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Hipparions of the Hipparion mediterraneum group from south-western USSR

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Samples of Turolian / Upper Sarmatian-Meotian *Hipparion* from southwestern USSR (Moldavia and the Ukraine) are analysed. They are compared with each other and with type *H. mediterraneum* from Pikermi, using univariate ($t = d/\sigma$ and χ^2), bivariate (scattergrams with 95 % equiprobability ellipses) and multivariate (clusters) methods. These hipparions are referred to *H. moldavicum* and *H.* cf. *moldavicum.*

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1. Introduction

Several Russian (Goronovič 190, Pržemyskij 1912, Alexeev 1916) and Soviet (Gromova 1952, Gabunia 1961, Tarabukin 1967) authors, in addition to a Romanian (Barbu 1959), have described ample fossil material of *Hipparion* from the Ukraine and Moldavia, southwestern USSR. This material has not been analysed statistically or compared with material from geographically related sites outside the USSR.

During a 2-month visit to Moscow in 1973 and a 2-year stay in Odessa in 1976—78 I had the opportunity to study these collections. The aim of this paper is to analyse certain local samples of *Hipparion* from the USSR and to compare them with the sample of type *H. mediterraneum* Roth & Wagner from Pikermi, Greece. *Hipparion mediterraneum* was chosen for comparison because of its close resemblance in skull morphology and in limb bone size and proportions.

2. Material, methods, and abbreviations

I examined samples of *Hipparion* from localities in southwestern USSR pertinent to this paper in the A. P. and M. V. Pavlov Museum and Palaeontological Museum of the Academy of Sciences in Moscow and Kiew, the Palaeontological Museum of the State University of Odessa and the District Museum in Kichinev, as well as in the Department of Geology and Geography of the University of Bucharest, Romania. I express my gratitude to the persons in charge of the collections studied.

For methods of measuring bones and teeth, see Forstén (1968, 1978).

Data on local samples were compared in scattergrams with the aid of 95 % equiprobability ellipses (Defriese-Gussenhoven 1955); changes in proportions appear as changes in the relative positions of the ellipses. Data on limb bones (14 characters, i.e. measurements in Table 10), and tooth size and morphology (10 characters in Table 9) were analysed, the sample means for each character being standardized by dividing by the mean standard deviation $\sqrt{\Sigma n_i \, s^2_i / \Sigma n_i}$ and used for calculation of the Euclidean distance between the samples (Sneath & Sokal 1973:124). The Euclidean distance was used to construct a phenogram of UPGMA clustering (Sneath & Sokal 1973:230—234), one each for limb bones and teeth. The phenograms show resemblances and differences between samples; the distance scale is in standard deviations. I thank Dr. S. Panelius for advice on these methods.

Figure 1 shows the sites from which the material had originated. Correlation of faunal stages in Western and Eastern Europe are approximate (Fig. 2).

Abbreviations:
Ch = Chimişlia, Moldavian SSR
Em = Novaja Emetovka, Ukrainian SSR
H = Hadji Bey, Ukrainian SSR
NE = Novo Elisavetovka, Ukrainian SSR
P = Pikermi, Greece
T = Ciobruci, Moldavian SSR
Ta = Taraklia, Moldavian SSR
Tu = Tudorovo, Moldavian SSR
AMNH = American Museum of Natural History, New York
Dept. Pal. Bucharest = Dept. Geology and Geography, University of Bucharest
MGRI = A. P. & M. V. Pavlov Museum, Moscow
Pal.Mus.Kiev = Palaeontological Museum, Academy of Sciences, Kiev
PIN = Palaeontological Institute and Museum, Academy of Sciences, Moşcow
OGUM = Palaeontological Museum, State University of Odessa

