Tableau 2 : Dimensions et paramètres statistiques de la dentition supérieure des spécimens de Mauer et paramètres statistiques de *S. etruscus*, *S. hundsheimensis* et *S. kirchbergensis* d'après C. Guérin (1980). Abréviations des mesures: BBL = longueur buccale, MBB = largeur mesiale.

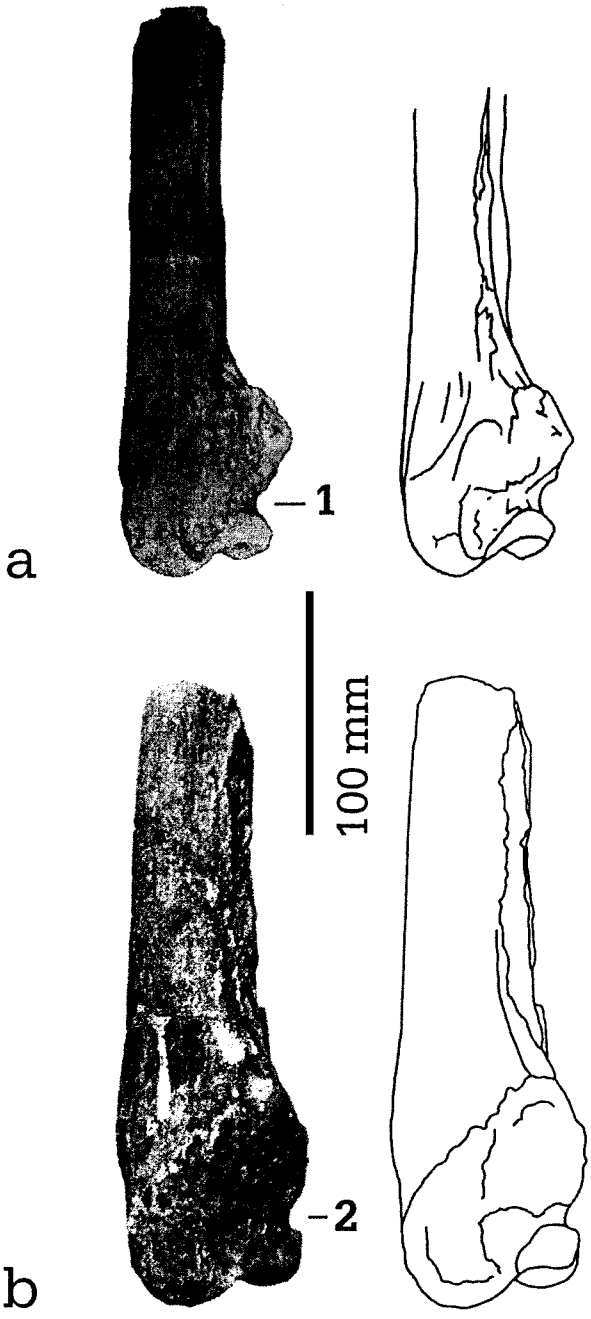

Figure 3: Characters on Radius of (a) *S. hundsheimensis* (Toula, 1902), Mauer, M.1730, SMNK, distal fragment, sin, lateral (photography and drawing), (b) *S. kirchbergensis* (Jäger, 1839), Mauer, M.478/479, SMNK, distal fragment, sin, lateral (photography and drawing). 1- slightly developed palmar transverse groove; 2- distinct and deep developed palmar transverse groove.

Figure 3 : Caractères morphologiques du radius de (a) *S. hundsheimensis* (Toula, 1902), Mauer, M.1730, SMNK, fragment distal, gauche, en vue latérale (photographie et dessin), (b) *S. kirchbergensis* (Jäger, 1839), Mauer, M.478/479, SMNK, extrémité distale, gauche, en vue latérale (photographie et dessin). 1- fosse transversale (en vue palmaire) moins distincte ; 2- fosse transversale (en vue palmaire) très distincte.

