

Hipparion primigenium (v. Meyer, 1829), an early three-toed horse

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The type sample of teeth and bones of *Hipparion primigenium* (v. Meyer) from the Rhine valley, FGR, is analysed. Other known Vallesian / Middle-Late Sarmatian forms are discussed, as are the ecological implications of the morphology of these early hipparions and the associated fauna.

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1. Introduction

In 1829 H.v. Meyer described a small sample of fossil equid teeth from Eppelsheim in the Rhine valley, Germany, naming them *Equus primigenius* and *E. angustidens*. Later he (v. MEYER, 1833) altered these names to *E. caballus primigenius*, *E. mulus primigenius*, and *E. asinus primigenius*. Subsequently KAUP (1833), using material from the same site but evidently unaware of v.Meyer's work, erected *Equus (Hippotherium) gracile* and *E. (H.) nanus*, which in 1835 he finally referred to his genus *Hippotherium*. Kaup's generic name "*Hippotherium*" has long since been dropped in favour of *Hipparion* de Christol 1832, which has priority by 1 year, but the specific name "*gracile*" Kaup, although clearly a junior synonym of *primigenium* v. Meyer, is still sometimes used. Since v.Meyer and Kaup, nobody has seriously doubted the homogeneity of the sample, the correct specific name of which is *H. primigenium* (v. Meyer).

The Rhine valley material occupies a significant position in *Hipparion* systematics. It is the earliest described material pertaining to the genus, and accordingly a reference sample for students of the group, and it derives from one of the stratigraphically earliest *Hipparion* populations in the Old World (TOBIEN 1938, 1967). *Hipparion primigenium* (*primigenium*: Lat., first formed or generated, primal) is thus doubly worthy of its name.

Although earlier workers often referred to this material, it has remained only superficially

known. This paper therefore presents a compilation and analysis of the data.

2. Material and methods

The Rhine valley material of isolated teeth and limb bones derives from several sites in which the fossiliferous sediment — the *Dinotherium* Sand — has been utilized commercially. Chief among these sites are Eppelsheim, Esselborn, Gau Weinheim, and Westhofen. Small samples, chiefly from the type locality Eppelsheim, can be found in most large museums of the world. Statistically important collections are kept in the Hessisches Landesmuseum, Darmstadt, where Kaup's original material is housed, and in the Naturhistorisches Museum and the Institut für Geologie und Paläontologie der Universität in Mainz. H.v. Meyer's originals from 1833 are in the Senckenberg Museum in Frankfurt a. Main. I studied these collections, in addition to material in the British Museum (Natural History), London; the Museum of Comparative Zoology of Harvard University, Cambridge U.S.A.; the Department of Paleontology, Princeton University, Princeton; the A.P. and M.V. Pavlov Museum, Moscow; the Departments of Paleontology of the Universities of Munich, Heidelberg, Tübingen, Göttingen, and Kiel; the Staatliches Museum für Naturkunde, Stuttgart-Ludwigsburg, and the Naturhistorisches Museum, Basel. Comparative collections are kept in these institutes, as well as in the Museum of Paleontology of the Academy of Sciences, Moscow, the Institute of Palaeobiology, Tbilisi, the Departments of Palaeontology of the Universities of Freiburg, Vienna, Barcelona, Utrecht, Lyons, and Montpellier, the Museum National d'Histoire Naturelle in Paris and in Lyons, the Museum in Sabadell, and the Geological Institute, Budapest. My sincere thanks are due to the keepers of these collections.

In examining the cheek teeth I measured the heights at the mesostyle and metaconid, and the length and breadth at the base of the crown, to establish a point

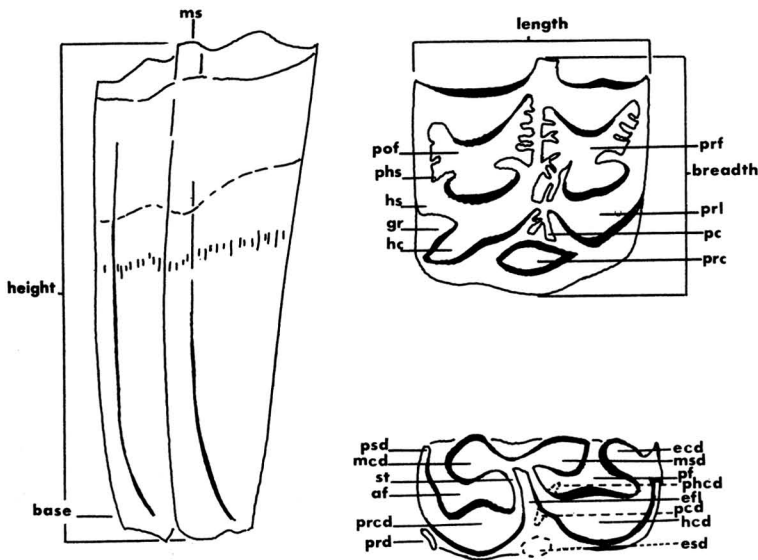


Fig. 1. Nomenclature of upper and lower horse teeth. Right P^3 or 4 and left $M_{1\text{ or }2}$ from Conclud, Spain. Abbreviations: af = anterior fossetula, ecd = entoconid, efl = ectoflexid, esd = ectostylid, gr = hypoconal groove, hc = hypocone, hcd = hypoconid, hs = hypostyle, mcd = metaconid, ms = mesostyle, msd = metastylid, pc = pli caballin, pcd = pli caballinid, pf = posterior fossetula, phcd = pli hypoconid, phs = pli hypostyle, pof = post-fossette, prc = protocone, prcd = protoconid, prd = protostylid, prf = prefossette, prl = protocomule, psd = parastylid, st = stalk.

of reference and to eliminate variation in size due to wear. As a reference point for measuring, the crown base has several advantages: it is easy to spot and all measurable teeth in a sample can be utilized even when very worn. HUSSAIN (1971:12) and ALBERDI (1974:149) claim that the two latter measurements are too variable because of irregularities in the shape of the tooth base, but give no evidence for their opinion. Since the measurements obtained by my method have coefficients of variation comparable to those found in homogeneous samples (Table 1), and no higher than those obtained by other methods, e.g. those used by HUSSAIN (1971) or ALBERDI (1974), I consider their criticism unwarranted.

I calculated the hypsodonty index according to $10 \times \text{height/length}$ at the base of the unworn or barely worn P_4^3 — M_2^3 . Measurements are in cm.

The number of enamel plications, counted at the occlusal surface of all available P_3^3 — M_2^3 , is given as a single total count per tooth to facilitate statistical comparison of samples; in contrast, GROMOVA's (1956) widely used plication formula does not easily yield to statistical comparison. The single total counts for the material examined are distributed fairly symmetrically around the sample mean. Since the plication count of a tooth generally decreases with wear, frequency distributions of small tooth samples may be skewed because of over-representation of extreme wear stages. In all samples this character, as well as protoconal length, has high coefficients of variation (Table 1).

I measured the volar length of the phalanges along the midline; this measurement is shorter than the total phalangeal length.

For easy comparison the proportions of the limb bones are compared in scattergrams with 95% equiprobability ellipses (DEFRIESE-GUSSENHOVEN, 1955). Too often measurements have been used to calculate indices, although allometric growth makes such indices unreliable. Most of the indices for the skull, jaw and limb bones, at one time or another considered "characteristic"

of species, are invalid: in scattergrams the observations mostly fall along a common growth axis, and the differences between indices are due solely to differences in size. True differences in proportions, i.e. position of scatters, are best expressed in scattergrams.