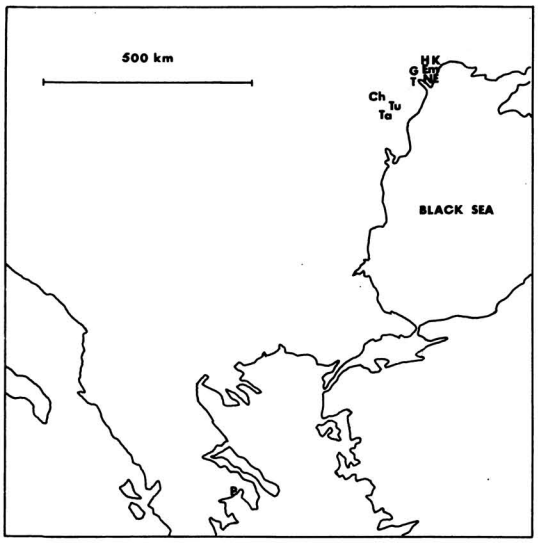

Fig. 1. Map showing SE Europe with fossil sites inserted.

3. Comparisons

3.1. Taraklia, Novo Elisavetovka, and Tudorovo

Goronovič (1906) identified *H. mediterraneum* from the Meotian of Taraklia, while Alexeev (1916), in his extensive study on the related fauna of Novo Elisavetovka, identified *H. gracile* Kaup. Gromova (1952) united these forms in a new species, *H. moldavicum,* which I (Forstén 1968:53) synonymized with *H. mediterraneum.* Gromova (1952:324) and Gabunia (1961:363) also pointed out that *H. moldavicum* is closely related to and may be identical with *H. mediterraneum.* A detailed analysis of limb bone, tooth, and skull data shows that the two species, although morphologically close, are not identical.

Gabunia (1961:99—113) described a new species, *H. tudorovense,* from the Meotian of Tudorovo (material in OGUM). In his view this species differs from the closely similar *H. moldavicum* in the more strongly developed cingular structures of its lower cheek teeth and the lower plication count of its uppers (but see Tables 2, 5, 9). Gabunia (1961:106) also drew attention to the occasional presence of enamel styles round the base of the uppers, especially around the protocone, infrequently reaching the occlusal surface. Such styles are, in fact, present in most samples of hipparions. Gabunia (1961:109) further assumed that the metapodials of *H. tudorovense* are relatively more massive than those of *H. moldavicum.* However, the limb bone measurements correspond fully to those from Taraklia and Novo Elisavetovka (Figs. 3—5, Table 10).

I consider *H. tudorovense* a synonym of *H. moldavicum* because of its overall similarity to that species. In the hipparion from Tudorovo the preorbital fossa, although similar in size and shape to that of type *H. moldavicum* and *H. mediterraneum,* is situated relatively slightly farther in front of the eye (Fig. 6).

The samples from Taraklia, Novo Elisavetovka, and Tudorovo are taxonomically heterogeneous. From Taraklia Gromova (1952:252—254) described two skull fragments as *H. platygenys* and (254—259) some large limb bones as *H.*sp. Some large specimens in the sample from Novo Elisavetovka may derive from the lower beds (Upper Sarmatian) at the site. The Upper Sarmatian hipparion has been identified as *H. "gromovae"* Gabunia = *H. verae* Gabunia (Korotkevič 1976: 66).

In addition to *H. tudorovense* Gabunia (1961: 113—116) described *H.*sp. from Tudorovo on the basis of a juvenile skull (OGUM 1779). He believed *H.*sp. to be larger than *H. tudorovense,* but the skull resembles those of juvenile *H. moldavicum*

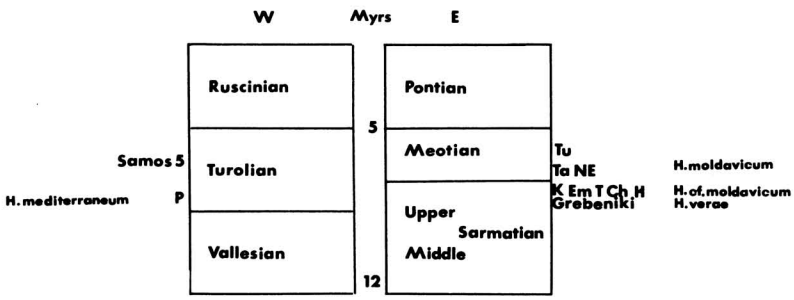

Fig. 2. Approximate correlation of stages in Western and Eastern Europe (after Van Couvering & Miller 1971, Korotkevič 1976).