Radius	GLr	Bpr	Tpr	KDr	KTr	Bdr	Tdr
Mauer: *S. hundsheimensis* (TOULA, 1902)							
M.477	-	-	-	-	-	100,5	62,5
M.480	378	95	62,5	43	34,4	89	60,5
M.481	(351,5)+50	93,5	63,5	48,5	33	-	-
M.482	-	101	~65	-	-	-	-
M.483	-	~87	~60	-	-	-	-
M.486	-	95	57	-	-	-	-
M.494	-	91	60	-	-	-	-
M.501	-	97,5	68,5	<53	<39	-	-
M.502	-	96,5	62,5	-	-	-	-
M.1730	-	-	-	-	-	103	66
Mau 143	-	98	61,5	-	-	-	-
Mau 145	-	>89	62	-	-	-	-
Mau 420	-	106	76,1	-	40	-	-
Mau 421	-	101	72,2	-	39,3	-	-
M.838	388	99	62	46	31	91	64
N	3	11	11	4	6	4	4
μ	-	96,59	64,48	47,63	36,12	95,88	63,25
min	351,5	87	57	43	31	89	60,5
max	388	106	76,1	53	40	103	66
σ	-	5,214	5,675	4,230	3,804	6,909	2,327
v	-	5,399	8,801	8,883	10,534	7,206	3,680
Med	-	96,5	62,5	47,25	36,7	95,75	63,25
Mauer: *S. kirchbergensis* (JÄGER, 1839)							
M.478/479	(430)+10	104	71,5	55	38	109	86
Hundsheim: *S. hundsheimensis* (TOULA, 1902); * TOULA (1902)							
holotype*	400	103,5	67,5	48	-	100,5	59
1909II.540	-	-	-	-	-	99	58
1909II.541	-	-	-	-	-	96	67
Ohne Nr.1	-	101	72	~57	38	-	-
C38	(386)+3	95	68	48	37	100	66
Ohne Nr.2	-	94	59	-	-	-	-
N	2	4	4	3	2	4	4
μ	-	98,38	66,63	-	-	98,88	62,5
min	386	94	59	48	37	96	58
max	400	103,5	72	57	38	100,5	67
σ	-	4,608	5,468	-	-	2,016	4,655
v	-	4,684	8,207	-	-	2,038	7,448
Med	-	98	67,75	-	-	99,5	62,5
S. etruscus (FALCONER, 1868)							
N	29	42	40	36	36	30	28
μ	373,55	86,14	57,49	47,57	36,04	86,92	57,38
min	342	77,5	50,5	40	30	79	49
max	415	94	65	56	42	93,5	63
S. hundsheimensis (TOULA, 1902)							
N	13	40	40	35	35	20	20
μ	379,96	97,64	65,96	52,64	39,9	93,88	59,53
min	358	80	57	45	33	86	54
max	404	112	80	64	53	102	65,5
S. kirchbergensis (JÄGER, 1839)							
N	5	18	18	9	9	10	10
μ	421,8	110,39	74,92	58,72	43,39	105	67,85
min	408	102	68	53	40,5	90,5	61
max	445	119	87	65	47	113,5	82

Table 3: Assemblage of measurements and statistical parameters of the radius from Mauer and statistical parameters for *S. etruscus*, *S. hundsheimensis* and *S. kirchbergensis* based on Guérin (1980). Abbreviations of dimensions: GLr = greatest lengt; Bpr = proximal breadt; Tpr = proximal dept; KDr = smallest breadth of diaphysi; KTr = smallest depth of diaphysi; Bdr = distal breadt; Tdr = distal depth.

Tableau 3 : Dimensions et paramètres statistiques du radius de Mauer et paramètres statistiques de *S. etruscus*, *S. hundsheimensis* et *S. kirchbergensis* d'après C. Guérin (1980). Abréviations des mesures: GLr = longueur maximale ; Bpr = largeur proximale ; Tpr = profondeur proximale ; KDr = largeur minimale de la diaphyse ; KTr = profondeur minimale de la diaphyse ; Bdr = largeur distale ; Tdr = profondeur distale.

An exception in Mauer is one radius (SMNK: M.478/479; fig. 3, b). It has a distinct and deep developed palmarly transverse groove which is characteristic for *S. kirchbergensis* and *C. antiquitatis* (Guérin, 1980) and its sizes lie on higher degrees (tabl. 3). The specimen M.478/479 from Mauer should be assigned to *S. kirchbergensis* (Jäger, 1839) because remains of *Coelodonta* do not usually occure in the early Middle Pleistocene of Europe. Its first occurrence in Western Europe dates in the Elsterian of Bornhausen, Neuekrug (both Harz) and Frankenhausen (Thuringia) (Sickenberg, 1962).

