Latest *Hipparion* Christol, 1832 in Europe. A review of the Pliocene *Hipparion crassum* Gervais Group and other finds (Mammalia, Equidae)

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ABSTRACT
The mainly late Miocene equid genus *Hipparion* Christol, 1832 still occurred in the early and middle Pliocene of Eurasia. Known European finds are here reviewed; most are referred to a "*H. crassum* Group", chiefly because of their common dental morphology, but also on their limb bone proportions when known. The group may comprise more than one species, as indicated by metapodial proportions, but new taxa are not formally described, because of the paucity of the material mostly consisting of isolated teeth. Some other finds from the same period, sometimes referred to *H. crassum* Gervais, 1859 but of uncertain relationship, are discussed.

KEY WORDS
Mammalia,
Equidae,
Hipparion crassum Group,
Pliocene,
Europe.

RÉSUMÉ
Les derniers Hipparion *Christol, 1832 en Europe. Examen du Groupe* Hipparion crassum *Gervais du Pliocène et autres découvertes (Mammalia, Equidae).*
Le genre *Hipparion* Christol, 1832, qui date principalement du Miocène supérieur, est encore présent dans le Pliocène de l'Eurasie. Les découvertes européennes connues sont examinées ici ; la plupart se réfèrent au « Groupe *H. crassum* », principalement en raison de leur morphologie dentaire, mais aussi des proportions des os de leurs membres. Certaines autres découvertes de la même époque, parfois se référant à *H. crassum* Gervais, 1859 mais dont les affinités sont incertaines, sont discutées. Les nouvelles espèces ne sont pas formellement décrites à cause de la pauvreté du matériel, constitué principalement de molaires isolées.

MOTS CLÉS
Mammalia,
Equidae,
Groupe *Hipparion crassum*,
Pliocène,
Europe.

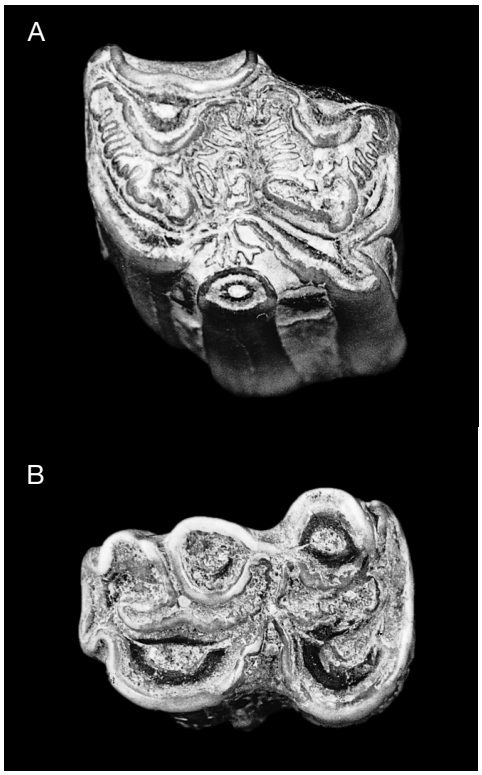

FIG. 1. — **A**, left upper M1-2 (Ipswich Borough Council Museum and Galleries R-1876-4.2) of *Hipparion* sp. of the *crassum* Group, probably from the Nodule Bed, Suffolk, England. Note strongly plicated enamel, short protocone, and open hypoconal groove; **B**, right lower p3-4 (IPSMG R-1876-4.11) of *Hipparion* sp. of the *crassum* Group, probably from the Nodule Bed, Suffolk, England. Note crenulated enamel and the lack of a protostylid.

INTRODUCTION

As late as in the Pliocene, *c.* 5.5-1.8 Ma ago, members of the mainly late Miocene equid genus *Hipparion* Christol, 1832 still occurred in Eurasia. In spite of the presence of the dentally more derived equid genus *Proboscidipparion* Sefve, 1927, and later of monodactyl *Equus* Linné, 1758, representatives of *Hipparion* were geographically widespread, in Europe from the British Islands in the west to the Caucasus in the east, although they were evidently not locally numerous, as indicated by the paucity of the material. Their time range may have spanned most of the Pliocene or some 3 Ma. Most European occurrences share morphological characters in common, indicating relatedness or, alternatively, similar ecological adaptations. Spain had its own, probably endemic forms of *Hipparion* (Alberdi & Alcala 1999), and farther east in Asia other species of the genus occurred, frequently in sympatry with *Proboscidipparion*, rarely with *Equus*.

The Pliocene members of *Hipparion* in Europe and the Middle East discussed here have been given various species names, i.e. *Hipparion gracile* Kaup, 1833, *H. crassum* Gervais, 1859, *H. moriturum* Kretzoi, 1954, *H. gracile complicatum* Pirlot, 1956, *H. apcheronicum* Gabuniya, 1959, *H. malustenense* Radulescu & Samson, 1967, *H. stavropolensis* Macarovici, 1967, and *H. heintzi* Eisenmann & Sondaar, 1998. They have also been given various generic names. Kretzoi (1954) coined the new genus name *Parahipparion* for *H. crassum*, without giving a formal definition of the new taxon. In 1964, Kretzoi substituted the name *Parahipparion* for *Pliohipparion*, and again in 1965 *Parahipparion* for *Perihipparion*, in both cases in footnotes without definitions. *Hipparion crassum* is a member of the genus *Hipparion* as shown by its cheek teeth, which have isolated protocones and convex enamel crests, but well-differentiated, rounded to rounded-triangular metaconids and metastylids of the lower cheek teeth, including the lower molars.

Some of these hipparions have erroneously been referred to "*Plesiohipparion*" Qiu, Huang & Guo, 1987 (Bernor *et al.* 1996). *Plesiohipparion* is a junior synonym of *Proboscidipparion*, a genus characterised by the derived, so called caballoid enamel pattern of its cheek teeth. In contrast to *Hipparion*, in the cheek teeth of *Proboscidipparion* the longitudinal enamel crests are straight, the metaconids and metastylids angular, and the upper tooth crowns noticeably straight (Forsten 1997).

Characters in common to many of the European Pliocene members of *Hipparion* are medium to large size and moderately high tooth crowns, with the enamel richly plicated and crenulated.

In the upper cheek teeth the protocones and hypocones are short relative to tooth occlusal length, and the hypoconal grooves are simple and widely open (Fig. 1A). In the lower cheek teeth, even in the lower deciduous teeth, the cingular stylids are weakly developed (Fig. 1B). The lectotype of *H. crassum* is a skull (Depéret 1890; Forsten 1968), the morphology and whereabouts of which are uncertain. There are three fragmentary skulls from Çalta, Turkey, referred to *H. heintzi* (Eisenmann & Sondaar 1998). Where preserved, the limb bones tend to be massive or broad in relation to their length. Alleged advanced characters of the metapodials (Depéret 1890; Samson 1975), interpreted as indicating incipient monodactyly, are probably dictated by the stratigraphically late age of the finds; Gromova (1952) refuted them regarding *H. crassum*. These hipparions may be united under the common denomination "the *H. crassum* Group" (*Hipparion* "morphotype" 4, according to Alberdi 1989) after the oldest valid and most commonly used species name. The group includes different species, not here formally described because of the paucity of the material. Other Pliocene finds, often referred to as *crassum*, cf. *crassum*, or ex gr. *crassum*, but of uncertain relationship, are briefly discussed.

LOCAL FINDS AND THEIR DESCRIPTION

ITALY

One of the stratigraphically earliest occurrences of a member of the *H. crassum* Group seems to be the still undescribed *Hipparion* from Baccinello V3, Italy, dated latest Miocene-earliest Pliocene or Mammalian biozones MN13-MN14 (Engesser 1989; Palombo 1994a; for Mammalian biozones see Mein 1990). Two species of *Hipparion* have been suggested (Rook 1988/1989; Palombo 1994a: 425, footnote), but I believe that the sample could belong to a single species. The sample seen is kept in the Naturhistorisches Museum, Basel. The height of the tooth crowns, measured from the tooth base to the top of the mesostyle/metaconid, is low to medium: in the little worn P3-4/p3-4 the crown heights vary between 43-53 mm. Protocone lengths and plication counts I measured/counted occlusally in upper P3-M2; all plications visible to the bare eye were counted. In this sample the protocones are short, mean length is 5.8 mm, the plication counts high, mean count 36 plications. In the lower cheek teeth the protostylids are weak or absent; one worn left p3-4 (without No.) from Cinigiano has an ectostylid in wear.

The limb bones, mainly phalanges, are small compared with those of *H. crassum* from Perpignan, but a calcaneum from Arcidosso (without No.) is as large or larger than those from Perpignan.

Hipparion "gracile" (junior synonym of *H. primigenium* [v. Meyer, 1829]) from the lignites of Casino, Italy (biozone MN13, Mein 1990; MN14, Palombo 1994b), probably also belongs to this group. In the Natural History Museum, London (NHM), is kept a small sample of cheek teeth of *Hipparion* from Casino (NHM coll. M 7160 and M 7161; Table 1); the main sample, in the Paleontological Museum, Pisa, has not been available. Unworn crown heights cannot be measured, since the available teeth are worn, but the protocones are slightly longer than in the teeth from Baccinello, mean 6.2 mm, and the plication counts, mean 41 plications, are high. The m1-2 have protostylids, weak in p3-4.