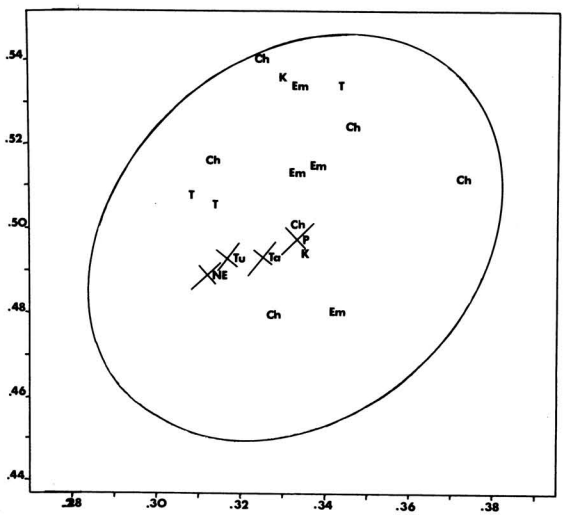

Fig. 3. MC III distal articular breadth plotted against total length in local samples of *mediterraneum*-like hipparions; log data; 95 % equiprobability ellipse drawn for sample from Pikermi (P), plotted means from NE, Tu, and single observations from T, Ch, K, and Em.

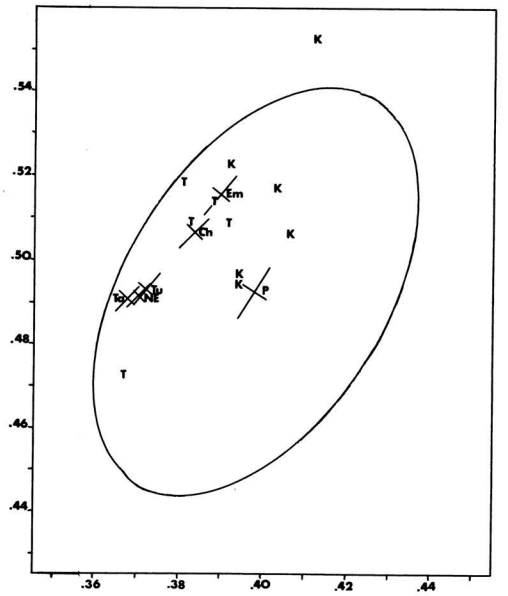

Fig. 4. MT III distal articular breadth plotted against total length in local samples of *mediterraneum*-like hipparions; log data; 95 % equiprobability ellipse drawn for sample from Pikermi (P), plotted means from Ta, NE, Tu, Ch, and Em, and single observations from T and K.

of the same individual age in samples from Taraklia and Novo Elisavetovka, and is no larger than these. Among the limb bones from Tudorovo are some specimens of a larger hipparation, e.g. a R complete MT III (OGUM 1696a) and two proximal MT III ends (OGUM 1978). These podials are as massive as the largest specimens of *H. verae*.

Most of the material from Taraklia, Novo Elisavetovka, and Tudorovo belongs to a medium-