Abbreviations used:

B = Braila, Moldavian SSR	K = Kalfa, Moldavian SSR
BD = Bled Douarah, Tunisia	M = Montredon, France
Ch = Chabeuil, France	N = Nombrevilla, Spain
Cs = Csakvar, Hungary	Nb = Nesebr, Bulgaria
E = Eppelsheim (s.l. and s.str.)	Ng = Nagri, India
El = Eldar, Georgian SSR	P = Pikermi, Greece
Ess = Esselborn, FGR	R = Roustavi, Georgian SSR
G = Grossoulovo, Ukrainian SSR	S = Soblay, France
Gb = Gaiselberg, Austria	SU = Seo de Urgel, Spain
GW = Gau Weinheim, FGR	VP = Valles-Penedes, Spain
Hw = Höwenegg, FGR	W = Westhofen, FGR

3. Description

Hipparion primigenium (v. Meyer, 1829)

For synonyms, diagnosis, etc., see FORSTÉN (1968).

Although v. Meyer and Kaup described two or even three different hipparions from Eppelsheim, later workers have recognized only one species. Sample distributions and coefficients of variation show clearly that each local sample is homogeneous (Table 1). The large local samples, e.g. those from Eppelsheim, Esselborn, Gau Weinheim, and Westhofen, though very similar, are not identical. Analysis of variance shows

Table 1. Measurements (cm) of various dimensions of cheek teeth.

	OR	N	M	σ	V
Eppelsheim					
P ³⁻⁴	l. 2.03 - 2.58	56	2.32 ± .018	0.1365	5.88
	br. 2.22 - 2.90	51	2.55 ± .019	0.1380	5.41
M ¹⁻²	l. 1.88 - 2.28	38	2.04 ± .014	0.0883	4.328
	br. 2.19 - 2.67	36	2.36 ± .016	0.0979	4.148
P ₃₋₄	l. 1.98 - 2.59	65	2.35 ± .017	0.1378	5.86
	br. 1.34 - 1.74	67	1.53 ± .013	0.1083	7.078
M ₁₋₂	l. 1.98 - 2.35	55	2.13 ± .0117	0.0869	4.0798
	br. 1.17 - 1.64	54	1.37 ± .015	0.1107	8.08
protoc. l.	0.57 - 1.01	94	0.75 ± .009	0.0879	11.72
plic.freq. 14	-50	46	32 ± 1.407	9.54	29.812
Esselborn					
P ³⁻⁴	l. 2.00 - 2.50	29	2.27 ± .0199	0.1077	4.74
	br. 2.31 - 2.77	29	2.51 ± .0247	0.1330	5.299
M ¹⁻²	l. 1.89 - 2.29	24	2.03 ± .0209	0.1028	5.069
	br. 2.14 - 2.55	21	2.33 ± .0224	0.1026	4.403
P ₃₋₄	l. 2.06 - 2.61	57	2.34 ± .0146	0.1105	4.722
	br. 1.30 - 1.72	56	1.50 ± .013	0.0980	6.533
M ₁₋₂	l. 1.89 - 2.27	42	2.05 ± .0147	0.0954	4.653
	br. 1.12 - 1.57	48	1.33 ± .0139	0.0969	7.303
protoc. l.	0.59 - 0.95	50	0.78 ± .0136	0.0960	12.339
plic.freq. 4	-52	39	30.8 ± 1.717	10.725	34.821
Gau Weinheim					
P ³⁻⁴	l. 2.12 - 2.56	42	2.29 ± .0165	0.1069	4.67
	br. 2.32 - 2.73	34	2.53 ± .016	0.0935	3.702
M ¹⁻²	l. 1.83 - 2.32	40	2.01 ± .018	0.1142	5.69
	br. 2.24 - 2.60	34	2.36 ± .014	0.0833	3.529
P ₃₋₄	l. 2.10 - 2.58	52	2.35 ± .0147	0.1060	4.51
	br. 1.38 - 1.75	57	1.52 ± .0135	0.1019	6.707
M ₁₋₂	l. 1.93 - 2.34	38	2.08 ± .0126	0.0775	3.726
	br. 1.18 - 1.59	40	1.37 ± .0154	0.0974	7.125
protoc. l.	0.63 - 1.03	80	0.84 ± .0093	0.0835	9.964
plic.freq. 7	-43	34	25.59 ± 1.59	9.27	36.225
Westhofen					
P ³⁻⁴	l. 2.09 - 2.45	23	2.29 ± .0193	0.0928	4.05
	br. 2.36 - 2.76	22	2.53 ± .0251	0.1178	4.66
M ¹⁻²	l. 1.98 - 2.21	11	2.07 ± .0213	0.0707	3.415
	br. 2.25 - 2.55	11	2.40 ± .0276	0.0916	3.817
P ₃₋₄	l. 2.06 - 2.53	53	2.34 ± .0154	0.1123	4.80
	br. 1.37 - 1.66	55	1.52 ± .010	0.0753	4.95
M ₁₋₂	l. 1.92 - 2.27	31	2.09 ± .0166	0.0925	4.434
	br. 1.18 - 1.44	33	1.32 ± .0128	0.0734	5.56
protoc. l.	0.58 - 0.97	37	0.78 ± .0165	0.1005	12.968
plic.freq. 19	-60	23	33.75 ± 1.978	9.485	28.104
Bermersheim					
P ³⁻⁴	l. 2.03 - 2.04	3	2.03		
	br. 2.60, 2.62	2	2.61		
M ¹⁻²	l. 2.00 - 2.15	3	2.07		
	br. 2.20 - 2.43	4	2.33		
P ₃₋₄	l. 2.19 - 2.66	11	2.42 ± .0518	0.1718	7.097
	br. 1.48 - 1.68	8	1.58 ± .0279	0.0790	5.00
M ₁₋₂	l. 1.96 - 2.31	8	2.13 ± .0420	0.1188	5.576
	br. 1.25 - 1.61	7	1.41 ± .0433	0.1144	8.143
protoc. l.	0.64 - 0.82	5	0.74		
plic.freq. 33		1			

slight heterogeneity, and certain character frequencies are significantly different between the samples when compared by χ^2 in a 2×2 contingency table with Yates's correction (Tables 8, 9).

Recently FRANZEN & STORCH (1975) briefly discussed the relative age of the Rhine valley fossil localities. They think that the faunal composition of the southern sites, Eppelsheim, Esselborn, Bermersheim, and Westhofen, is distinct from that of the more northern Wissberg and Gau Weinheim. As seen from the tables, however, this distinction, whether temporal, ecological, or both, is not reflected in the differences between the local *Hipparion* samples of the Rhine valley, since the means for two localities in one part of the area may differ significantly, while resembling the means for samples from the other area. In spite of these erratic differences, I believe that the whole material is drawn from a single population.

The size ranges of the teeth in the local samples overlap widely, and the mean differences are generally slight (Table 1), except that M₁—M₂ for the Eppelsheim sample are significantly longer and broader than those for the three other samples. Protoconal length and plication count are generally similar, but in the Gau Weinheim sample the plication count is significantly lower and the protocone longer (Table 7).

The protocone in all samples is often fish-shaped or concave, or may bear an anterolabial tip. It unites with the protoconule at a mesostylar height of some 1.00—1.50, in P² slightly earlier or at a height of some 2.00.

The frequency of open and/or confluent fossettes, i.e. disconnected lophs, in the permanent uppers and the frequency of cingular stylids in the lowers varies erratically from sample to sample (Tables 4, 8). The fossettes may remain open in early wear, but they usually close towards the tooth base, except in P², where they may remain open even in advanced wear. The frequency of this character may depend on the age class distribution in a sample.