FRANCE

The type locality of *H.crassum* is said to be "sur la route de Perpignan au Canet" (Gervais 1859), France; in the collections material marked "Perpignan" derives from several localities in the area (Alberdi & Aymar 1995). The fauna is dated to zone MN15 (Mein 1990). Material studied is kept in the Centre des Sciences de la Terre, Université Claude Bernard and Musée Guimet, Lyon; Centre des Sciences, Université de Montpellier; Muséum national d'Histoire naturelle, Paris (MNHN); the Museum Ordzonikidze, Moscow, and the American Museum of Natural History, New York. The material consists of isolated cheek teeth and

TABLE 1. — Measurements on the teeth from Casino, Italy (length and breadth taken at the base of the tooth, in mm). Abbreviations: **a**., approximate; **L**, left; **NHM**, Natural History Museum, London; **R**, right.

Specimen	Height	Length	Breadth	Protocone	Plications	Tooth
NHM 7160	29	23.1	24.3	6.7	a.43	P3-4 R
"	34.1	24.4	19.7	a.5.1	a.33	M3 R
"	34.1	20.7	23.3	a.6.2	–	M1-2 R
"	37.6	20.8	–	5.5	33	M1-2 R
"	35.9	32.5	24.4	5.2	–	P2 L
NHM 7161	37.1	21	20.7	6.1	48	P3-4 L
"	23.9	30.7	22.9	6.5	39	P2 R
"	24.3	29.9	–	7.4	37	P2 L
"	34.1	20.7	22.7	6.2	a.38	M1-2 L
"	36.5	21.1	25	a.6.2	43	P3-4 R
"	34.2	24.5	20.4	5.3	–	M3 L
NHM 7160	41.2	22.5	15.3			p3-4 L
"	38.7	–	12.7			m1-2 R
"	> 31	a.20.4	–			m1-2 R
"	37.1	22.4	15.1			p3-4 R
"	33.4	25.9	11.5			m2 R

jaws, of which several deciduous, and limb bones. Little worn P3-4/p3-4 have crown heights of 48-55 mm, an m1-2 (Lyon, Centre des Sciences 40994) measures 58 mm in height (Table 2). As in the preceding samples, the protocones are short, mean 6.3 mm, the plication counts high, mean 30 plications. In the lower cheek teeth the enamel is crenulated and the protostylids are mostly weak, low or scar-like. In the lower deciduous teeth there may be a protostylid, but an ectostylid is low or absent.

Although mid-shaft width even in adult specimens is quite small, the metapodials (Table 11) and proximal phalanges from Perpignan show the relatively massive proportions of the limbs of this hipparion. As the hypodigm, they will here serve as a model for comparison with other local finds. I measured the bones according to Gromova (1952) and compare them in Simpson's ratio diagrams (Simpson 1941), using arbitrary standards for MT and MCIII (see figure captions Figs 2-11). An arbitrary standard, which does not represent a species, a sample, or a specimen, allows for comparison of any samples or single specimens with one another.

Eisenmann & Sondaar (1989) stress the broad distal articular breadth in relation to distal protuberance breadth of the metapodials of *crassum*. In the sample from Perpignan measured by me six out of nine measureable metapodials have greater protuberance than articular width, as is usual in *Hipparion*, but in comparison with some other finds, the distal protuberances are little developed (Figs 2; 6). The distal sagittal keel is prominent.

The facet for the fourth carpal (unciform) proximally on MCIII is very broad and usually lacks a synovial notch; there is no facet for the second carpal.

Isolated teeth and a MTIII, said to come from Roussillon, France, are kept in the Naturhistorisches Museum, Basel, and in the Museum Ordzonikidze, Moscow. The cheek teeth seem to have longer protocones (mean 7.3 mm, n = 2; Table 3) than the other French local finds, but the sample is very small. The plication counts are high (mean 37 plications, n = 2). One upper P2 (Basel, Rss 17) is very large; the few other cheek teeth correspond in size to those from Perpignan. A lower milktooth (Basel, Rss 9) has a protostylid, but no visible ectostylid.

The MTIII (Basel, Rss 80) from Roussillon is longer and distally broader than the bones from Perpignan (Fig. 2; Table 11), but corresponds in its overall proportions to the MT from Iarăs-Cariera Nouă, Romania, and, although narrower, to those from Çalta, Turkey, referred to *H. heintzi* (Figs 4; 9).

TABLE 2. — Measurements on the teeth from Perpignan, France (length and breadth taken at the base of the tooth, in mm). Abbreviations: **a**., approximate; **L**, left; **R**, right.

Specimen	Height	Length	Breadth	Protocone	Plications	Tooth
Musée Guimet, Lyon						
Pp 217	21.3	24.6	24.1	6.5	33	P3-4 R
”	a.20	23.4	26.2	7	a.36	P3-4 R
”	18.7	21.8	24.2	7.2	33	M1-2 R
”	35.6	23.9	23.4	6	35	M1-2 R
”	30.1	24.8	22.2	4.9	–	M3 R
”	17.4	35	24.6	7.2	31	P2 R
Pp 214	14.3	–	22.7	7	a.16	P3-4 L
”	–	–	–	7.8	19	P3-4 L
”	–	–	–	6.7	22	M1-2 L
”	–	–	–	6.7	19	M1-2 L
Pp 213b	18.5	26.2	22.6			Pd3-4L
Pp 216	35.2	26	16.1			p3-4 L
”	(25)	30.1	15.1			p2 L
”	28.8	22.9	15			p/m L
”	34.6	22.8	13.3			m1-2 L
”	30	–	12.8			m1-2 L
”	23	29.8	12.7			m3 L
Pp 218	> 41	–	a.13.3			p/m R
”	24.9	27.4	15.8			pd3-4 R
”	16.1	36.4	15.5			pd2 R
”	23.5	27.7	–			pd3-4 L
”	> 24	28.4	–			pd3-4 R
”	23.3	–	–			pd3-4 L
”	16.7	36.8	16.4			pd2 L
Pp 218	13.5	37.7	15			pd2 L
”	12.6	37.2	15.2			pd2 R
Centre des Sciences, Université Claude Bernard, Lyon						
40961	> 29	–	–	5.8	42	P2 L
No No.	24.8	21.9	23.3	6.2	31	P/M L
40994	58.5	22.8	16.6			m1-2 L
40990	48.4	24.2	14.7			p3-4 R
40956	–	–	–			p2 L
40957	(34)	33.1	12.8			m3 L
No No.	a.30	24.7	16.3			p/m L
40980	36.3	28.7	17.1			p3-4 L
40982	28	27.5	16.6			p3-4 R
40978	38.3	24.5	13.7			m1-2 R
40981	36.5	23.3	16.1			m1-2 R
No No.	55.1	22.6	15.7			p3-4 R
40977	35	29.5	12.4			m3 L
40980	37	(28.6)	11.6			m3 L
40975	47.7	a.30.1	12.2			m3 L
40960	20	24.5	24	6.8	38	P3-4 L
40962	25.6	a.24.2	–	–	33	M3 L
40965	16.5	34.9	25	7.1	28	P2 L
40968	12.9	24.5	27	7.8	24	P3-4
40966	20.5	23.7	26.3	6.9	34	P/M L
40963	18.1	21.5	25	6.4	a.24	M1-2 L
40967	19.1	23.8	21.5	6.9	28	M3 L
40964	> 33	25.7	–	6.3	a.43	P3-4 L
Centre des Sciences, Université de Montpellier						
No No.	> 44	> 23.5	–	5.5	34	P3-4 R

Specimen	Height	Length	Breadth	Protocone	Plications	Tooth
Muséum national d'Histoire naturelle, Paris						
No No.	25.9	–	25.8	6.7	32	P2
"	32	35	23	6.2	31	P2
"	32	25	28.5	6.7	42	P3-4
"	54.3	25.2	25.6	5.9	18	P3-4
"	40.5	27	15.6			p3-4
"	48.3	25	15.9			p3-4
American Museum of Natural History, New York						
10545	40.6	24	14.8			p3-4
10545	38.6	25.8	a.24.3	5.8	51	P3-4
Museum Ordzonikidze, Moscow						
1985	24.2	23.8	21.3	5.7	28	M3 R
1986	13.8	26.5	26			Pd3-4 R
1984	15.2	28.7	26.4			Pd3-4 L
1993	33.5	25.2	15.5			m1-2 L
1991	35.3	23.7	14.1			m1-2 L
1992	38.7	23.5	14.1			p3-4 L
1988	25	34.1	16.3			p2 L

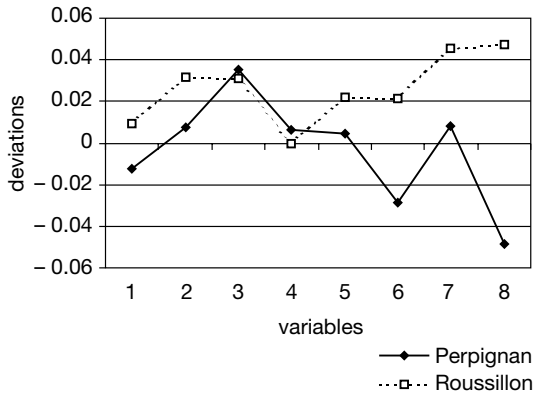

FIG. 2. — Simpson's ratio diagram, comparing the means of the hypodigm sample of MTIII from Perpignan (data own and Samson 1975: table 8) with single specimen from Roussillon. Standard (in common logs) and measurements (in mm): **1**, length 2.36; **2**, proximal breadth 1.63; **3**, proximal diameter 1.55; **4**, diameter of proximal articular surface 1.50; **5**, distal articular breadth 1.58; **6**, distal protuberance breadth 1.62; **7**, distal keel diameter 1.50; **8**, midshaft breadth 1.47.