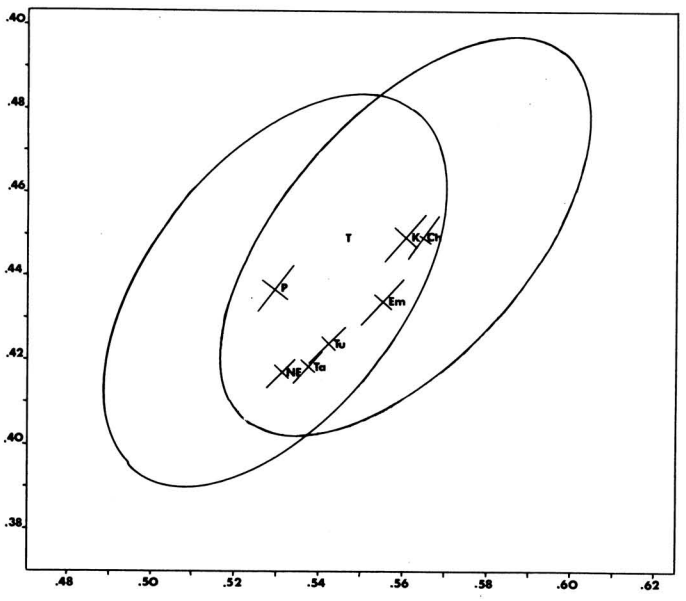

Fig. 5. Phalanx 2 mid-shaft width plotted against volar length in samples of *mediterraneum*-like hipparions; log data; 95 % equiprobability ellipses drawn for samples from Pikermi (P) and Kuijalnik (K), plotted means from NE, Ta, Tu, Em, and Ch, and single observations from T.

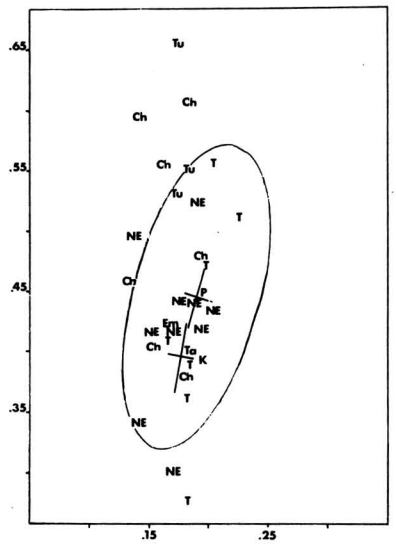

Fig. 6. Distance orbit-preorbital fossa plotted against distance P^2-orbit in samples of *mediterraneum*-like hipparions; log data; 95% equiprobability ellipse drawn for sample from Pikermi (P), plotted mean for sample from Ta, and single observations from NE, T, Em, K, Ch, and Tu.

sized hipparion. The three samples are similar in limb bone size and proportions (Figs. 3—5, Table 10). The volar V-scar of the oblique sesamoid ligament on phalanx 1, which in most hipparions is short, is often long and flattened. There is a rather high frequency of MT III lacking a facet for the cuneiform (Table 10). The teeth are hypsodont and moderately to richly plicated (Tables 3 and 9).

Hipparion moldavicum differs from type *H. mediterraneum* in being smaller in all respects, with slightly shorter and relatively slightly more massive metapodials, but a narrower phalanx 2 (Figs. 3—5). The frequency of MT III lacking a facet for the cuneiform is higher than in type *H. mediterraneum*. The upper cheek teeth are more plicated (Tables 8 and 9). The skull, although slightly smaller, has a similarly well-defined, triangular preorbital fossa.

3.2. Ciobruci

Gabunia (1961:78—86, 90—99) distinguished two species of *Hipparion* from the Meotian of Ciobruci (material in MGRI and OGUM): *H.*cf. *verae* from the lower, and *H.*cf. *moldavicum* from the upper beds. Korotkevič (1978, pers.comm.) does not believe that there are two separate beds at Ciobruci. Most of the material in the OGUM seems to belong to a single, medium-sized hipparion, there being a few specimens of a larger form. All metapodials are more slender than those of type *H. verae* from Grebeniki, and closer to those of *H. moldavicum* (Figs. 3 and 4). One of 16 MT III lacks a facet for the cuneiform. The calcaneum is also comparable to that of *H. moldavicum*, as are four astragali, in addition to which there is one very large astragalus (AMNH 21925).

The small sample of teeth from Ciobruci kept in the OGUM seems homogeneous, except for three upper premolars (OGUM 3078), which are larger than the others and bluish in colour, while the rest are brown. Those teeth (OGUM 3077), which Gabunia (1961:95—96) believed to belong to a large form, do not differ from the rest of the sample. I did not include the MGRI isolated teeth in the calculations, since their locality data are lacking or uncertain, but measured plication count and protoconal length on the skullmaterial in the MGRI and OGUM collections. Tooth measurements are given in table 9.