The frequency of an ectostylid is highest in P₃—P₄ in the Gau Weinheim sample, followed by the small samples from Wissberg and Bermersheim; the frequency of an ectostylid in M₁—M₂ is high in the sample from Esselborn (Tables 5 and 9). While a protostylid is found in most lower molars, it is lacking from some

Table 2. Measurements (cm) of the jaw

	OR	N	M	σ	V
Gonion- I ₁					
length	±44.00	1			
gonion- P ₂ l.	30.2	1			
P ₂ - M ₃ l.	15.4 - 16.5	8	15.9 ± .137	0.388	2.439
P ₂ - P ₄ l.	7.3 - 8.96	15	8.14 ± .102	0.395	4.849
M ₁ - M ₃ l.	7.02 - 8.24	13	7.66 ± .062	0.225	2.932
depth at P ₂	4.11 - 5.93	11	5.06 ± .194	0.643	12.718
depth at P ₄	5.26 - 7.29	9	6.51 ± .200	0.601	9.225
depth at M ₃	9.30 - 11.1	3	10.0		
P ² - P ⁴ l.	8.61	1			
M ¹ - M ³ l.	6.92 - 7.20	3	7.06		

Table 3. Measurements of limb bones

	OR	N	M	σ	V
MC III l.	20.9 - 22.0	3	21.5		
prox.br.	3.96, 4.17	2	4.07		
prox. diam.	2.89, 3.12	2	3.00		
prox.diam.art.	2.55, 2.88	2	2.72		
dist. br.	3.66 - 3.69	3	3.68		
br. protub.	3.78 - 4.11	3	3.90		
dist.diam.	2.71, 2.74	2	2.73		
MT III l.	23.80 - 24.90	6	24.29 ± .1536	0.376	1.549
prox. br.	3.98 - 4.64	4	4.32		
prox.diam.	3.42 - 3.85	4	3.72		
prox.diam.art.	2.63 - 3.40	6	3.10 ± .1188	0.291	9.405
dist. br.	3.55 - 4.08	6	3.84 ± .0749	0.183	4.778
br. protub.	3.96 - 4.43	6	4.23 ± .0712	0.174	4.125
dist.diam.	2.88 - 3.38	4	3.16		
Astragalus					
dist. br.	3.85 - 4.60	12	4.34 ± .0586	0.203	4.676
height	5.20 - 5.95	12	5.61 ± .0607	0.210	3.748
Phal.I vol.l.	5.06 - 5.96	10	5.63 ± .0962	0.304	5.403
least br.	2.70 - 3.12	10	2.97 ± .045	0.143	4.81
Phal.2 vol.l.	3.62 - 4.24	13	3.90 ± .055	0.198	5.08
mid-br.	2.95 - 3.45	13	3.20 ± .042	0.151	4.72

P₃-P₄ in the Eppelsheim, Westhofen, and Wissberg samples (Tables 5, 9).

Other morphological characters of the teeth commonly used for taxonomic purposes also vary erratically. Thus there is often a pli hypostyle, sometimes separated as a small foramen, and the hypoconal groove may be partly closed by one or several plication-like lingual extensions from the hypostyle; occasionally the groove is enclosed as a lake. The pli caballin is mostly many-branched. Styles of varying height may rise from the cingulum, especially between the protocone and protoconule. A pli caballinid, sometimes visible even

Table 4. Frequency of fossettes, whether open or confluent, in relation to total number of teeth investigated.

	P ²	P ³⁻⁴	M ¹⁻²	M ³
Eppelsheim	14/29	3/54	1/45	1/17
Esselborn	15/24	2/33	0/26	1/16
Gau Weinheim	14/21	1/52	2/49	3/20
Westhofen	18/23	1/25	1/12	2/9
Wissberg	4/5	0/5	0/4	0/4

Table 5. Frequency of protostylid and ectostylid, in relation to total number of teeth investigated.

	P ₃₋₄		M ₁₋₂	
	protostylid	ectostylid	protostylid	ectostylid
Eppelsheim	75/81	13/81	67/68	15/68
Esselborn	67/67	18/67	62/62	27/62
Gau Weinheim	65/65	28/65	56/56	11/56
Westhofen	64/65	12/65	36/36	5/36
Wissberg	19/21	8/21	19/19	6/19
Bermersheim	12/12	4/12	8/8	3/8

Table 6. Frequency of crenellated enamel in the upper and lower cheek teeth, in relation to total number of teeth investigated.

		P ²	P ³⁻⁴	M ¹⁻²	M ³
		Eppelsheim	upper	2/28	2/48
	lower	5/18	38/61	32/59	2/24
Esselborn	upper	0/24	4/32	3/26	0/16
	lower	4/27	50/67	43/64	6/23
Gau Weinheim	upper	0/19	0/41	0/42	0/17
	lower	1/14	23/63	13/59	0/20
Westhofen	upper	0/17	0/15	0/10	0/5
	lower	0/7	39/53	10/29	1/8
Wissberg	upper	0/6	0/12	0/8	0/6
	lower	-	14/22	4/19	0/3

in late wear, and a pli hypoconid are usually present in the little-worn lowers. Additional plications occur in the lowers, e.g. anteriorly on the metaconid-metastylid "stalk", lingually between the metaconid and metastylid, underneath the metastylid, posteriorly along the parastylid, and as a simple or branching entoconid tip, occasionally separated as an entostylid. In P₂ there is often a plication between the paraconid and protoconid in the anterior fossetula. The ectoflexid of the lower premolars is often deep, resembling that of the molars.

In correlation with the high plication number in this material the enamel is often crenellated.

Table 7. Table of $t = d/\sigma$ for statistics on dimensions (cm) of the teeth.

	E-Ess	E-GW	E-W	Ess-GW	Ess-W	GW-W
P^{3-4} length	1.864	1.300	0.797	0.817	0.913	0.179
breadth	1.285	0.803	0.727	0.549	0.477	0.026
M^{1-2} length	0.474	1.315	1.176	0.744	1.407	2.253*
breadth	1.089	0.023	1.252	1.115	1.970	1.307
P_{3-4} length	0.492	—	0.480	0.537	—	0.524
breadth	1.628	0.534	0.608	1.069	1.217	—
M_{1-2} length	4.341***	2.988***	2.200***	1.581	1.630	0.289
breadth	2.075*	0.117	2.565**	1.928	0.424	2.406***
protocon l.	0.541	3.060***	0.721	2.226*	1.126	3.246***
plicat.freq.	1.704	4.869***	1.344	3.690***	0.164	2.828***

Significance level adopted at $P = .05$; significant differences indicated with asterisks: * $P < .05$, ** $P < .02$, *** $P < .01$.

Table 8. Table of χ^2 comparing frequencies of fossettes, whether open or confluent, in P^2 , P^{3-4} , M^{1-2} , and M^3 for local samples of *H. primigenium*. (Yates' correction for small samples).

	P^2					
	Epp.	Ess.	GW.	W.	Wiss.	
P^{3-4}	Eppelsheim	—	1.07	1.67	4.87*	3.23
	Esselborn	0.32	—	0.02	1.39	1.60
	Gau Weinheim	0.22	0.16	—	0.27	1.25
	Westhofen	0.06	0.06	0.05	—	0.04
	Wissberg	0.27	0.25	2.16	0.82	—
M^{1-2}	M^3					
	Eppelsheim	—	0.59	2.02	3.55	0.65
	Esselborn	0.07	—	1.14	3.31	0.59
	Gau Weinheim	1.20	3.22	—	0.00	0.00
	Westhofen	3.62	6.66**	0.06	—	0.03
Wissberg	2.38	0.00	0.90	0.35	—	

Significance level adopted as in Table 7.

This is more common in the lowers than in the uppers: 3/4 of P_3 — M_2 , but only a fraction of the uppers, are crenellated (Table 6).

The mean hypsodonty index differs from sample to sample, but hardly significantly. For the Rhine valley material as a whole the mean index of P^4 varies from 18.3 to 21.8, of M^1 — M^2 from 21.6 to 25.5, of P_4 from 19.5 to 21.7, and of M_1 — M_2 from 20.6 to 23.2.