The dimensions of the radius from Mauer and Hundsheim are similar to *S. hundsheimensis* and *S. etruscus* (tabl. 3). Only the specimen M.478/479 from Mauer is larger and has the same degrees like *S. kirchbergensis*. The other specimens from Mauer are assigned to *S. hundsheimensis* (Toula, 1902).

II Metacarpal

The specimen M.1415 (SMNK) from Mauer has palmarly a slight pronounced tuberculum on the proximal epiphysis (fig. 4, a). Some other specimens from Mauer (SMNK: M.1409, HMLD: Mau 153) and Hundsheim (NMW: Holotype-specimens, Toula 1902, IPW: A109, C57, C157) have just a weak developed palmar tuberculum. These characters are mentioned for *S. hundsheimensis* by Guérin (1980).

On the other hand there is one specimen from Mauer (HLMD: Mau 149) which shows a strong pronounced palmar tuberculum (fig. 4, b). This feature is characteristic for *S. kirchbergensis* (Guérin 1980). Additionally, the specimen Mau 149 has the similar dimensions like *S. kirchbergensis* (tabl. 4). The other specimens from Mauer are smaller (in Bp) than *S. hundsheimensis* and

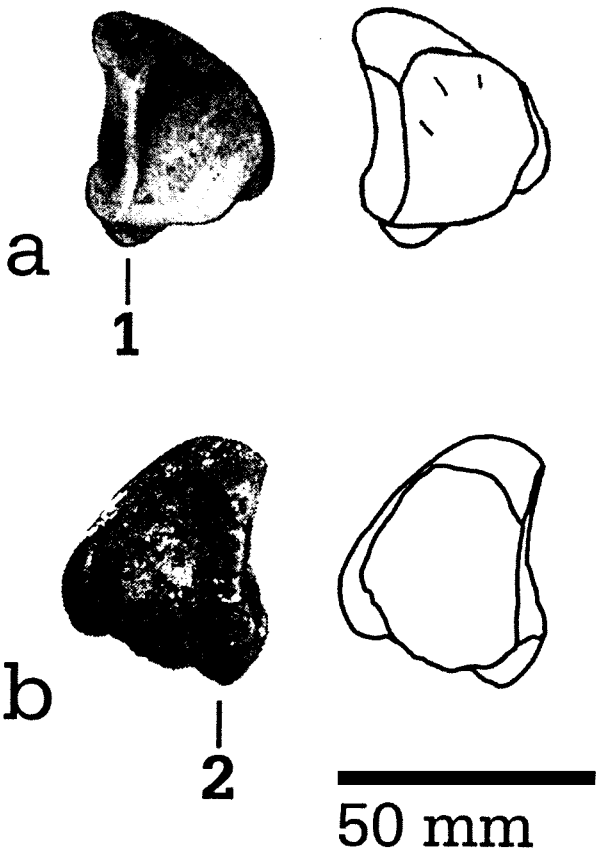

Figure 4: Characters on II Metacarpal of (a) *S. hundsheimensis* (Toula, 1902), Mauer, M.1415, SMNK, proximal fragment, proximal, sin (photography and drawing), (b) *S. kirchbergensis* (Jäger, 1839), Mauer, Mau 149, HLMD, proximal, dex (photography and drawing). 1- slightly pronounced palmar tuberculum of the proximal epiphysis; 2- strong pronounced palmar tuberculum.

Figure 4 : Caractères morphologiques du métacarpien II de (a) *S. hundsheimensis* (Toula, 1902), Mauer, M.1415, SMNK, gauche, en vue proximale (photographie et dessin), (b) *S. kirchbergensis* (Jäger, 1839), Mauer, Mau 149, HLMD, droit, en vue proximale (photographie et dessin). 1- tubercule (en vue palmaire) de l'épiphyse proximale moins accentué ; 2- tubercule (en vue palmaire) très accentué.

S. etruscus. The II Metacarpal from Hundsheim are in the sizes of *S. hundsheimensis*, somewhat larger than *S. etruscus* and larger than the specimens from Mauer. Just in the case of the proximal depth (Tp) the metacarpals are similar.