Hipparion crassum was referred from Montpellier, France (Depéret 1890) (material in the Centre des Sciences de la Terre, Université Claude Bernard, Lyon; and in the Naturhistorisches Museum, Basel), dated to zone MN14 (Mein 1990). Interestingly, there is a lower p3-4 of a stenonid *Equus* (Lyon, No. 40644) among the teeth of *Hipparion*. The *Hipparion* material seen is scarce and consists of a few isolated cheek teeth and a MTIII (Tables 4; 11). The little worn tooth crowns reach + 50 mm in height. With the exception of two large specimens, left lower p2 and right p3-4 (Lyon, Nos 40643 and 40641), corresponding in size to those from Perpignan, the teeth are medium sized with short protocones, mean 5.6 mm, and high plication counts, mean 36 plications. Two lowers have protostylids, which in four specimens are only scar-like; the enamel is crenulated. The single MTIII from Montpellier (Basel, MP 125) is short and proximally narrow compared with the bones of *H. crassum* from Perpignan/Roussillon (Fig. 3). Plotted on its distal articular breadth to length it falls just beneath the range of the bones from Perpignan. Recently *H. crassum* was referred from the locality Le Soler, France, dated > 4 Ma ago (Alberdi & Aymar 1995). As noted by the authors, the teeth are narrow occlusally and the protocones long (Alberdi & Aymar 1995: table 1), probably due to their mainly early stage of wear, and the limb bones (MC, MT, two proximal and one medial phalanges, astragalus) are longer and proximally more slender than those of *H. crassum* from Perpignan, although their distal and

TABLE 3. — Measurements on the teeth from Roussillon, France (length and breadth taken at the base of the tooth, in mm). Abbreviations: **L**, left; **R**, right.

Specimen	Height	Length	Breadth	Protocone	Plications	Tooth
Naturhistorisches Museum, Basel						
Rss 10	23.1	24.5	28.3	7.2	41	P/M R
Rss 17	8.1	36.7	25.2	7.3	25	P2 L
Rss 9	21.8	27	16.7			pd3-4 L
Rss 8	31.1	24.7	17			m1-2
Museum Ordzonikidze, Moscow						
No No.	–	26.7	–			p3-4 L
”	23.5	24.4	–	7.4	33	P3-4 L

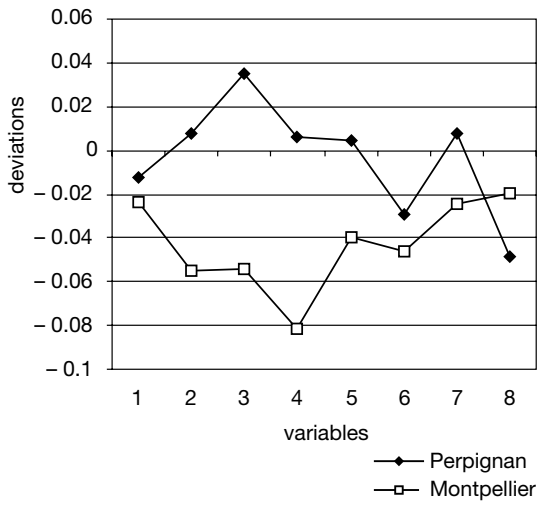

FIG. 3. — Simpson's ratio diagram, comparing the means of the hypodigm sample of MTIII from Perpignan (own data and Samson 1975: table 8) with single specimen from Montpellier. Standard (in common logs) and measurements (in mm): **1**, length 2.36; **2**, proximal breadth 1.63; **3**, proximal diameter 1.55; **4**, diameter of proximal articular surface 1.50; **5**, distal articular breadth 1.58; **6**, distal protuberance breadth 1.62; **7**, distal keel diameter 1.50; **8**, midshaft breadth 1.47.

mid-shaft breadths are considerable (Alberdi & Aymar 1995: table 2). The metapodials have very flat distal sagittal keels, possibly due to abrasion (Fig. 5).

Two lesser finds from France, referred to *H. crassum*, are an upper tooth fragment and a lower m3 from Ravin de la Chapelle at Puimoisson (Guérin *et al.* 1970) and two uppers from Saint-Laurent-des-Arbres (Crégut-Bonnoure 1982-1984). *Hipparion* cf. *crassum* from Puimoisson comes from a small fauna comprising *Zygolophodon borsoni* (Hays, 1834) and *Gazella* sp. (three teeth of *Equus* cf. *stenonis* Cocchi, 1867 are believed to have a different preservation), considered Pliocene in age. The upper tooth fragment is said to have much plicated enamel, but there are no pictures, nor measurements (Guérin *et al.* 1970). A single, much worn upper M1-2 (MNHN without No.) from Puimoisson has crenulated enamel, a protocone measuring 7.5 mm and 26 plications; the hypoconal groove is shallow.

The fauna from Saint-Laurent-des-Arbres is dated to zone MN14 (Crégut-Bonnoure 1982-1984). The worn right upper P3-4 and M1-2 (without No.), tentatively referred to *H. crassum*, are kept in the Gagnière Collection, Musée Réquien, Avignon. The teeth are of medium size with short, rounded protocones, measuring 5.6 and 6.4 mm, respectively; the enamel is crenulated, the plications cannot be counted, but seem numerous.

SPAIN

Alberdi (1974) described *H. crassum* from the lignites of Alcoy-Mina, Spain, dated to zone MN14, but Eisenmann & Sondaar (1989) doubted the specific identification. However, the cheek teeth are much plicated (Alberdi 1974: lamina 7:4; 5), with rather long-flat protocones in early wear; in later wear the protocones are oval. There is information neither on crown height, nor on the development of the cingular stylids in the lower cheek teeth.

TABLE 4. — Measurements on the teeth from Montpellier, France (length and breadth taken at the base of the tooth, in mm). Abbreviations: **a**., approximate; **L**, left; **R**, right.

Specimen	Height	Length	Breadth	Protocone	Plications	Tooth
Centre des Sciences, Université Claude Bernard, Lyon						
40655	–	(23.3)	–	5.5	a.31	P3-4 R
40645	> 38	–	–	5.2	–	P3-4 R
40641	34.6	28.2	27.6	6.3	50	P3-4 R
40643	30.4	40.6	27.7	7	39	P2 L
40649	44.1	19.1	22.7	5.1	a.48	M1-2 L
40642	31.2	20.1	22.2	5.4	35	P3-4 L
40640	50.2	19	20.7	6	18	M1-2 R
40639	51.1	21.6	14.8			p3-4 L
Musée Guimet, Lyon						
M3	29.8	22.8	14.8			p3-4 R
”	32.4	21.6	–			p3-4 R
”	27.6	a.19.6	14.7			m1-2 R
”	28.4	21.6	13.3			m1-2 R
”	26.2	20.8	15			m1-2 L

TABLE 5. — Measurements on the teeth from Gödöllö, Hungary (Hungarian Geological Institute, Budapest) (length and breadth taken at the base of the tooth, in mm). Abbreviations: **L**, left; **R**, right.

Specimen	Height	Length	Breadth	Tooth
Ob 5388	33.7	28.1	16.6	p2 L
”	35	29.7	16.3	p2 R
”	50.8	22.1	16.8	p3-4 L
”	46	22.8	17.2	p3-4 R
”	42.8	22.4	17	m1-2 L
”	48.5	22.6	15.3	m1-2 L

Among the material from Alcoy there is an equid proximal MCIII (Alberdi 1974: lamina 7:1), measuring some 50 mm in breadth, with the unciform facet divided by a synovial notch, which Eisenmann & Sondaar (1989) considered un-*Hipparion* like. However, proximal MCIII with notched unciform facets are not uncommon in the hipparions from Polgardi and Baltavar, and also occur in *H. primigenium* from Höwenegg. The Alcoy MC is proximally broader than any specimen seen from Perpignan, the broadest of which measures 47 mm in breadth (Table 11). If this bone represents *Equus*, Alcoy would be yet another locality, allegedly comprising *Equus* as well as *Hipparion* (see Montpellier above and Kislang, Malusteni, Beresti, Khapryi, and Kosiakino/Stavropol below).

ENGLAND

Hipparion is known since the middle of the 19th century from the “crags” of Suffolk, south-eastern England. The crags are marine deposits, which comprise washed-in bones and teeth of land mammals, dating mainly to the Pliocene. The *Hipparion* material from the crags consists of isolated, fragmentary and rolled upper and lower cheek teeth, kept in the Ipswich Borough Council Museum and Galleries (IPSMG), the Natural History Museum, London, and the Museum of Comparative Zoology, USA. Although said to come from the Red Crag, I believe that the *Hipparion* derives from the Nodule Bed beneath the Red Crag, dated to > 2.6 Ma ago (Gibbard *et al.* 1998), because the fossil material from there, representing the species *Dicerorhinus megarhinus* Christol, 1835,

TABLE 6. — Measurements on the teeth from Kislang, Hungary (Hungarian Geological Institute, Budapest) (length and breadth taken at the base of the tooth, in mm). Abbreviations: **a**., approximate; **L**, left; **R**, right.