The limb bones are often rolled and measurements are then not fully reliable. Too little material is available for comparisons between local samples, but the pooled data do not indicate heterogeneity. Usually the size range observed in the Eppelsheim sample, which is

Table 9. Table of χ^2 comparing frequencies of protostylid and ectostylid in local samples of P_{3-4} and M_{1-2} (Yates' correction for small samples).

	protostylid						
	Epp.	Ess.	GW.	W.	Wiss.	Ber.	
P_{3-4}	Eppelsheim	—	2.59	13.0***	0.15	4.96	5.37*
	Esselborn	7.25**	—	3.82	1.33	0.97	0.66
	Gau Weinheim	7.08**	0.00	—	9.24**	0.16	0.9
	Westhofen	4.16*	0.00	0.00	—	3.43	0.61
	Wissberg	0.60	11.5***	11.2***	5.85*	—	0.01
	Bermersheim	0.12	0.00	0.00	0.91	2.20	—
M_{1-2}	protostylid						
	Eppelsheim	—	6.85**	0.11	1.0	0.76	0.28
	Esselborn	3.86	—	7.70**	9.11**	0.86	0.49
	Gau Weinheim	3.69	0.00	—	0.5	1.15	0.47
	Westhofen	3.19	0.00	0.00	—	2.43	1.12
	Wissberg	0.47	0.00	0.00	0.00	—	0.56
Bermersheim	1.68	0.00	0.00	0.00	0.00	—	

Significance level adopted as in Table 7.

the largest, includes the measurements of specimens from the other sites (Table 3). GROMOVA (1955: 218) gave measurements of a very large femur and tibia from Eppelsheim based on material figured in the literature. I have not been able to relocate these bones in the collections, but a cast (BMNH No. 2645) in the British Museum (Nat.Hist.) may represent the femur in question. Whether these two bones really belong to *Hipparion* remains uncertain, since the Rhine valley material is contaminated with stratigraphically younger specimens, i.e. of *Equus*. The proximal phalanx BMNH No. 27481 from Eppelsheim, which PIRLOT (1956: 30) measured and referred to *Hipparion*, a left MC III from Wissberg (Mainz Museum No. 1926/412), and some isolated teeth in Darmstadt belong to *Equus*.

The facet for the second cuneiform is absent from four out of seven MT III studied, and its presence is uncertain in one more.

The volar ligamental scars of the proximal phalanx are typical of *Hipparion*. The V-shaped scar of the oblique sesamoid ligament is short, sometimes very short, and concave. The scar of the ligamentum sesamoideum rectum is either long and narrow, being a direct distal continuation of the V-shaped scar, or a small, central rugosity. There are always paired, lateral volar scars.

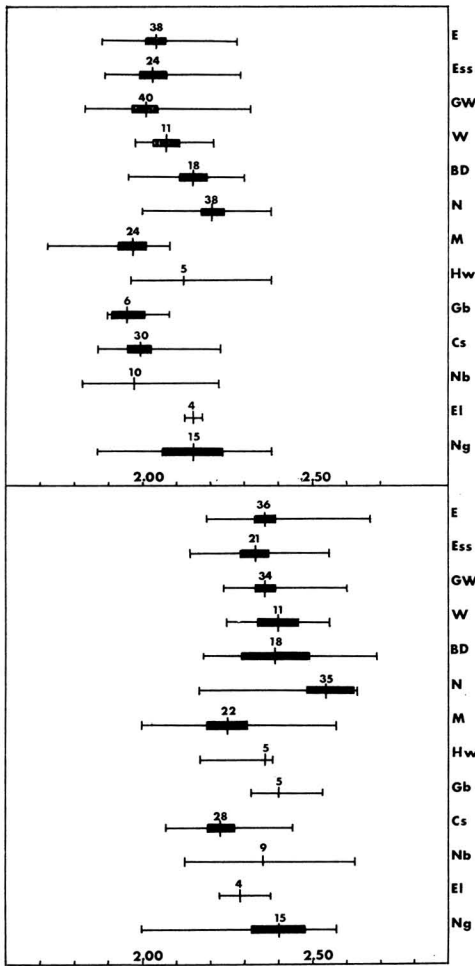


Fig. 2. M^1-M^2 length (above) in various Vallesian forms of *H. primigenium*. Horizontal line = observed range; black rectangle includes 95 % confidence limits of the mean, vertical crossbar = the mean. M^1-M^2 breadth (below) in various Vallesian forms of *H. primigenium*. Symbols as above.

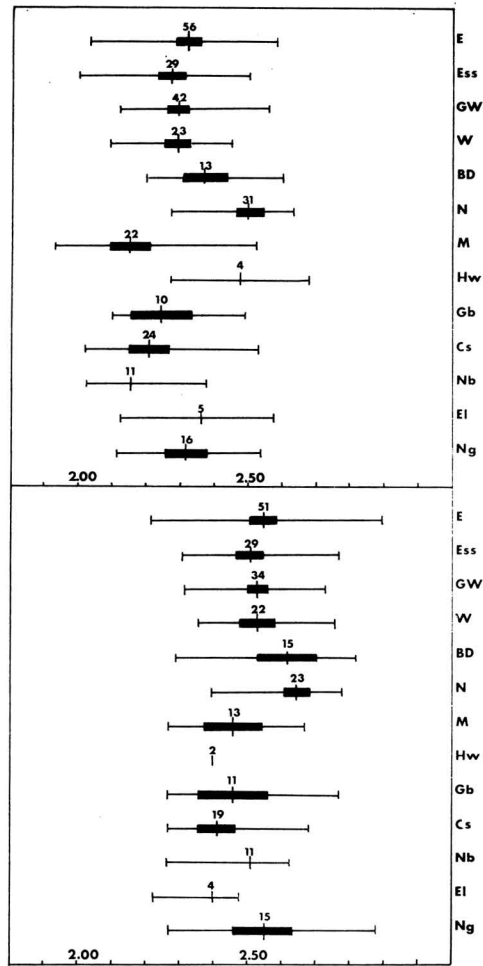


Fig. 3. P^3-P^4 length (above) and breadth (below) in various Vallesian forms of *H. primigenium*. Symbols as in Fig. 2.

4. Comparisons and discussion

The early, i.e. Vallesian/Sarmatian, finds of *Hipparion* in the Old World are scattered over a geographically wide area, extending from India in the east to France and Spain in the west. This huge area was inhabited by a rather large and massive hipparion (GROMOVA 1955, PIRLOT 1956, ARAMBOURG 1959, TOBIEN 1959, GABUNIA 1961, SONDAAR 1962, 1974, OZANSOY 1965, FORSTÉN 1968, 1972, HUSSAIN 1971, LUNGU 1973, NIKOLOV 1973, ALBERDI 1974, HOOIJER 1975).

In the Soviet Union GROMOVA (1955) reported *Hipparion* from the Middle Sarmatian at Sirez, Lopouchna, and tentatively at Sevastopol, and in the Upper Sarmatian at Kouialnik.