II Mc	GL	Bp	Tp	KD	TD	Bd	Td
Mauer: *S. hundsheimensis* (TOULA, 1902)							
M.1409	-	33	43	-	-	-	-
M.1415	-	36	46	-	-	-	-
Mau 153	-	32	45	-	-	-	-
Mauer: *S. kirchbergensis* (JÄGER, 1839); * FORTELIUS et al. (1993)							
Mau 149*	204	48,3	43	39,7	24,2	53,3	44,5
Hundsheim: *S. hundsheimensis* (TOULA, 1902); * TOULA (1902)							
holotype*	190	-	-	39	20	-	43,5
A109	189	43	46	34	28	43	41
C57	177	39	42	37	24	43	41
Ohne Nr.1	189	41	44	34	27	44	42
N	4	3	3	4	4	3	4
μ	186,25	-	-	36	24,75	-	41,88
min	177	39	42	34	20	43	41
max	190	43	46	39	28	44	43,5
σ	6,185	-	-	2,449	3,594	-	1,181
v	3,321	-	-	6,804	14,521	-	2,821
Med	189	-	-	35,5	25,5	-	41,5
S. etruscus (FALCONER, 1868)							
N	19	25	25	19	19	18	18
μ	176	39,3	40,66	32,47	22,61	42,58	37,89
min	162	27	34	24	17	38	36
max	186	47	46,5	38	28	48	41
S. hundsheimensis (TOULA, 1902)							
N	11	9	13	11	11	11	11
μ	181,59	44,5	42,92	35,59	23,27	45,23	39,45
min	174	39,5	37	30	20	42	36
max	194	49	45,5	41	28	49	41
S. kirchbergensis (JÄGER, 1839)							
N	13	12	12	13	13	12	12
μ	195,35	48	48,17	38,58	27,85	48,92	45
min	179	41	42,5	33,5	24,5	45	37,5
max	212	57	60	41,5	33	56	53,5

Table 4: Assemblage of measurements and statistical parameters of the II Metacarpal from Mauer and statistical parameters for *S. etruscus*, *S. hundsheimensis* and *S. kirchbergensis* based on Guérin (1980). Abbreviations of dimensions: GL – greatest length, Bp – proximal breadth, Tp – proximal depth, KD – smallest breadth of diaphsysis, KT – smallest depth of diaphysis, Bd – distal breadth, Td – distal depth.

Tableau 4 : Dimensions et paramètres statistiques du métacarpien II de Mauer et paramètres statistiques de *S. etruscus*, *S. hundsheimensis* et *S. kirchbergensis* d'après C. Guérin (1980). Abréviations des mesures: GL – longueur maximale, Bp – largeur proximale, Tp – profondeur proximale, KD – largeur minimale de la diaphyse, KT – profondeur minimale de la diaphyse, Bd – largeur distale, Td – profondeur distale.

The II Metacarpal from Mauer are assigned to *S. hundsheimensis* (Toula, 1902) except the specimen Mau 149 that is referred to *S. kirchbergensis* (Jäger, 1839) in agreement with Fortelius *et al.* (1993).

Astragalus

The astragali from Mauer do not belong to one mophological type because of their morphological differences on the plantar articular surfaces to the calcaneum. Two morphotypes are differentiated.

Morphotype 1 contains two conditions, which are connected by transitional types. The first one is Morphotype 1a (fig. 5, a): The plantar mesio-distal facet has a rectangular outline, it stays proximally and distally at the same width. The plantar proximo-lateral facet shows a four or five angular polygonal outline and has a mesio-distal extension which causes a mesio-lateral stretching. Morphotyp 1b (fig. 5, b) has a triangular plantar mesio-distal facet which is slender proximal and wider distal. The outline of the plantar proximo-lateral facet is triangularly shaped, without a mesio-distal extension. The transitional types show features of both conditions.

Morphotype 2 (fig. 5, c) are distinctly different. A rather convex extension occurs disto-laterally on the