Specimen	Height	Length	Breadth	Protocone	Plications	Tooth
V 13445	37.3	24.3	24.2	6.4	a.25	P3-4 R
V 13445	36.5	a.23.0	15.4			p3-4 L

Tapirus arvernensis Croizet & Joubert, 1828, *Zygolophodon borsoni*, *Parailurus anglicus* Boyd Dawkins, 1888, and *Ursus minimus* Devèze & Bouillet, 1827 (Stuart 1982), is similarly fragmentary and rolled. In addition the age, i.e. Ruscinian, of the Nodule Bed fauna corresponds to the occurrence of similar hipparions in Continental Europe.

Hipparion from the crags has earlier been identified as *H. gracile* (see Lankester 1870), *H. crassum* (see Depéret 1885, as cited in Lydekker 1886), *H. gracile complicatum* (see Pirlot 1956), and *H. moriturum* (see Koenigswald 1970), but it should be referred simply as *Hipparion* sp., because limb bones and skulls are lacking. It belongs to the *H. crassum* Group, as shown by its cheek teeth, which are medium sized with moderately high crowns (a p3-4, IPSMG R 1939 85.57.3, in early wear has a crown height of 51 mm), the protocones are short, mean 5.9 mm, the plication counts high, mean 38 plications (Fig. 1A). In the lower cheek teeth the enamel is crenulated and the cingular stylids are weak or lacking (Fig. 1B).

HUNGARY

Mottl (1939) identified *H. crassum* from Gödöllö, Hungary, dated to zone MN14 (Mein 1990), on some broad lower cheek teeth (Hungarian Geological Institute, Ob 5388) probably more or less of one individual, a humerus (Ob 5387), and distal tibia (Ob 5390). One little worn left p3-4 has a crown height of 51 mm (Table 5). The enamel is crenulated and plicated, the metaconid-metastylid double knots of the premolars in early wear tend to droop; in m1-2 the protostylids are developed, in p3-4 they are weak. The tibia and humerus are distally broad (69.3 mm and 76 mm, respectively) compared with those from Perpignan (63.6-67.5 mm and 72.2-73.8 mm, respectively).

Kretzoi (1954) described a new species called *H. moriturum* on a P3-4 and p3-4 from Kislang, Hungary (Hungarian Geological Institute, V 13445), in a fauna comprising *Equus*. Alekseeva (1977) considered the fauna mixed, with the main part belonging in the Khaprov Faunal Complex or middle Villafranchian equivalent. In the holotype of *H. moriturum*, a right P3-4 (not M1, as stated by Kretzoi 1954), the protocone is 6.4 mm, the plication count approximately 25 plications (Table 6). The enamel of the left p3-4 is crenulated, there is no protostylid, only a scar.

Kretzoi (1954) also referred a MTIII (V 13411) from Ercsi, Hungary, to *H. moriturum*, but this bone may belong to *Proboscidipparion rocinantis* Hernandez-Pacheco, 1921 (see Eisenmann & Brunet 1973; Forsten 1997: fig. 15).

BULGARIA

Alberdi & Alcala (1999) referred *H.* cf. *H. crassum* from Dorkovo, Bulgaria, dated to zone MN14 (Mein 1990). Little worn crown heights are > 50 mm; the protocones of P3-M2 are short, mean 6.1 mm, and the plications are said to be numerous (Alberdi & Alcala 1999: tables 1, 2, fig. 7). The lower premolars are said to have protostylids, rudimentary in the molars. For their measurements the few limb bones (two distal metapodials, single proximal phalanx and astragalus; Alberdi & Alcala 1999: tables 3-5) fall within the observed range of *H. crassum* from Perpignan, but metapodial breadth:length proportions are unknown.

Nikolov (1971, 1973) referred *H.* cf. *crassum* from the middle Pontian (Meotian or lower-middle Turolian, zones MN11-12, according to

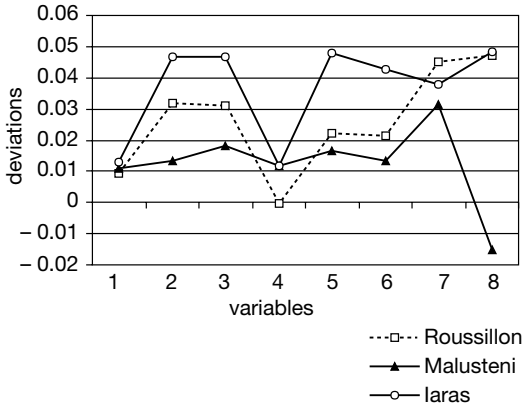

FIG. 4. — Simpson's ratio diagram, comparing single MTIII from Roussillon, Mălusteni and Iarăs-Cariera (data Samson 1975: table 8). Standard (in common logs) and measurements (in mm): **1**, length 2.36; **2**, proximal breadth 1.63; **3**, proximal diameter 1.55; **4**, diameter of proximal articular surface 1.50; **5**, distal articular breadth 1.58; **6**, distal protuberance breadth 1.62; **7**, distal keel diameter 1.50; **8**, midshaft breadth 1.47.

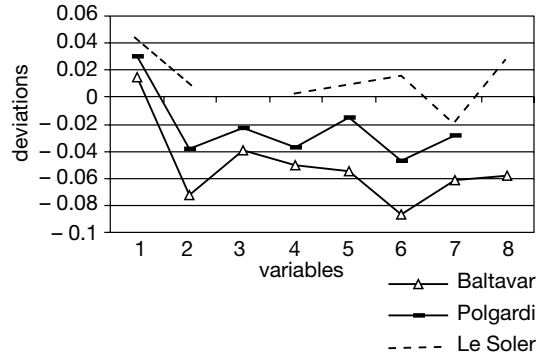

FIG. 5. — Simpson's ratio diagram, comparing single MCIII from Le Soler (data Alberdi & Aymar 1995: table 2) with sample means from Polgardi and Baltavar (own data). Standard (in common logs) and measurements (in mm): **1**, length 2.29; **2**, proximal breadth 1.63; **3**, proximal diameter 1.485; **4**, diameter of proximal articular surface 1.445; **5**, distal articular breadth 1.59; **6**, distal protuberance breadth 1.63; **7**, keel diameter 1.48; **8**, midshaft breadth 1.49.

Nikolov 1985: 44, 55) of Kalimantsi, Bulgaria, but the material from Kalimantsi pertains to two species, resembling *H. brachypus* Hensel, 1862 and *H. mediterraneum* Roth & Wagner, 1855 from Pikermi, Greece (Forsten 1978b: figs 2-5). Later Nikolov (1985) referred *H. praesulcatum* Nikolov, 1971 and *H. mediterraneum* from the uppermost lignite levels of Hrabrsko, Bulgaria, in a fauna with *Anancus arvernensis* (Croizet & Joubert, 1828), *Zygolophodon borsoni*, *Tapirus arvernensis*, and *Dicerorhinus schleiermacheri* Kaup, 1832, believed to be Pontian in age (middle-upper Turolian or zones MN12-13, according to Nikolov 1985: 44). Gabuniya (1986); (see also Kojumdgieva & Nikolov 1975; Alekseeva 1977) dated this fauna to the Pliocene in accordance with Mein's (1975) characterisation of zone MN15 faunas on the association of *Anancus arvernensis* + *Zygolophodon borsoni* + *Dicerorhinus* (*megarhinus*) + *Hipparion* (*crassum*). More recent studies seem to support Nikolov's original dating of the fauna to the late Turolian or zone MN13 (Spassov pers. comm.).

The *Hipparion* material from Hrabrsko, in the University of Sofia (coll. 290), consists of isolated cheek teeth and three distal metapodials. The tooth crowns appear to be low, 40-44 mm in little worn lower premolars (possibly all p3); the protocones are short, mean 6.5 mm, the plication counts very high, mean 50 plications, including a branched pli caballin (Table 7). In the lower cheek teeth the protostylids are scarlike or absent. The distal articular breadth of the metapodials is > 40 mm, but since the total length of the bones is unknown, nothing can be said about their relative massivity. This *Hipparion* belongs to the *H. crassum* Group on its dental morphology.

Of the species referred by Nikolov (1985) from Hrabrsko, *Hipparion mediterraneum*, originally from the Turolian (zone MN12) of Pikermi, is a species with less plicated cheek teeth and slender metapodials (Forsten 1968), while *Hipparion praesulcatum* (junior synonym of *H. primigenium*), originally described from the Vallesian equivalent (zones MN9-10) of Nesebr, Bulgaria (Nikolov 1971), has high plication counts, but flatter protocones of its upper and better developed cingular stylids of its lower cheek teeth (Forsten 1978a).

The locality Byala Slatina, Bulgaria, has a mammalian fauna identified as *Dicerorhinus schleiermacheri*, *H. mediterraneum*, *Zygolophodon borsoni*, and *Anancus arvernensis*, dated Levant,

TABLE 7. — Measurements on the teeth from Hrabrsko, Bulgaria (University of Sofia) (length and breadth taken at the base of the tooth, in mm). Abbreviations: **a**., approximate; **L**, left; **R**, right.