From Sirez she reported a large jaw: the length of P_2-M_3 is about 16 cm. In P_3 (GROMOVA 1955: fig. 53) the ectoflexid is deep, as is often the case in the Rhine valley lower pre-molars. The plication number and protoconal length of the rather worn P^2-M^2 from Lopouchna are inside the range, although below the mean, of the Rhine valley sample. Upper P^2 is similar in that the fossettes are confluent,

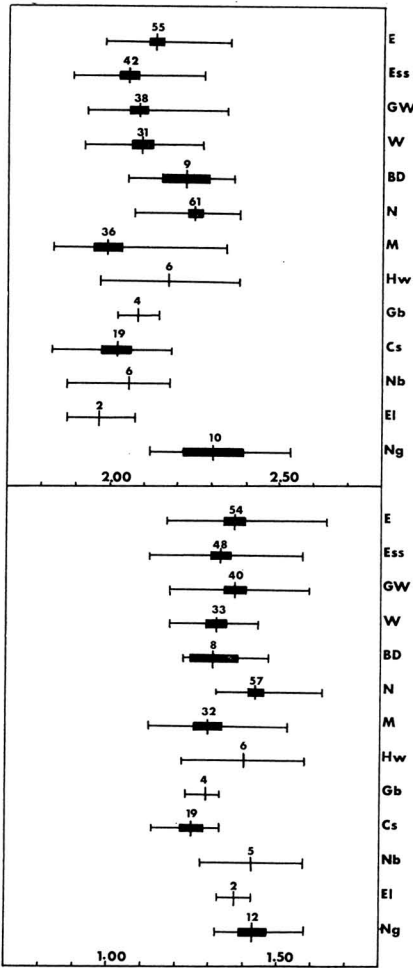


Fig. 4. M_1-M_2 length (above) and breadth (below) in various Vallesian forms of *H. primigenium*. Symbols as in Fig. 2.

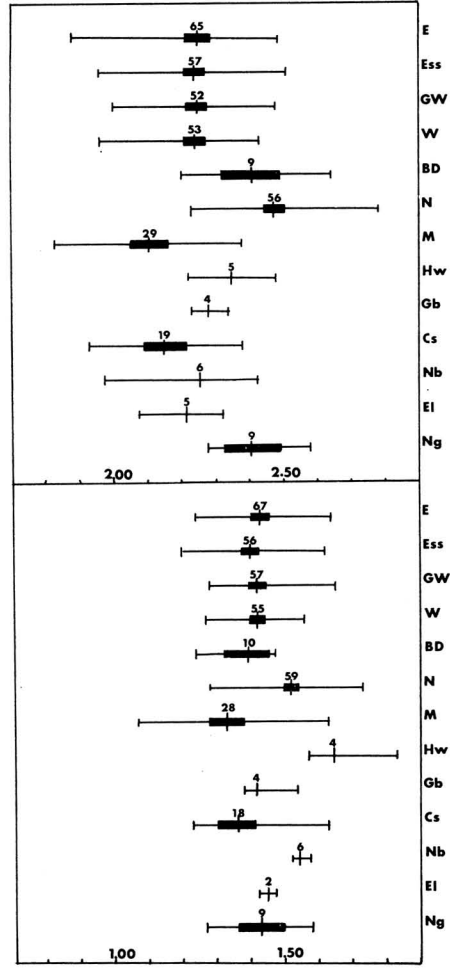


Fig. 5. P_3-P_4 length (above) and breadth (below) in various Vallesian forms of *H. primigenium*. Symbols as in Fig. 2.

and P^3 bears a style in front of the protocone. The Kouialnik upper tooth row, though very worn, is long (according to GROMOVA 1955: 204, 14.3 cm long), and the protocones are long and narrow.

In addition to these same finds, GABUNIA (1961) reported *Hipparion* from the Middle Sarmatian at Bourlatskoe near Stavropol, from the Upper Sarmatian at Grossoulovo, Kichinev, Eldar, and Roustavi, and from the Upper Sarmatian or Mcoctian at Arkneti and Djaparidze.

GABUNIA (1961:137) compared the size and massiveness of the limb bones of *Hipparion* from Grossoulovo with those of *H. primigenium* and

H. giganteum Gromova, and even with those of *H. crassum* Gervais. According to his measurements (Table LXXXV), MC III conforms well with the corresponding bones of other early hipparions (Fig. 12:G), as do the other limb bones (Figs. 8, 9:G). The teeth, which Gabunia compared with those from Eldar, are strongly plicated and the protocone varies from long, narrow and concave, to short and rounded (GABUNIA 1961: 134, 135, 138, fig. 11d). In the lower teeth the cingular structures are said to be weakly developed.

The two upper teeth (P^2 and P^3) from Bourlatskoe (Gabunia 1961:158) are moderately worn; the plication number is considerable (P^2

in Fig. 11B about 25), and the protocone narrow. The teeth are said to be slightly smaller than those from Braila and Lopouchna.

From Kichinev there is a single distal end of a massive MC III, which compares with that from Grossoulovo. From the Upper Sarmatian of the Sevastopol area there are some teeth and bones of a very large hipparion, which GABUNIA (1961: 155—156) compared with *H. giganteum*.

GABUNIA (1961: 168—192) described a new species, *H. eldaricum*, from the Upper Sarmatian of Eldar, and believed that there may be a second, even larger and possibly stratigraphically slightly older form at the same site. The morphology of the teeth is rather similar, but size differences in the teeth and tooth rows may indicate two forms.

Both forms at Eldar are large and relatively brachyodont. The uppers (GABUNIA 1961: figs. 5, 11e, f, g) are strongly plicated, usually with lingually indented hypocone and with long hypostylar plication extending lingually and almost closing the hypoconal groove. Open and confluent fossettes are common; the protocone is long and narrow and markedly concave, or short and broad (GABUNIA 1961: fig. 5). The lowers are often crenellated and bear a pli caballinid. Cingular structures are weak: an ectostylid is seldom developed in the permanent teeth, and the protostylid is frequently absent or weak. The preorbital fossa is mostly small and weak, and the limb bones rather massive.

The single MC III from Roustavi (GABUNIA 1961: 213) is moderately massive. A MT III (PIN —) is as long as, but slightly less massive than, most Rhine valley specimens (Fig. 11:R).

Eight teeth have been found at Djaparidze (GABUNIA 1961: 209—210). They are low-crowned, large, and strongly plicated, with a long protocone. Lower P_3 or P_4 has a deep ectoflexid; cingular structures are weak. Gabunia compared these specimens with teeth from Eldar.

In the teeth from Arkneti the plication count is also very high (in P^3 — M^3 it varies from 61—37), and the protocone is moderately long. The metapodials seem very massive (GABUNIA 1961: Tables LXXXV and LXXXVIII), but are, in fact, crushed antero-posteriorly; the astragalus and calcaneum correspond to those from the Rhine valley, but the radius seems comparatively gracile.

A new species, *H. sarmaticum*, was erected on material from the Moldavian Middle Sarmatian

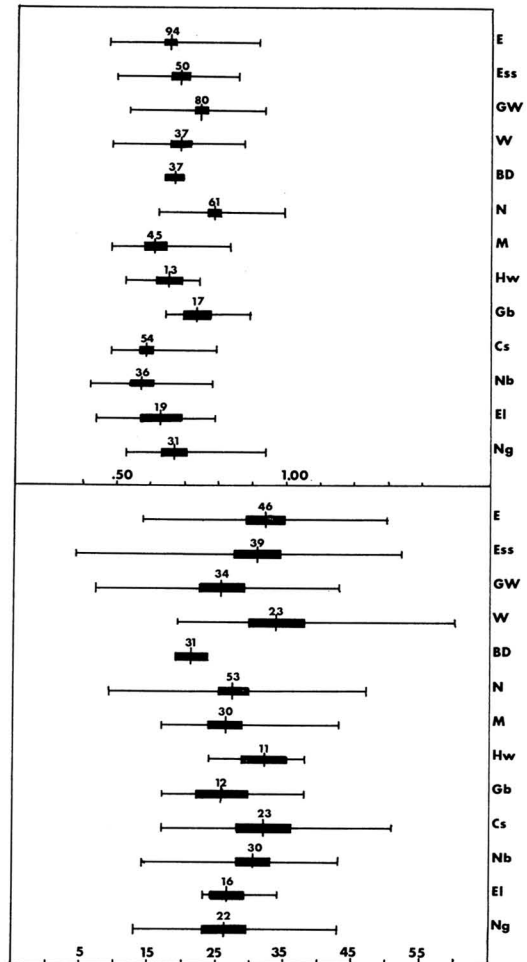


Fig. 6. Protoconal length (above) and plication count (below) in various Vallesian forms of *H. primigenium*. Symbols as in Fig. 2.

sites of Braila, Kalfa, Sirez, Lopouchna, Buschori, Varniza, Gidigitch, and Malie Mileschti (LUNGU 1973). LUNGU compared this large, massive form, which had rather low-crowned, strongly plicated teeth and a variable protocone, with other early hipparions of the Old World, and found similarities with *H. primigenium*, which he thinks (LUNGU 1973: 109) "do not exclude a relationship". Comparison of the samples from Kalfa and the Rhine valley shows complete overlap in the size and proportions of the teeth and limb bones (Figs. 7—12:K), and morphological similarity, except that in the Kalfa sample the protocone (mean length 0.69 ± 0.006) of the uppers is significantly

shorter than in any of the Rhine valley samples.