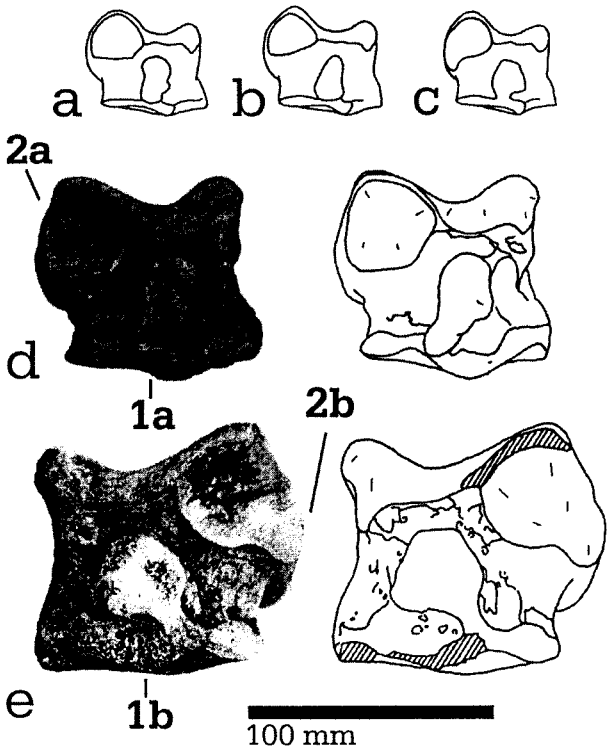

Figure 5: Morphotypes of the Astragalus, (a) sketch of morphotype 1a, (b) sketch of morphotype 1b, (c) sketch of morphotype 2, and the characters on Astragalus of (d) *S. hundsheimensis* (Toula, 1902), Mauer, M.1443, SMNK, palmar, sin (photography and drawing), (e) *S. kirchbergensis* (Jäger, 1839), Mauer, M.362, SMNK, palmar, dex (photography and drawing). 1a- rectangular outline of the plantar mesio-distal facet, proximal slender, distal wide, vertical pronounced; 1b- variable, triangular or circular outline, slightly vertically pronounced; 2a- triangular outline of the plantar proximo-lateral articular surface, without mesio-distal extension, 2b- distal extension laterally on the plantar proximo-lateral facet, proximo-distal pronounced.

Figure 5 : Morphotypes du talus: dessin du (a) morphotype 1a, (b) morphotype 1b, (c) morphotype 2 ; Caractères morphologiques du talus gauche de (d) *S. hundsheimensis* (Toula, 1902), Mauer, M.1443, SMNK, en vue palmaire (photographie et dessin), et droit de (e) *S. kirchbergensis* (Jäger, 1839), Mauer, M.362, SMNK, en vue palmaire (photographie et dessin). 1a- facette mesio-distale plantaire de contour rectangulaire, proximalement mince, large distalement, accentuée verticalement ; 1b- ou bien contour variable, triangulaire ou circulaire, non accentuée verticalement ; 2a- facette proximo-latérale plantaire de contour triangulaire, sans extension mesio-distale ; 2b- facette proximo-latérale plantaire avec latéralement extension distale, accentuée proximo-distalement.

proximo-lateral facet which produces a proximo-distal pronounciation. The mesio-distal facet has no special shape. It is variable rectangular, triangular or even circular, and just slightly vertically pronounced.

Twenty specimens from Mauer represent the Morphotype 1 (eg. M.1443, fig. 5, d), three of them (SMNK: M.363, M.1443 und M.1583) are referred to type 1a and seven specimens are transitional types (SMNK: M.364, M.365, M.366, M.1417a, M.1440, M.1444, M.1520, M.1725). Ten specimens belong to Morphtype 1b (SMNK: M.382, M.874, M.966, M.1419, M.1424, M.1425, M.1427, M.1441, M.1445, FS 39/344). The latter specimens are assigned to *S. hundsheimensis*. The other ten specimens, especially the three astragali of Morphotype 1a, should provisionally be assigned to *S.* cf. *hundheimensis*. Four specimens from Mauer (SMNK: M.362 (fig. 5, e), M.1418,