Specimen	Height	Length	Breadth	Protocone	Plications	Tooth
290/1	43.6	21.9	26.7	6.7	48	P3-4 R
”	–	–	–	6.5	48	M1-2 R
”	42.2	–	20.8	5.6	56	M3 R
No No.	–	–	–	6.5	57	P2 L
”	–	–	–	6.4	69	P3-4 L
”	–	–	–	6.5	54	P3-4 L
”	–	–	–	6.6	34	M1-2 L
290/2	43.7	22.4	16			p3-4 L
”	35.4	23.6	16			p3-4 R
”	43.1	21.8	14			m1-2 L
”	44.3	22.7	15.4			p3-4 R
”	a.40.7	21.5	15.5			m1-2 L
”	45	21.5	14.3			m1-2 R
”	45.9	27.3	1.32			m3 L

Pliocene (Nikolov 1965). Of *Hipparion* there is a distal humerus, the distal articular surface of which measures 70 mm (Nikolov 1965). The breadth is slightly less than that of the humeri from Perpignan and Gödöllö (72-76 mm), but greater than in *H. mediterraneum* from Pikermi, 57-66 mm (own data).

Nikolov (1985) lists *H. mediterraneum* from a number of other sites in Bulgaria, in faunas allegedly comprising *Anancus arvernensis* and *Zygolophodon borsoni*, but also *Dicerorhinus schleiermacheri* and *Deinotherium giganteum* Kaup, 1829, in Nikolov (1985) dated Pont-Pliocene. They are Kotina, Malorad, Hairedin, Bolshevik mine, and the upper lignite of Aldomirovci; the material is kept in the University of Sofia. From Kotina I have seen four large lower cheek teeth (SU 605); p3 and p4 in early wear measure 45 and 48 mm in crown height, the protostylids vary from scar-like to well-developed, and the enamel is plicated and crenulated (Table 8). From Malorad there is a lower jaw (SU 53) with well-worn teeth, the tooth row measures 148 mm at the alveoli, the enamel is crenulated, but protostylids are not visible. The scarce material from Bolshevik mine comprises a p3-4 (SU 56) with crenulated enamel, but lacking protostylid, and a fragmentary MTIII (SU 464), measuring approximately 220-230 mm in length and > 40 mm in proximal breadth. The lowers from Hrabrsko, Kotina, Malorad, and Bolshevik resemble one another closely.

GREECE

Sickenberg (1972) referred to *H.* cf. *crassum* from Megalo Emvolon (Karaburun), Greece. This locality is presently believed to date to zone MN15 and to comprise *H. longipes* Gromova, 1952 (Eisenmann & Sondaar 1989; Koufos & Kostopoulos 1997). Koufos & Kostopoulos (1997) referred to a hipparion close to *H. crassum* from Apollakia, Greece, dated to zone MN15.

From the lignites of Ptolemais, Greece, Koufos (1982) described *H. crassum* (but see Eisenmann & Sondaar 1989). The faunal levels from Ptolemais have been dated to zones MN14-15 (Mein 1990); the fauna with *H. crassum* is believed to come from the upper levels of the site, dated to zone MN15 (Koufos 1982). The *Hipparion* sample consists of some carpals, left upper Pd1, P2-3 in a jaw fragment, a MCIII, and a fragmentary proximal phalanx. The enamel of the teeth is little plicated, probably partly because the specimens are in early wear, but the pli caballins are bifid and the mesostyles well-grooved; the crowns are low and the protocones very short, in P3 only 5.7 mm (Koufos 1982: plate 1, table p. 231). There is a well-individualised pli

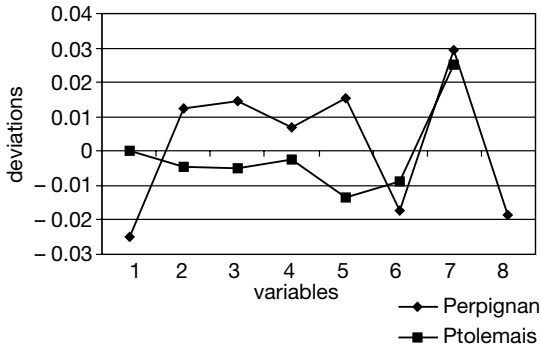

FIG. 6. — Simpson's ratio diagram, comparing the means of the hypodigm sample of MCIII from Perpignan (own data) with single specimen from Ptolemais (data Koufos 1982: 232, table). Standard (in common logs) and measurements (in mm): **1**, length 2.29; **2**, proximal breadth 1.63; **3**, proximal diameter 1.485; **4**, diameter of proximal articular surface 1.445; **5**, distal articular breadth 1.59; **6**, distal protuberance breadth 1.63; **7**, distal keel diameter 1.48; **8**, midshaft breadth 1.49.

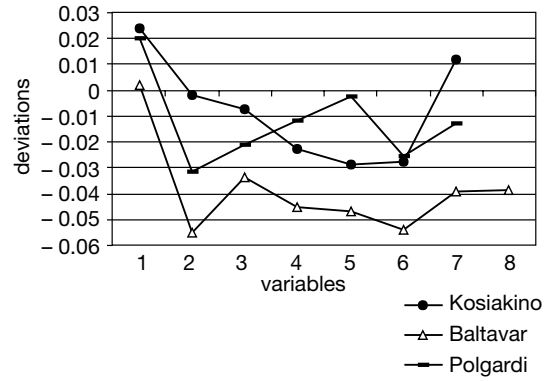

FIG. 7. — Simpson's ratio diagram, comparing the means of two MTIII from Kosiakino (data own) with sample means from Polgardi and Baltavar (own data). Standard (in common logs) and measurements (in mm): **1**, length 2.36; **2**, proximal breadth 1.63; **3**, proximal diameter 1.55; **4**, diameter of proximal articular surface 1.50; **5**, distal articular breadth 1.58; **6**, distal protuberance breadth 1.62; **7**, distal keel diameter 1.50; **8**, midshaft breadth 1.47.

hypostyle overhanging the hypoconal groove, in contrast to the hipparions of the *crassum* Group, which usually have simple, open grooves.
The MCIII from Ptolemais is relatively long for its breadth values (Koufos 1982: table p. 232, fig. 2) and falls beyond the scatter of MC from Perpignan. As in the latter sample, the distal sagittal keel is well developed (Fig. 6).

ROMANIA

Radulescu & Samson (1967) described a new *Hipparion* species, called *H. malustenense*, on seven isolated teeth and two MTIII from Mălusteni, Beresti, and Iarăs-Cariera Nouă, Romania. Later, Macarovici (1967) referred the hipparion from Mălusteni and Beresti to *H. stavropolensis*, a name originally given to the *Hipparion* from Stavropol, Russia, described as *Hipparion* sp. by Gabuniya (1959). The material is kept in the Geological Institute, University of Jassy, the Laboratory of Paleontology, University of Bucarest, and Museum Sf. Gheorge, Romania. The three local faunas are dated lower Villafranchian and about 3.8 Ma ago (Samson 1975: table 1), but Mein (1990) places Mălusteni and Beresti in zone MN15 or late Ruscinian. These two faunas have been considered mixed (Macarovici 1976; Eisenmann & Sondaar 1989; Azzaroli 1990 citing Gabuniya), because they comprise *Equus* and *Hipparion*. However, in comprising *Equus* as well as *Hipparion* they correspond to some other local faunas in eastern Europe and the northern Caucasus (see below).
The protocones of *H. malustenense* are as a mean 6.4 mm, the plication counts are high (28 plication in left P3-4; Macarovici 1967: taf. 2:2), also the two p3-4 in early wear have plicated enamel; of these one (LPB 191) measures 54 mm in crown height (Samson 1975: table 7; fig. 5). There is a protostylid (parastylid in Samson 1975) reaching two thirds of the height of the crown. The two MTIII (of which the one from Mălusteni, LGI 25, is the holotype) are longer and slightly more massive than those from Perpignan (Samson 1975: fig. 7, table 8) (Fig. 9), but the MT from Iarăs-Cariera (MSG P 165), referred to *H. malustenense*, corresponds closely in its over-all proportions to the single MT from Roussillon (Basel, Rss. 80) and to MT from Çalta (Figs 4; 9).

UKRAINE

From the Pontian limestone of Orto Mamai, near Eupatoria on the Crimea, Ukraine, there is an equid tibia (Odessa Paleontological Museum,

TABLE 8. — Measurements on the teeth from Kotina, Bulgaria (University of Sofia) (length and breadth taken at the base of the tooth, in mm). Abbreviations: **L**, left; **R**, right.

Specimen	Height	Length	Breadth	Tooth
SU 605	–	–	12.9	p2 R
"	48.1	22.7	–	p3-4 L
"	44.8	23.6	15.5	p3-4 L
"	42.9	21.4	14.7	m1-2 L

TABLE 9. — Measurements on the teeth from Kosiakino/Stavropol, Russia (Paleontological Institute and Museum, Moscow) (length and breadth taken at the base of the tooth, in mm). Abbreviations: **a.**, approximate; **L**, left; **R**, right.