NIKOLOV (1973) recently identified three species, *H. mediterraneum* Roth & Wagner, *H. nesebricum* Nikolov, and *H. praesulcatum* Nikolov, from the Middle Sarmatian of Nesebr, Bulgaria. A critical analysis (FORSTÉN 1978) shows that the material probably comprises only a single species with robust metapodials (Figs. 11, 12: Nb), high plication count, short protocone (Figs. 2—6) and well-developed protostylid, but weak ectostylid.

TOBIEN (1938, 1956, 1959) reported on *Hipparion* from the fossil-bearing site at Höwennegg, FGR. This large, massive form, dated at ± 12 million years (VAN COUVERING & MILLER, 1971), is one of the earliest hipparions in the Old World. The teeth are as large as or even larger than those from the Rhine valley (Figs. 2—5). The uppers are strongly plicated with a moderately long protocone (Fig. 6), and

P² frequently with open or confluent fossettes; the lowers have crenellated enamel and cingular stylids. Limb bone measurements are as in *H. primigenium* from the type locality (Figs. 7—12: Hw).

The Austrian locality Gaiselberg is considered Vallesian (MEIN 1975). The isolated teeth correspond in morphology to those from the Rhine valley; they are slightly smaller in mean size and slightly less plicated, but have a longer protocone than the latter (Figs. 2—6).

Hipparion from the Vallesian of Csakvar, Hungary, has been identified as *H. primigenium* (FORSTÉN 1968) on the basis of tooth morphology (Figs. 2—6) and limb bone size and proportions (Fig. 8—11:Cs).

PIRLOT (1956) described a new species, *H. catalaunicum*, from the Vallesian of Valles-Penedes, Spain, which he considered primitive on account of the frequent absence of a facet

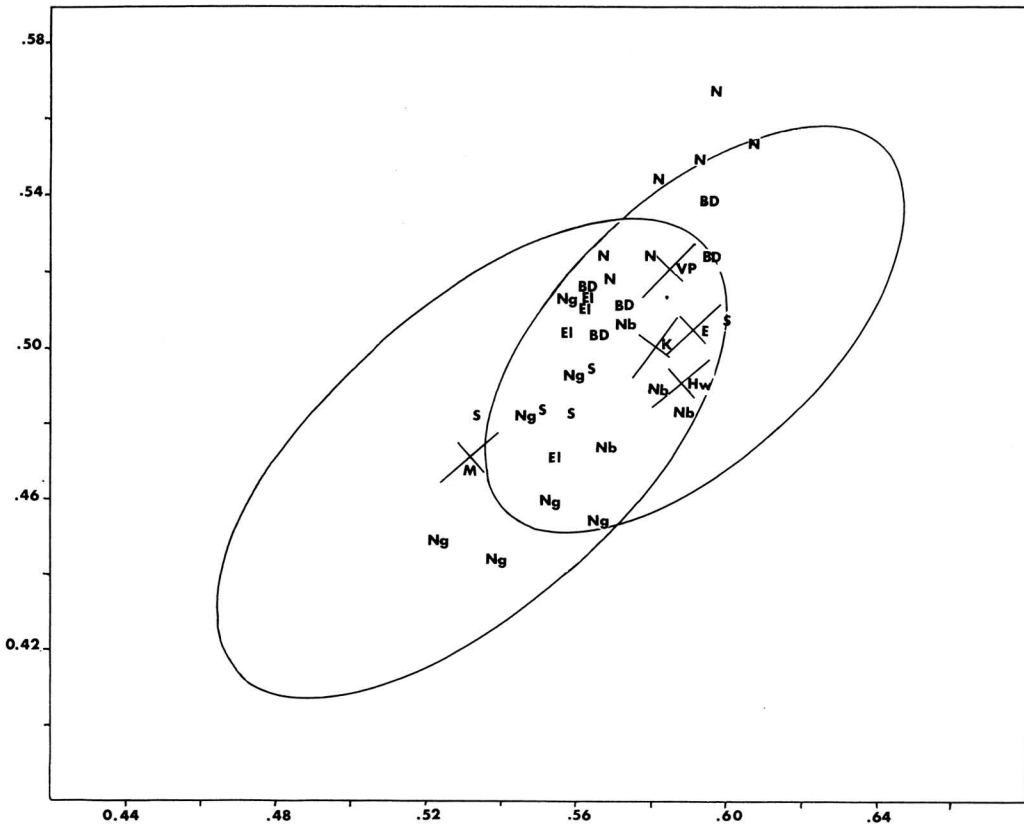


Fig. 7. Phalanx 2 volar length plotted against mid-shaft breadth in various Vallesian forms of *H. primigenium*; log. data. 95 % equiprobability ellipses drawn for samples from Eppelsheim s.l. (E) and Montredon (M).

I identified *H. primigenium* from the Vallesian of Bled Douarah, S. Tunisia, in a decidedly sylvan fauna (FORSTÉN 1972). The teeth are rather low-crowned, moderately to strongly plicated, and with a rather long protocone (Figs. 2—6). The cingular stylids are weak. Measurements of the limb bones (Figs. 7—10: BD) correspond to those of Rhine valley *H. primigenium*.

HOOIJER (1975) described *H. primigenium* from the Ngorora Formation of Kenya in beds 12—9 million years old. The large upper premolar described (p. 13—14, Plate 3:1) has a complex enamel pattern and long protocone; the enamel of the lowers (p. 14, Plate 1) is crenellated and there is a well-developed proto-stylid. A proximal, evidently posterior phalanx (p. 15, Plate 3:5—6) is massive.

OZANSOY (1965), in a review of the Late Tertiary faunas of Turkey, identified a new species, *H. galaticum*, from the Infra-Pikermian at Inönu, the lowermost of his faunal levels with *Hipparion*. The large P_3 (rather P_4) pictured is little worn, but has a deep ectoflexid, multiple pli caballinid, drooping metaconid-metastylid, and plicated enamel, characters also common in *H. primigenium*; a lower M_1 or M_2 is not quite so plicated. A distal fragment of MC III is

said to be massive, but there are no measurements.

HUSSAIN (1971) described a new species, *H. nagriense*, from the Nagri of the Siwaliks, India and Pakistan. This species was recently synonymized with *H. primigenium* (HOOIJER 1975:4). COLBERT (1935) and v. KOENIGSWALD (1975, pers.comm.) reported isolated teeth of *Hipparion* in the Chinji Lower Siwaliks. These teeth are large and strongly plicated, as are those of *H. nagriense*.