Astragalus	Lm	GB	Bd	TmT	BT
Mauer: *S. hundsheimensis* (TOULA, 1902); ** *S.* cf. *hu.*					
M.363**	76,5	86,5	77,1	57,8	62
M.364**	75	88	80	55	~64
M.365**	~71	~78	~68	~45	~51
M.366**	80	90	80	62	~63
M.382	80	88	(78)+4	55	61
M.874	75	90	76	53	54
M.966	74	90	82	54	58
M.1417a**	78	87,5	77,5	(54)+4	~64
M.1419	~68	~80	~65	~44	~55
M.1424	76	91,5	81,5	53	~61
M.1425	81	93,5	83	(53)+3	~67
M.1427	70	82,5	72,5	55	56
M.1440**	73	86	72	50	~54
M.1441	84	86,5	81	61,5	~64
M.1443**	74	79,5	76,4	50,4	57
M.1444**	73	~88	76	(56)+4	~57
M.1445	66,5	83,5	(75)+5	44	58
M.1520**	74	-	-	47	-
M.1583**	76	82	74	54	~63
M.1725**	71,5	80,5	77,3	52	~55
N	20	19	19	20	19
μ	74,83	85,87	76,44	52,79	59,16
min	66,5	78	65	44	51
max	84	93,5	83	62	67
σ	4,384	4,447	4,692	5,016	4,425
v	5,859	5,179	6,138	9,504	7,481
Med	74,5	86,5	77,1	53,5	58
Mauer: *S. kirchbergensis* (JÄGER, 1839)					
M.362	87	101	85	~62	~68
M.1418	81	92	79,8	53,7	~60
M.1572	81	95	79	57	~66
Mau 411	-	-	-	-	-
Hundsheim: *S. hundsheimensis* (TOULA, 1902); * TOULA (1902)					
holotype*	80	-	-	-	-
1909II569**	75	90	80	~53	~63
C69	75	86	76	52	~59
C71	74	(89)+5	(77)+5	~50	~60
C155**	71	84	73	50	56
F3	71	79	71	(51)+3	~56
Ohne Nr.1	78	87	75	~53	~62
N	7	6	6	6	6
μ	74,86	85,83	75,33	51,5	59,33
min	71	79	71	50	56
max	80	90	80	53	63
σ	3,338	3,971	3,141	1,378	2,944
v	4,459	4,626	4,170	2,677	4,962
Med	75	86,5	75,5	51,5	59,5
S. etruscus (FALCONER, 1868)					
N	46	46	42	45	47
μ	77,01	80,88	69,89	53,5	55,36
min	71	73	60	47	49
max	84	88	78	58	62
S. hundsheimensis (TOULA, 1902)					
N	40	39	35	34	37
μ	79,95	86,01	73,7	55,66	60,35
min	67	76	61	46	52
max	89	107	82	68	71
S. kirchbergensis (JÄGER, 1839)					
N	29	31	30	28	27
μ	95,81	101,66	88,97	67,02	73,98
min	85	93	79	55	63,5
max	105	113	99	83	91

Table 5: Assemblage of measurements and statistical parameters of the astragalus from Mauer and statistical parameters for *S. etruscus*, *S. hundsheimensis* and *S. kirchbergensis* based on Guérin (1980). Abbreviations of dimensions: Lm – medial length, GB – greatest breadth, Bd – distal breadth, TmT – depth at the medial lip of the trochlea, BT – distance of the trochlear lips.

Tableau 5 : Dimensions et paramètres statistiques du talus de Mauer et paramètres statistiques de *S. etruscus*, *S. hundsheimensis* et *S. kirchbergensis* d'après C. Guérin (1980). Abréviations des mesures: Lm – longueur médiale, GB – largeur maximale, Bd – largeur distale, TmT – profondeur de la trochlée médiale, BT – distance des lèvres trochléennes.

M.1572 and HMLD: Mau 411) indicate Morphotype 2, which are assigned to *S. kirchbergensis*.

The conditions of Morphotype 1a are called *'etruscus'* by Toula (1902). In his revision Mazza (1988) named no contrary details and Guérin (1980) gives no statement to the features in the fossil taxa. The conditions of Morphotype 1b correspond to the description of the holotype of *S. hundsheimensis* (Toula 1902) and could be proved by some other specimens from Hundsheim (IPW: C69, C71, C155, C164, F3).

The ten specimens from Mauer (see above) and two specimens from Hundsheim (NMW: 1909II569 (Type 1a), IPW: C155) show transitional features between type 1a and 1b. Therefore it is not possible to seperate both types completely and at the same time it is not possible to fit them in the species *etruscus* or *hundsheimensis*. However, in the present context it is not useful to propose an final assignment to any taxonomical categorie, because there is still lacking a comprehensive review for the astragali of the Pleistocene rhinoceroses in Europe. In the present paper these specimens are treated as *S.* cf. *hundsheimensis*.

The Morphotype 2 is assigned to *S. kirchbergensis*. Schroeder (1930, Taf. 16, Fig. 64) has pictured an astragalus from Phöben (E-Germany), and assigned it to *,merckii'* (= *kirchbergensis*). This specimen shows the conditions of Morphotype 2.

The dimensions of the astragalus are similar (tabl. 5). The specimens from Mauer and Hundsheim have the same sizes. The values of *S. etruscus* are somewhat smaller and the astragali of *S. kirchbergensis* are usually larger. The four specimens (M.362, M.1418, M.1572, Mau 411) from Mauer are similar to *S. kirchbergensis*, just a little larger than the other specimens from Mauer.