Specimen	Height	Length	Breadth	Protocone	Plications	Tooth
PIN 225/15	49.5	–	–	–	–	P3-4 R
-/13	13.7	18.9	23.2	8.3	15	M1-2 R
-/18	36.5	24.4	24.4	5.6	48	P3-4 L
-/14	a.29	21.9	24.3	6.2	39	P3-4 L
-/11	36.4	19.8	22.9	6	a.38	P3-4 R
-/17	30	29.5	22.4	6.5	41	P2 R
-/10	26.7	a.32	24.8	6.3	39	P2 R
-/10	30.7	26.1	26.4	5.7	38	P3-4 R
-/10	–	–	–	6.2	48	P3-4 R
-/10	–	–	–	5.9	44	M1-2 R
-/10	40.2	–	23.1	5.6	34	M1-2 R
-/12	10.9	26.8	–	6.3	31	Pd3-4 R
-/30	44.9	23.6	15.9			p3-4 L
-/23	34.2	23.5	15.4			p3-4 R
-/20	34.1	21.2	13.9			p3-4 R
-/16	30.9	23	14			p3-4 R
-/31	53.5	22.3	14			m1-2 L
-/24	48.5	19.7	11.9			m1-2 L
-/28	33.8	21.1	13.8			p3-4 L
-/26	51.9	22	12.3			m1-2 L
-/21	46.6	21.8	a.15			p3-4 R
-/27	30.9	24.2	11.3			m3 L
-/25	28	19.8	11.7			m1-2 L
-/19	28.2	19.9	13.2			p3-4 L

OGU without No.), which by its size (length 341 mm, distal maximal breadth 67.5 mm) corresponds to those of *H. crassum* from Perpignan (Lyon 41292: 340 × 67.5 mm) and Roussillon (Lyon 40867 and 40868: 306 and 320 × 64.4 mm). Gabuniya (1986) lists *Hipparion* sp., *Palaeoryx pallasi* (Wagner, 1857), and *Paracamelus* sp. in the fauna from Mamai, which Mein (1990) places in zone MN13 or latest Turolian.

Gabuniya (1981, 1986) listed *Zygolophodon borsoni*, *H.* ex gr. *crassum*, *Dicerorhinus megarhinus*, *Eostyloceros pidoplitschkoi* Korotkevich, 1964, and *Muntiacus pliocaenicus* Korotkevich, 1965 from Kuchurgan, Ukraine (material mainly in the Zoological Institute, National Academy of Sciences, Kiev; see Dubrovo & Kapelist 1979); the fauna is believed to date to zone MN14 (see also Mein 1990). There is no information on the morphology of the *Hipparion*.

MOLDOVA

Hipparion crassum has been referred from several localities of the Pliocene "Moldavian Roussillon" in the Prut, Kagul, and Bolshaya Salcha river valleys, Moldova (Khomenko 1914, 1915; Eberzine 1948 cited in Gabuniya 1959; Alekseeva 1961, 1977; Nikiforova 1965; for critical views, see

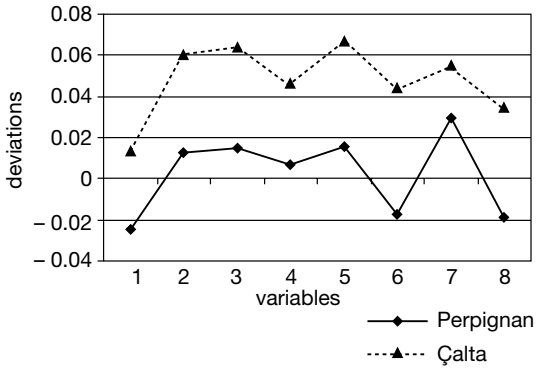

FIG. 8. — Simpson's ratio diagram, comparing the means of the hypodigm sample of MCIII from Perpignan (own data) with sample means from Çalta (own data and Eisenmann & Sondaar 1998: table 13). Standard (in common logs) and measurements (in mm): **1**, length 2.29; **2**, proximal breadth 1.63; **3**, proximal diameter 1.485; **4**, diameter of proximal articular surface 1.445; **5**, distal articular breadth 1.59; **6**, distal protuberance breadth 1.63; **7**, distal keel diameter 1.48; **8**, midshaft breadth 1.49.

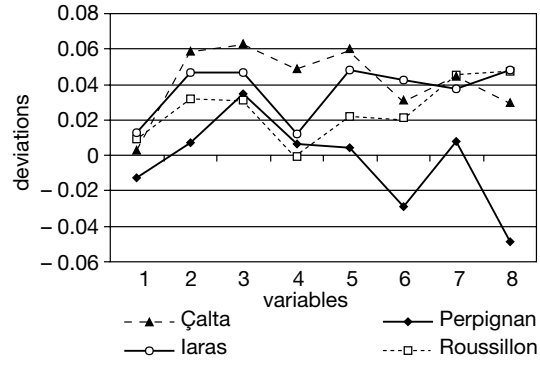

FIG. 9. — Simpson's ratio diagram, comparing the means of the hypodigm sample of MTIII from Perpignan (own data and Samson 1975: table 8) with sample means from Çalta (data own and Eisenmann & Sondaar 1998: table 13) and single specimens from Roussillon and Iarăs-Cariera (data Samson 1975: table 8). Standard (in common logs) and measurements (in mm): **1**, length 2.36; **2**, proximal breadth 1.63; **3**, proximal diameter 1.55; **4**, diameter of proximal articular surface 1.50; **5**, distal articular breadth 1.58; **6**, distal protuberance breadth 1.62; **7**, distal keel diameter 1.50; **8**, midshaft breadth 1.47.

Gromova 1952; Pevzner *et al.* 1996). Faunal elements listed together with *Hipparion* are *Castor fiber* Linné, 1758, *Vulpes vulpes* (Linné, 1758), *Lynx brevirostris* Croizet & Jobert, 1828, *Anancus arvernensis*, *Camelus bessarabiensis* Khomenko, 1912, and *Rusa* sp.; the age is believed to be zone MN15 (Gabuniya 1981; Mein 1990) or as late as lower Villafranchian equivalent (MN16) (Nikiforova *et al.* 1976).

Sinzov (1900) believed a short MTIII and a distal MCIII from Babel, Moldova, to belong to *H. crassum*, but Gromova (1952) doubted the identification. The MT (collection unknown) total length is 213 mm at a mid-shaft width of 24 mm; the MC measures 36.5 mm distally (Sinzov 1900). On these combined measurements the MT would plot in the lowermost range of *H. crassum* from Perpignan, rather near the bone from Montpellier (Basel, MP 125).

From Mikhailovka, Moldova, in a fauna with *Dicerorhinus* sp., *Cervus* (*Axis*) sp., and *Gazella* sp., believed to be Pliocene in age, David & Shushpanov (1972) referred a proximal phalanx (V 8/7), a distal tibia (V 8/5), a canine and incisor to *Hipparion* cf. *crassum*. The specimens are kept in the Dept. of Paleontology and Stratigraphy, National Academy of Sciences, Chisnau, Moldova. Plotted on its mid-shaft width to length, the phalanx falls in among the phalanges of *H. crassum* from Perpignan. With a distal breadth of 67 mm, the tibia corresponds to those from Perpignan and Orto Mamai.

In the Geological Institute, Russian Academy of Sciences, Moscow, are kept single finds of hipparions from faunas of the "Moldavian Roussillon" of Moldova (Vangengeim pers. comm. 1990). From Tataresti there is a right m3 (No. 428/311) and from Novye Kurgany a distal MTIII (No. 428/109) with an articular width of 37.6 mm. The m3 has a protostylid and the MT is slightly narrower than those from Perpignan, but corresponds to the bone from Montpellier. From an unknown locality in Moldova there is a right ramus fragment with large p2-m1 (without No.), in which the p2-p4 row measures 84 mm. The enamel of the teeth is crenulated and the m1 has a protostylid.

RUSSIA

Three cheek teeth of *Hipparion* have recently been described from the Khapryi fauna, Russia (Titov 2000), dated middle Villafranchian and

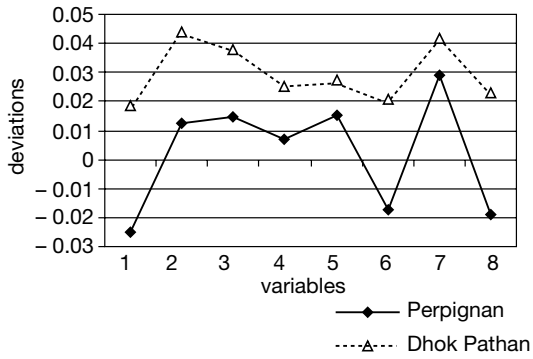

FIG. 10. — Simpson's ratio diagram, comparing the means of the hypodigm sample of MCIII from Perpignan (own data) with sample means of *Hipparion theobaldi* Lydekker, 1877 from the Dhok Pathan, Siwaliks (own data). Standard (in common logs) and measurements (in mm): **1**, length 2.29; **2**, proximal breadth 1.63; **3**, proximal diameter 1.485; **4**, diameter of proximal articular surface 1.445; **5**, distal articular breadth 1.59; **6**, distal protuberance breadth 1.63; **7**, distal keel diameter 1.48; **8**, midshaft breadth 1.49.