Recently SONDAAR (1974) referred *H. cf. primigenium* from the Lower Vallesian of Valreas, St. Jean de Bournay, St. Fons, Vaison la Romaine, and the railway of Croix Rouse in the Rhone valley, France. He described a new species, *H. depereti*, from the Upper Vallesian of Soblay and Montredon. SONDAAR believes the latter to be slightly smaller than type *H. primigenium*, but even more massive in mid-metapodial breadth relative to metapodial length. Measurements indicate that, although shorter, the metapodials are distally relatively as massive in *H. depereti* as in *H. primigenium* (Figs. 11, 12:M). The teeth are strongly plicated, the protocone rather short (Fig. 6). The proto-stylid is well developed, the ectostylid weak or absent. *Hipparion depereti* from Montredon,

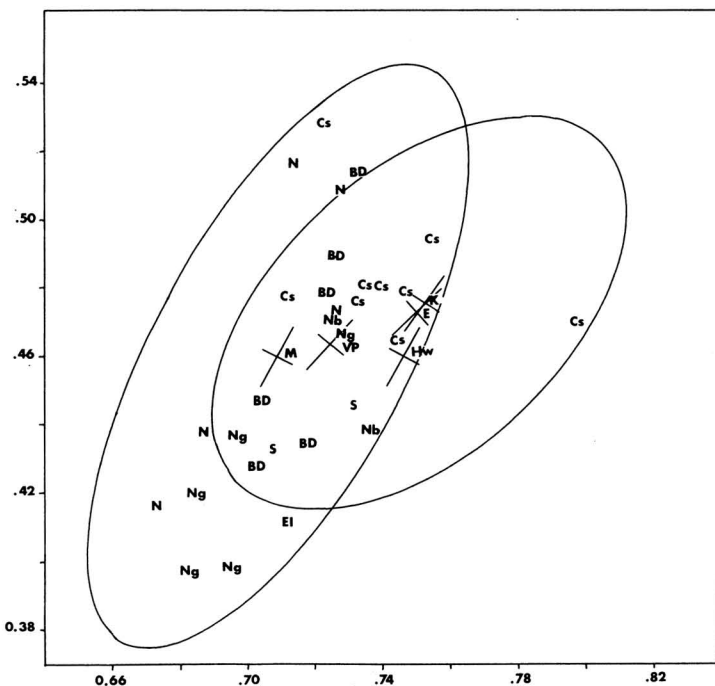


Fig. 10. Phalanx 1 volar length plotted against mid-shaft breadth in various Vallesian forms of *H. primigenium*; log. data. 95 % equiprobability ellipses drawn for samples from Eppelsheim s.l. (E) and Montredon (M).

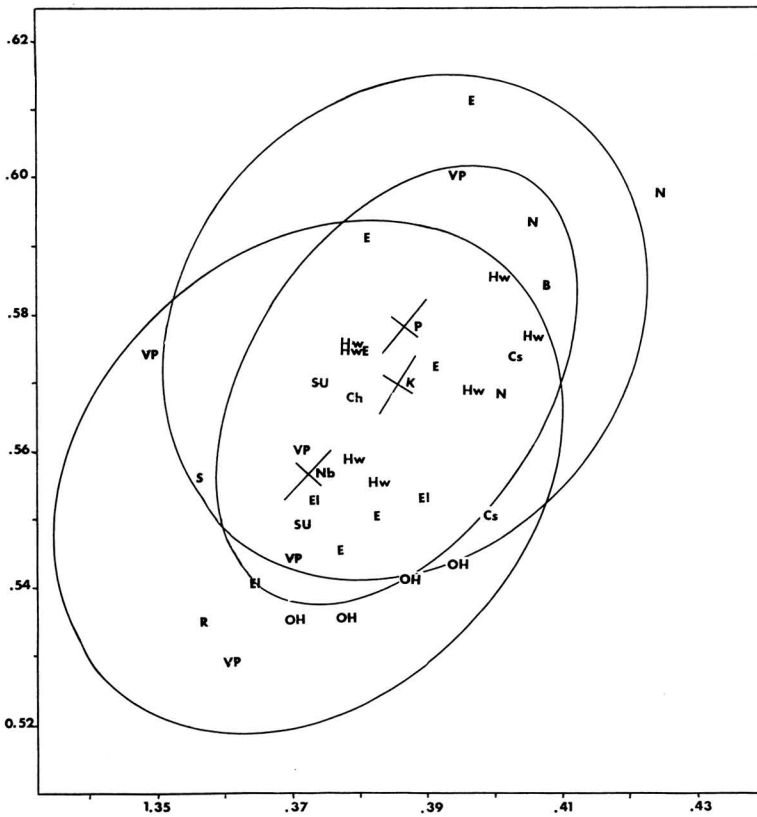


Fig. 11. MT III total length plotted against distal articular breadth in various Vallesian forms of *H. primigenium*; log. data. 95 % equiprobability ellipses drawn for samples from Pikermi (P), Kalfa (K), and Nesebr (Nb).

though over-all smaller, is morphologically very similar to the Rhine valley type form of *H. primigenium*.

In my opinion all these early occurrences should be regarded as locally and temporally differentiated forms of a single, widespread species, *H. primigenium*. Possibly some might better be classed as semispecies, already differentiated close to the point where genetic interchange was no longer possible. This may be the case with some marginal populations, such as those from Nombrevilla, Monteredon, and Eldar. In that case *H. primigenium* would have to be defined as a superspecies. However, the great morphological similarities between the local populations of early (and some later) *Hipparion*, and their undoubtedly close genetic interrelationship, must be formally recognized.

The Sevastopol locality, which BORISSIAK (1914) considered Sarmatian, has yielded a hipparion called *H. sevastopolitanum* Boriss. The age of the Sevastopol local fauna has been much debated (TOBIEN 1938, KOENIGSWALD

1939, GROMOVA 1955, GABUNIA 1961, VAN COUVERING & MILLER 1971). Recently, however, KOROTKEVITCH (1976) referred Sevastopol to the Middle Sarmatian on the basis of the fauna as a whole.

Hipparion sevastopolitanum was considerably smaller than *H. primigenium* and, although not a slender-built horse, was not nearly as massive as the latter. It was intermediate in limb proportions between *H. primigenium* and the slender forms of the *H. mediterraneum* group, but was small even in comparison with most of the latter. Possibly, *H. sevastopolitanum* represents a separate, very localized form already contemporaneous with, but different from, early *H. primigenium*, which would be rather surprising in view of the wide occurrence and sole dominance of the latter. Alternatively, *H. sevastopolitanum* derives from a fauna younger than Sarmatian.

Recently there has been discussion regarding how to express in terms of formal taxonomy the known and interpreted morphology, ecology,