III Metatarsal

Two III Metatarsal are derived from Mauer (SMNK: M.758, M.1791 (fig. 6, c)). The dorsal border of their proximal epiphysis have a concave outline caused by a depression (fig. 6, b). That feature is described for *S. kirchbergensis* by (Guérin, 1980). There exists a convex outline on the dorsal border in *S. hundsheimensis* (fig. 6, a). A distinct groove lies on the dorsal diaphysis which is connected with the depression on the proximal epiphysis. This groove is distinct for *S. kirchbergensis* (Fortelius *et al.*, 1993) and both III Metatarsals show this character. The dorsal groove is sligthly marked on the material from Hundsheim (NMW: Holotype-specimens, Toula (1902), 1909II.571, 1909No 87, IPW: A38, C99, C129, D16).

Additionally, both specimens from Mauer show the same proportional feature on the diaphysis as *S. kirchbergensis* described by Fortelius *et al.* (1993). Their diaphysis are relatively dorso-plantarly flattened (tabl. 6). Both III Metatarsals from Mauer (M.758 and M.1791) have higher values in the dimensions than *S. hundsheimensis* and the specimens from Hundsheim but show similar values for the smallest depth of the diaphysis (TD). *S. etruscus* is usually smaller. The

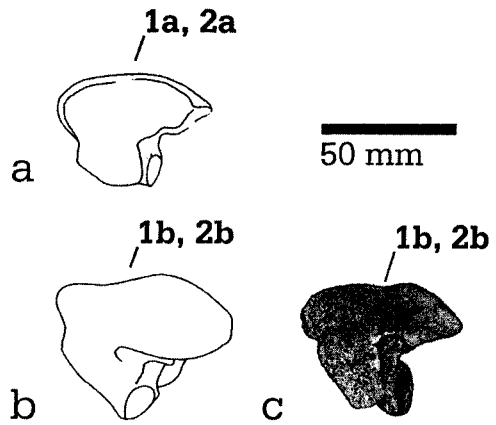

Figure 6: Characters on III Metatarsal of (a) *S. hundsheimensis* (Toula, 1902), Isernia, IS.I.378, MNI, proximal, dex (Fortelius et al. 1993, pl. 16, fig. 18), (b) *S. kirchbergensis* (Jäger, 1939), Mosbach, 1957/242, NMM, proximal, dex (Fortelius *et al.* 1993, pl. 16, fig.19), (c) *S. kirchbergensis* (Jäger, 1839), Mauer, M.1791, SMNK, proximal, dex (photography). 1a- dorsal border of the proximal epiphysis with konvex outline, 1b- dorsal border with concave outline, with depression, 2a- dorsal diaphysis with a slightly marked or without a groove; 2b- dorsal diaphysis with distinct groove.

Figure 6 : Caractères morphologiques du métatarsien III de (a) *S. hundsheimensis* (Toula, 1902), Isernia, IS.I.378, MNI, spécimen droit en vue proximale (Fortelius *et al.* 1993, pl. 16, fig. 18), (b) *S. kirchbergensis* (Jäger, 1939), Mosbach, 1957/242, NMM, spécimen droit en vue proximale (Fortelius *et al.* 1993, pl. 16, fig.19), (c) *S. kirchbergensis* (Jäger, 1839), Mauer, M.1791, SMNK, spécimen droit en vue proximale (photographie). 1a- contour convexe du bord dorsal de l'épiphyse proximale, 1b- contour concave du bord dorsal ; 2a- présence ou absence de fosse sur la diaphyse dorsale, 2b- fosse distincte sur la diaphyse dorsale.