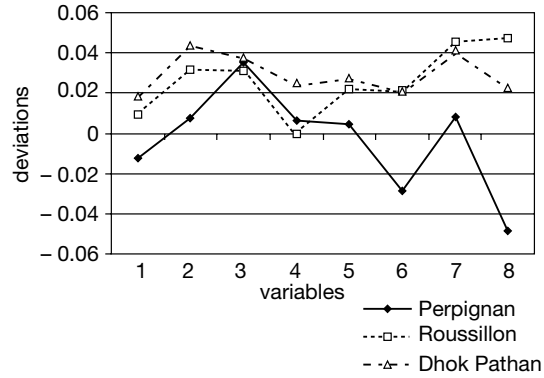

FIG. 11. — Simpson's ratio diagram, comparing the means of the hypodigm sample of MTIII from Perpignan (data own and Samson 1975: table 8) with sample means of *Hipparion theobaldi* Lydekker, 1877 from Dhok Pathan, Siwaliks (own data) and with single specimen from Roussillon. Standard (in common logs) and measurements (in mm): **1**, length 2.36; **2**, proximal breadth 1.63; **3**, proximal diameter 1.55; **4**, diameter of proximal articular surface 1.50; **5**, distal articular breadth 1.58; **6**, distal protuberance breadth 1.62; **7**, distal keel diameter 1.50; **8**, midshaft breadth 1.47.

comprising *Equus*. These are two right upper P or M (GGM-125-2/PV-557 cast and without number) and left lower p3-4 (RGU-675) (Titov 2000: fig. 1:3, 5, 4). The specimens are kept in the State Geological Museum (GGM), Russian Academy of Sciences, Moscow, and the Rostov State University (RGU), Rostov, Russia. In the uppers the protocones are long and the hypoconal grooves very shallow, probably due to wear; the lower tooth resembles that from Kislang. The upper tooth without a number, called *H.* cf. *moriturum*, was earlier described as *Hipparion* sp. by Gabuniya (1959); the cast and the lower tooth are identified as *H.* ex gr. *elegans* Gromova, 1952 (Titov 2000). These three specimens could belong to a *Hipparion* of the *crassum* Group.

Some other specimens, from Valovaya Balka (RGU-676 and -677) and from an unknown locality on the Taman peninsula (GGM-125-5/PV-558 cast, -559, and -560), Russia, are identified as *H.* ex gr. *elegans* or as *Hipparion* sp. "A" and "B", respectively (Titov 2000: figs 1:1, 2, 2:1, 2). The two uppers from Valovaya Balka, in a fauna dated middle Villafranchian, have few plications, but they are in early wear. The worn upper tooth (GGM-125-5/PV-560) from the Taman peninsula, resembles those of the *crassum* Group in having rich enamel plications and a simple, shallow hypoconal groove. These specimens may be smaller than those in the *crassum* Group and they are believed to be redeposited (Titov 2000).

Gabuniya (1959, 1986) dated the fauna from Kosiakino, near Stavropol, northern Caucasus, Russia, late Kimmerian-early Akchagylian or late Ruscinian-early Villafranchian equivalent, and differentiated two closely aged faunas (Gabuniya 1972). Mein (1990) places Kosiakino in zone MN14. The fauna comprises *Amphicyon* and *Dinotherium*, but also *Tapirus arvernensis*, *Anancus arvernensis*, and *Dicerorhinus* aff. *megarhinus*, as well as *Equus* gr. *stenonis* and *Archidiskodon* ex gr. *meridionalis* Nesti, 1825 (Gabuniya 1959). There is a medium-sized *Hipparion* (sample in the Paleontological Institute, Russian Academy of Sciences, Moscow, PIN coll. 225), called *Hipparion* sp. (Gabuniya 1959: pl. 11:1), *H.* cf. *crassum* (Gabuniya 1971), and *H. stavropolensis* (Gabuniya 1986). A small upper cheek tooth (PIN 225-22) may belong to a different species (see also Gabuniya 1959).

The little worn cheek teeth of the common hipparion from Kosiakino/Stavropol have crown

heights of 44 mm (lower p3-4) and 49-54 mm (m1-2). The protocones are as a mean 6.2 mm long, the mean plication count is 38 plications (Table 9). The lower premolars lack or have weak protostylids, in the lower molars they are thin. The limb bones studied comprise two MTIII, four proximal phalanges of which two juvenile/subadult, one astragalus and calcaneum, and two each of distal humerus, radius, and tibia. The metatarsals are longer and narrower than those from Perpignan, but resemble the podials from Polgardi, Hungary (Fig. 7; Table 11); the humeri and the measureable tibia (distal breadth 70.4-73.3 and 67 mm, respectively) correspond in breadth to those from Perpignan, the measurable phalanx is small, but a fragmentary calcaneum (PIN 225-56) is large, it may belong to *Equus*. Dentally this hipparion resembles those in the *crassum* Group, but its MT are proximally and distally more slender than those in the hypodigm. From Armavir in northern Caucasus, Russia, Gabuniya (1971) cited *Hipparion* sp. in a fauna together with *Equus* and *Archidiskodon*, later (Gabuniya 1972; see also Alekseeva 1977) he also listed *Zygolophodon borsoni*, *Anancus arvernensis*, and *Dicerorhinus megarhinus*, possibly indicating two faunas of different Pliocene age from this locality. A sample of *Hipparion* from Armavir is kept in PIN (coll. 665), comprising isolated teeth and some limb bones; *Equus* may be represented by a proximal MTIII, a medial phalanx, and some lower snouts (PIN 665-15, -16, -17). In the upper cheek teeth the protocones are medium long, mean 6.8 mm, occasionally with an anterior tip reaching towards the protoconule, uncommon in the *H. crassum* Group, and the plication counts are quite low, mean 19.6 plications (n = 3) (Table 10); the lower cheek teeth have protostylids. A proximal phalanx (PIN 665-) is slender compared with the bones of *H. crassum*. Dentally and skeletally this sample does not correspond to hipparions in the *H. crassum* Group.

TURKEY

Hipparion crassum was referred from Çalta, Turkey (Ginsburg *et al.* 1974), but was recently described as a new species, *H. heintzi*, by Eisenmann & Sondaar (1998). The fauna is dated to zone MN15 (Mein 1990). Materials are kept in the MNHN, and the Genel Müdürlügü Tabiat Tarihi Müzesi, Ankara, Turkey. There are three fragmentary skulls referred to this species rather than to *H.* cf. *longipes*, also found from Çalta. In one immature skull (MNHN, ACA 336) the preorbital fossa of the cheek is lacking or is only a shallow triangular depression; the nasal slit reaches level with the metacone of Pd2. Cheek teeth are rare in relation to the number of limb bones. Little worn P3-4 and M1-2 are 55 and 51 mm high, respectively; cut at midcrown, the protocones measure 7 and 6 mm, the plication counts about 39 and 25 plications, respectively (Eisenmann & Sondaar 1998: figs 9, 10). In the deciduous lowers of a jaw (MNHN, ACA 337) the protostylids are developed, but ectostylids are not visible.

The metapodials from Çalta, referred to *H. heintzi*, are longer and more massive than those from Perpignan (data Eisenmann & Sondaar 1998: table 13; and own). All measureable specimens have greater distal protuberance than articular widths, but like in the sample from Perpignan the protuberances are relatively weak and the distal sagittal keel prominent (Figs 8; 9). Also the proximal and medial phalanges, and the astragali are larger than those from Perpignan (data Eisenmann & Sondaar 1998: tables 11, 14; and own), the astragali also relatively broad. However, although shorter and broader, the MT resemble the specimens from Roussillon and Iarăs-Cariera in general proportions (Fig. 9); the MC correspond to those from Perpignan (Fig. 8).

AZERBAIDJAN

Gabuniya (1959: figs 12j, k, 27a) described a lower jaw from Cap Chicov on the Apcheron peninsula, Azerbaidjan, as a new species, *H. apcheronicum*. No other vertebrates were found, but the mollusc fauna from the site is said to indicate a late Apcheronian age, equivalent to the late Villafranchian. The lower tooth row measures 178 mm, indicating large teeth, cingular stylids are poorly developed and the talonid

TABLE 10. — Measurements on the teeth from Armavir, Russia (Paleontological Institute and Museum, Moscow) (length and breadth taken at the base of the tooth, in mm). Abbreviations: **a.**, approximate; **L**, left; **R**, right.

Specimen	Height	Length	Breadth	Protocone	Plications	Tooth
PIN 665/12	–	–	–	7.1	–	P3-4 L
”	–	–	–	7.3		M1-2 L
”	–	–	–	7.4		M1-2 L
-/11	–	–	–	7.9	–	P3-4 R
”	–	–	–	6.7	> 24	M1-2 R
”	–	–	–	7.4	–	M1-2 R
”	–	–	–	7.6	–	M3 R
-/98	> 47	< 20	–	6.5	–	M1-2 R
-/21	> 30	a.34	–	6.3	–	P2 L
-/25	42.5	> 20	24.9	7.8	–	P/M L
-/24	26.7	20.6	21.2	6.1	22	M1-2 R
-/23	28	–	20.9	6.2	–	M1-2 L
-/23	26.8	22.8	21.7	6.5	24	P3-4 L
No No.	33.5	19.3	23	6.5	–	M1-2 L
-/26	28	a.20	a.21	5.7	> 22	M1-2 L
-/27	27.2	23.2	18.7	6.2	20	M3 R
-/22	–	–	–	5.7	13	M1-2 R
-/30	18.4	> 20.5	15.8			p3-4 R
-/30	12.9	18.8	13.9			m1-2 R

of m3 is simple (Gabuniya 1959: fig. 12j). The specimen could represent a stenonid *Equus*, rather than *Hipparion*.