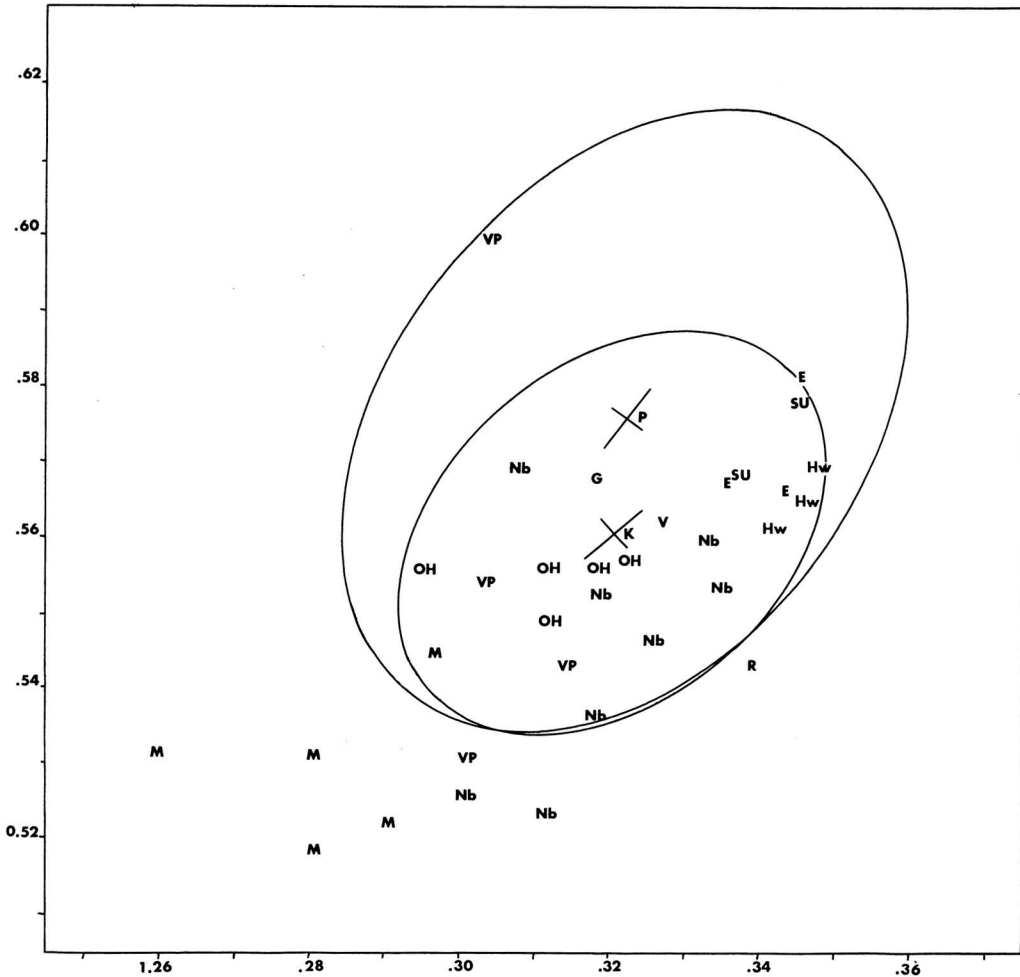


Fig. 12. MC III total length plotted against distal articular breadth in various Vallesian forms of *H. primigenium*; log. data. 95 % equi-probability ellipses drawn for samples from Pikermi (P) and Kalfa (K).

and functioning of fossil horses. I have stressed (FORSTÉN 1968, 1973) that local populations of a species vary in space and time, and that this has to be acknowledged by applying the concept of polytypic species in palaeontology. SONDAAR (1974) thinks that similarities or differences, or both, can be utilized to unite or separate finds when classifying them, but he does not seem to believe that these properties can be used for drawing biologically significant conclusions about the relationships of the animals involved. He regrets that no characters are consistently distinct enough to serve as infallible criteria for identifying species, and concludes that classification of *Hipparion* is simply a matter of personal taste.

But delimitation of species in a genus is not just a matter of personal taste, as SONDAAR (1974:305) would have us believe. Only sympatry affords unequivocal evidence of specific difference, but the status of recent or fossil allopatric forms should not be decided solely on the basis of morphological factors. Identical ecological roles, as inferred from similarities in morphology and associated fauna and flora, indicate geographic replacement. This is one of the criteria of a polytypic species in MAYR's (1964) definition of species. In recent species contemporaneous but geographically separated forms vary, and in fossil forms they must also have varied, especially since their differentiation may have been enhanced by temporal differences

not great enough to be discernible in the stratigraphic column or in the fauna as a whole. The most important mechanism in the evolution of morphological differences is adaptation. Differentiation in the species *H. primigenium*, as in the genus *Hipparion* as a whole, seems chiefly to have been due to local adaptation, resulting in populations of which no two were identical. These local populations seldom entered new or decidedly different adaptive zones, as defined by SIMPSON (1944). Speciation, i.e. the occupation of new zones, did occur, but evolution mainly gave rise to forms which, while maximally adapted to local subzones, shared a common, specific adaptive zone.

The adaptive zone, i.e. ecological niche, of early *H. primigenium* is reflected in the sum of the diagnostic features of this species. Although each feature is variable within a population and the means vary from one population to another, these features are shared in a general way by all local forms of the species and must have been adaptive. The relatively low-crowned teeth in early *H. primigenium*, inherited from the species' closest ancestors, are primitive, but were probably well adapted to the kind of vegetation it ate.

Students have long been trying to infer the ecology of species of fossil horses; the foremost theorists are Antonius, Gromova, and Gabunia. Arguments are based on the general morphology of the group of horses in question, the structure of the particular fossil form, and the associated fauna. The consensus seems to be that since hipparions of *H. primigenium* type are regularly associated with faunal, and in some cases floral, elements of sylvan type, these forms should be considered forest animals (THENIUS 1950). ANTONIUS (1919), GROMOVA (1955), and GABUNIA (1961) inferred the ecological and functional significance of the morphological features of these hipparions — features which regularly include large size, massive build, and complicated enamel. They believe these properties to be adaptations to a sylvan environment, particularly since the opposite traits, e.g. dwarfism, dolichopody, marked hypsodonty, and simplicity of enamel structure, tend to characterize hipparions associated with faunal elements typifying the open savanna or steppe. SONDAAR (1968, 1974), however rejects the idea of a "forest hipparion", pointing out that a fossil assemblage does not necessarily correspond to an original animal community. However, the

regularity with which *H. primigenium* type hipparions occur in faunas of a decidedly sylvan character cannot simply be explained away by claiming a mixture of faunal elements derived from different biotopes.

Hipparion was a ubiquitous genus comprising species adapted to many different ecological niches (TOBIEN 1960). *Hipparion primigenium*, if not exactly a deerlike browser of the dense forest, was certainly adapted to a different niche than the dwarf and the long-legged hipparions. These latter, for one thing, showed marked hypsodonty, a character regarded as adaptive to a xerophytic environment, where the grass is rich in abrading silica. The difference in tooth height between the hypsodont "steppe hipparions" and the relatively low-crowned *H. primigenium* resulted from differences in ecology. Although the general tendency in the Equidae was towards higher crowns, hypsodonty did not increase orthogenetically, but in relation to the selective pressure in a given environment and the ability of the given population to adapt accordingly. As a result, at any one time relatively low-crowned and markedly more hypsodont horses co-existed, but not in the same niche. Probably the low-crowned teeth of *H. primigenium* were adapted to less abrasive food than those of the "steppe forms".

Central Europe seems to have remained forested throughout the temporal range of *H. primigenium* (THENIUS 1949, BERGER 1950, KURTÉN 1972: map p. 32), which in terms of marine stratigraphy extended from the Late Miocene well into the Pliocene. This area was the centre of the geographic range of the species. The forest is a relatively stable biotope, where extremes of temperature, moisture, and other physical factors are smoothed. Thus, for a species adapted to this environment, Central Europe would for a long period have continuously offered fairly stable ecological conditions. Under such conditions evolution may be slow or arrested (see also TOBIEN 1960). Another feature indicating that *H. primigenium* was a forest form is its conservatism. Although the species did evolve with time, it retained its general characteristics, and presumably its ecological requirements. The species was still extant in the Pikermian. Typical late representatives were Ruscinian *H. crassum*, which, except for added massiveness, had changed little since primordial *H. primigenium*, and *H. "gracile complicatum"* Pirlot from the Red Crag, England,

recently erected, on insufficient evidence, as a separate species, *H. complicatum* Pirlot (KOENIGSWALD 1970). In the geographically marginal areas in the south and east where, at least intermittently, conditions were xerophytic and thus ecologically more labile and exacting, several different *Hipparion* species succeeded one another.

The local forms of early *H. primigenium*, although variable and occurring in geographi-

cally distant areas, show similar combinations of characteristics, indicating that they replaced each other geographically, thus conforming to the criteria of local populations of a polytypic species (MAYR 1964). Together these forms, sharing the same characters and evidently also ecology, form a "basic unit in evolution", the spatial and temporal populations of an evolving species (SIMPSON 1951).

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