III Mt	GL	Bp	Tp	KD	TD	Bd	Td
Mauer: *S. kirchbergensis* (JÄGER, 1839)							
M.758	200	59	46	52	23	69,5	45
M.1791	201,5	59	47,5	46	23,4	61	43,5
Hundsheim: *S. hundsheimensis* (TOULA, 1902); * TOULA (1902)							
holotype*	197	58	36	45,7	25,6	61	46,4
"2.Extremität"*	188	58,5	41	43,6	25,3	57,3	41,4
1909II.571	189	53	41	43	24,5	57	43
1909No 87	181	52	42	41	21	50	43
A38	(194)+3	(52)+5	43	42	22,5	55	43
C99	188	55	45	40	24	47	~40
C129	(186)+8	(51)+5	40	40	22	52	39
D16	187	56	46	40	24	52	41
N	8	8	8	8	8	8	8
μ	188,75	54,438	41,75	41,91	23,61	53,913	42,10
min	181	51	36	40	21	47	39
max	197	58,5	46	45,7	25,6	61	46,4
σ	4,892	2,872	3,105	2,077	1,628	4,517	2,288
v	2,592	5,275	7,438	4,955	6,894	8,379	5,434
Med	188	54	41,5	41,5	24	53,5	42,2
S. etruscus (FALCONER, 1868)							
N	18	24	18	19	15	16	15
μ	175,92	48,54	41,86	40,18	22,9	52,13	36,73
min	165	43	38	33,5	21,5	48	32
max	187	56	47	45	25	59	40
S. hundsheimensis (TOULA, 1902)							
N	12	17	16	17	17	13	13
μ	186,58	50,12	43,41	40,65	23,91	53,96	39,88
min	167	37	39,5	33	20	46	33,5
max	197	54,5	47,5	46	29	59,5	43
S. kirchbergensis (JÄGER, 1839)							
N	10	12	10	11	11	10	11
μ	209,05	61,33	50,6	56	25,32	71,4	49,27
min	198	54	46	52	23,5	64,5	44
max	222	66	56	63	28,5	77,5	56

Table 6: Assemblage of measurements and statistical parameters of the III Metatarsal from Mauer and statistical parameters for *S. etruscus*, *S. hundsheimensis* and *S. kirchbergensis* based on Guérin (1980). Abbreviations see tabl. 4 (II Metacarpal).

Tableau 6 : Dimensions et paramètres statistiques du métatarsien III de Mauer et paramètres statistiques de *S. etruscus*, *S. hundsheimensis* et *S. kirchbergensis* d'après C. Guérin (1980). Abréviations des mesures: voir tableau 4 (métacarpien II).

III Metatarsals from Mauer are assigned to *S. kirchbergensis* (Jäger, 1839).

CONCLUSION

By using morphological and metric characters of the skull, dentition and postcranial bones it is possible to assign the fossil remains of rhinoceroses from Mauer mainly to *Stephanorhinus hundsheimensis* (Toula, 1902). It emerges that there is a great correspondence to the fossil remains from the type locality Hundsheim.

The variability of characters in context to the other European Pleistocene rhinoceroses is also analysed and the fossils of Mauer are similar in morphology and metric to *S. hundsheimensis* characterised by Toula (1902), Guérin (1980) and Fortelius *et al.* (1993).

According to that it is possible to identify the species *S. kirchbergensis* (Jäger, 1839) in Mauer by some specimens of the radius, II Metacarpal, Astragalus and III Metatarsal.

The co-occurence of *S. hundsheimensis* and *S. kirchbergensis* at Mauer, first mentioned in Guérin (1980), supports the results of other early Middle Pleistocene localities in Europe. Guérin (1980) notes the occurence of both taxa in Mosbach (Germany), Solilhac, Vergranne (both France), Forest Bed (England) and Tegelen (Netherlands). These co-occurences suggest a possible sympatry of *S. hundsheimensis* and *S. kirchbergensis* in the early Middle Pleistocene.

ACKNOWLEDGEMENT

The present paper is based on a diploma thesis, which was supported by Prof. Wighart von Koenigswald (IPB). I am greatly indebted to all members of the visited institutions, who supported my working in the collections (alphabethical order by cities): Dr. Gabriele Gruber (HLMD), K. Riedelsberger (GPIH), Dr. Eberhard Frey and Wolfgang Munk (SMNK), Dr. Herbert Lutz and Thomas Engel (NMM), Dr. Gudrun Höck (NMW) and Prof. Gernot Rabeder and Charly Rauscher (IPW).

ACRONYMS

GPIH – Geologisch-Paläontologisches Institut der Universität Heidelberg, HLMD – Hessisches Landesmuseum Darmstadt, IPB – Institut für Paläontologie der Universität Bonn, MNI – Museo Nazionale Isernia, NMM – Naturhistorisches Museum Mainz, NMW – Naturhistorisches Museum Wien, SMNK – Staatlisches Museum für Naturkunde Karlsruhe, IPW – Institut für Paläontologie der Universität Wien

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