ASIA

Farther east in Asia there are no typical representatives of the *H. crassum* Group. Zhegallo (1978) believed *H. tchicoicum* Ivanjev, 1966, from the Ruscinian equivalent of China, Mongolia, and Russia, to be an Asiatic vicar of this group, but although large and relatively brachyodont, having uppers with a rounded protocone and shallow hypoconal groove, and lowers with weakly developed stylids, *H. tchicoicum* differs from the European and Middle East/Caucasian forms in having more strongly curved, truncated upper tooth crowns, thinner and less plicated/crenulated enamel, and an often deep ectoflexid in the lower premolars. In addition the lower I3 lacks an infundibulum (Forsten 1992).

EARLIER FORMS WITH SIMILAR MORPHOLOGIES

Late Turolian hipparions, dentally resembling the forms of the *H. crassum* Group, are the hipparions from Polgardi and Baltavar, Hungary, dated to zone MN13 (Mein 1990). They share dental size, moderate hypsodonty, the fairly rich enamel plications (means 27 plications), and the protocone lengths (means 6.7 and 6.9 mm, respectively) with the majority of the occurrences listed above, but the protocones are oval rather than rounded and the cingular stylids of the lowers are more developed, especially in the milk lowers. The metapodials are longer and proximally and distally narrower than those from Perpignan/Roussillon, Çalta, and Romania, but they resemble the bones from Montpellier, Le Soler, and Kosiakino/Stavropol in proximal slenderness (Figs 5; 7). The podials from Polgardi and Baltavar share the relatively weak distal protuberances and prominent distal sagittal keel with the bones from Perpignan. The proximal phalanges are more slender and the medial phalanges smaller than those from Perpignan. The astragali cover the whole size range from Perpignan.

Hipparion theobaldi Lydekker, 1877, from the Dhok Pathan Stage of the middle Siwaliks, Indian Subcontinent, resembles *H. crassum* in metapodial proportions (Figs 10; 11). The upper cheek teeth of *H. theobaldi*, although richly pli-

TABLE 11. — Measurements on the metapodials (in mm): **1**, length; **2**, proximal breadth; **3**, proximal diameter; **4**, diameter of proximal articular surface; **5**, distal articular breadth; **6**, distal protuberance breadth; **7**, distal keel diameter; **8**, midshaft breadth. Abbreviations: **a.**, approximate; **L**, left; **R**, right.

	1	2	3	4	5	6	7	8
MT Perpignan								
Pp224 (juv.)	221	(40)	(38.1)	(28.7)	38.4	38.2	33.5	24.6
Pp	> 190	–	a.34	a.30.4	–	(37)	–	–
No No.	–	–	–	–	a.33.5	–	31.1	–
Per 41	210	43.2	38.6	29.8	38.8	39	32.1	26.4
CSU18	223	> 42	> 36.5	(33)	–	–	–	25.7
Unknown	226	44.7	40.6	32.4	39.3	(39.8)	(31.7)	–
41299	226	43.9	(41.7)	(32.9)	39.2	–	(32.)	–
MT Montpellier, Roussillon, and Kosiakino/Stavropol								
MP 125	217	37.6	31.3	26.2	34.7	37.5	29.9	28.2
Rss 80	234	45.9	38.1	31.6	40	43.8	35.1	32.9
225/697	242	–	(35.2)	–	–	38.7	32.3	–
225/-	242	425	34.6	30	35.6	39.6	32.6	–
MC Perpignan								
Pp 223	183	47.3	37.7	30.9	42.1	43.6	33.2	32
Pp 241	178	42.8	30.4	26.2	38.5	37.7	29.7	27.5
Pp 241	187.5	45.3	32.2	29.7	> 40	40.9	32.9	31.7
CSU 19	189	40.9	30.2	26.6	37.6	38.8	–	27.1
CSU 17		41.2	29	27.4				
PER 45		> 40	(29.1)	(26)				
40905	183	46.8	32.4	30	42.9	44.1	33.3	
41079		43.3	29.4	27.6				

cated and often crenulated, differ in having longer, oval protocones; the permanent lowers have well-developed protostylids and occasional ectostylids, almost constantly present in the lower milk teeth. These dental characters are common to late Miocene *Hipparion* in Eurasia and Africa and can be considered "primitive" in relation to those of the *crassum* Group.

DISCUSSION

Although dental morphology is common to most of the finds discussed above, they probably do not belong in one species. Nor do similar metapodial proportions in a Simpson's ratio diagram guarantee species unity. Both dental morphology and limb proportions may have been ecological adaptations, which evolved repeatedly in different lineages under similar selective regimes. On the other hand, shared adaptations, as evidence of similar developmental reactions to environmental pressure, may indicate relationship.

With the exception of the smallest dwarfs, the hipparions generally have relatively complicated enamel patterns, especially compared with the New World pliohippines of the *Equus* lineage from the same period. In *Hipparion* richly plicated teeth also tend to be relatively low crowned (Forsten 1981). Among the Old World hipparions, particularly richly plicated enamel and massive limb proportions are found, on the one hand, in the early, Vallesian to Turolian hipparions of the *H. primigenium* Group, and on the other, in the late, Ruscinian *H. crassum* Group. According to "Antonius' Rule" (Antonius 1919), enamel complication in equid teeth correlates with tree density, i.e. with the degree of woodedness of the horse's environment. Both the early *primigenium* and the *crassum* Group hipparions are found in faunas of a sylvan character, comprising mastodonts, tapirs, deer, and pigs. However, richly plicated enamel also occurs in hipparions in faunas, which are not sylvan, e.g., Pikermi and Samos, as do massive

limb proportions, like plicated teeth considered adaptive in a sylvan environment where the surface is soft. Both "rules" should be critically re-evaluated.

Within the *H. crassum* Group I differentiate two taxa, identified primarily on the morphology of their cheek teeth, secondarily on their limb bone size and proportions. To *H. crassum*, chiefly of a late Ruscinian age, probably belong *H. morituru*m and *H. malustenense*; *H. heintzi* I regard as a geographic form of *H. crassum*. The hipparions from the early Ruscinian localities Montpellier, Le Soler, and Kosiakino, although dentally similar to *H. crassum*, differ for their limb bone size and proportions. They may belong to a related form, possibly ancestral, since it resembles late Turolian hipparions. I do not name it. A third, heterogeneous category remains as *Hipparion* sp. of the *crassum* Group or of uncertain affinity, because of a lack of material.

In Europe, the Ruscinian environment of the *H. crassum* Group was warm, humid, and densely vegetated (Palombo 1994b: 431, scheme), as also shown by the several finds from lignite deposits. The fauna from Çalta has, on the basis of the fossil rodents, been characterized as a steppe fauna and as untypical of a hipparion of the *crassum* Group (Eisenmann & Sondaar 1998), but Turkey, although probably more arid than Central Europe, probably had a mosaic vegetation, furnishing suitable environments for an ecologically diverse fauna. Also Spain, with a *Hipparion* fauna of its own (Alberdi & Alcala 1999), seems to have been more arid. At the end of the Ruscinian the climate was still warm, but drier and with cooler intervals, heralding the beginning glaciations at the Gauss-Matuyama shift (Palombo 1994b: 431, scheme). The hipparion in these and in the succeeding middle Villafranchian faunas belongs to the genus *Proboscidipparion*.

Species of *Proboscidipparion* occur together with *Equus* in the Pliocene and Pleistocene of Asia, Europe, and Africa (Eisenmann 1976, 1983, 1985; Forsten 1986), but the presence of *Hipparion* together with *Equus* has been considered controversial. The finds of *Equus* and a *Hipparion* of the *crassum* Group in the same faunas, e.g., from Kislang and Khapryi (zone MN?17), Mălusteni, Beresti, and Kosiakino (zones MN14-15), questionably from Montpellier and Alcoy, are generally believed to be due to the mixing/redeposition of material of different age. This would be true for faunas older than 2.5 Ma, which is the supposed date of the dispersal of *Equus* in the Old World (Lindsay *et al.* 1980). However, in Eastern Europe faunas comprising *Equus* have been dated on paleomagnetics to > 2.5 Ma, to the early Gauss or even late Gilbert chron (Khubka *et al.* 1983; Pevzner & Vangengeim 1986; Vangengeim & Pevzner 1991) or late zone MN15, which would not exclude the presence of *Hipparion*.

CONCLUSION

It has been maintained that the hipparions all but disappeared from Europe in the Pliocene, but this is an exaggeration. Although not as diverse or as locally numerous as in the late Miocene, hipparions are regularly found in European Pliocene mammalian faunas, from the beginning of the Ruscinian into the middle Villafranchian. Members of the *H. crassum* Group occurred throughout the Ruscinian (zones MN14-15), possibly even into the Villafranchian (Khapryi, Kislang). In Europe the *crassum* Group was succeeded by *Proboscidipparion rocinantis* in the early to middle Villafranchian (zones MN16-17). The two hipparions, well differentiable on their dental morphology, have not been found from the same sites, with the sole known exception of the Suffolk Crags, where both taxa occur, but probably deriving from differently aged beds. It is interesting that *P. rocinantis* and *H. crassum* have not been found together, since both allegedly occur together with *Equus*. Either the two hipparions did not, in fact, overlap in time in Europe, or they had different ecologies.

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NDLR : Le décès récent de Ann Forsten ne lui a pas permis de relire ses épreuves. Il restera donc quelques coquilles dans son article, dont j'espère les spécialistes des Hipparions ne nous tiendront pas rigueur. Nous vous remercions de votre compréhension.

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