The skull of hipparion from Ciobruci is larger than the skull of *H. moldavicum* from Taraklia or Novo Elisavetovka and as large as that of *H. mediterraneum* from Pikermi. The preorbital fossa, as in these forms, is situated close in front of the eye (Fig. 6).

3.3. Cimişlia, Novaja Emetovka, and Kuijalnik

Barbu (1959) identified three species, *Hipparion gracile, H. mediterraneum,* and *H. matthewi* Abel, from the Meotian of Cimişlia (material in Dept. Pal., Bucharest). Recently Tarabukin (1967) described a new species, *H. praegiganteum,* on the sample from Cimişlia in the District Museum at Kichinev, USSR.

The Cimişlia collection in Bucharest is mixed with specimens from Taraklia and Ciobruci (Barbu 1959:4), which cannot be sorted out, since the preservation of the bones and teeth at these three sites is similar and locality data are lacking. The limb bone material (combined samples in Bucharest and Kichinev) comprises two hipparions: a medium-sized form, morphologically similar to *H. moldavicum* but larger, and more rarely a large form resembling *H. verae.*

The metapodials do not fall into two well-defined groups, as there is a whole gradation from relatively slender specimens to relatively massive ones. The phalanges, especially phalanx 2, clearly fall into two groups: some specimens are relatively slender, resembling but longer than phalanges of

type *H. moldavicum*; others are massive, like those of *H. verae.*

I analysed the teeth as a single sample, since two or more groups cannot be sorted out on the basis of size or morphology. Variation, however, is not unusually high (Table 9).

Gabunia (1961:139—141) complained that the formerly large fossil collection from Novaja Emetovka in the Palaeontological Museum of the Academy of Sciences at Kiev is small as a result of destruction during the war. The old collections have evidently been relocated since then, for they now comprise much more than the few specimens that Gabunia studied in the 1950s. Moreover, recent excavations at the site have added to the sample and clarified its stratigraphic position (Korotkevič 1978 pers.comm.). I did not see the new collections from Novaja Emetovka, which are also kept in Kiev, but I saw the old ones and some specimens in the OGUM and the Naturhistorisches Museum in Stuttgart-Ludwigsburg, FGR.

The material derives from two stratigraphic levels, an Upper Sarmatian and a Meotian (Korotkevič 1978, pers.comm.). The older collection is mixed, although the specimens probably were mainly from the younger, Meotian, level. The limb bones indicate a slender build similar to that of the hipparion from Cimişlia, i.e. larger than the type form of *H. moldavicum* (see also Gabunia 1961:140—141), in addition to rare specimens of a large to very large form.

Most of the tooth material belongs to the smaller form at Novaja Emetovka; only a few specimens are too large to belong to the sample.

Pržemyskij (1912) described a Meotian fauna from Kuijalnik near Odessa (material in OGUM). In its entirety this fauna, which derives from two stratigraphic levels (a clay and a sand level), resembles the fauna at Pikermi, Samos, and Maragha (Pržemyskij 1912, Alexeev 1916). Pržemyskij described two forms of *Hipparion:* the large *H. gracile* (from the clay and sand) and the small *H.*sp. *minor* Pavlov (from the sand). Gromova (1952:295) compared the larger form to *H. moldavicum,* whereas Gabunia (1961:124) believed it to be closer to *H. verae.* In fact, the limb bones from Kuijalnik suggest three forms: a rare, very small hipparion (*H.* sp. "*minor*"), comparable to *H. matthewi* from Samos, a medium-sized to large form comparable to *H. mediterraneum* or *H. verae,* and a third, very large species.

Medium-sized teeth are in the majority in the Kuijalnik material; very small and very large specimens are lacking. The three forms cannot be sorted out. Gabunia (1961:125) referred some permanent lowers (OGUM 1011) and some deciduous uppers (OGUM 988) to the small form, but these teeth are large and should probably be referred to the medium-sized form.

The medium-sized hipparions from Cimişlia, Novaja Emetovka, and Kuijalnik were similar in limb bone size and proportions, being larger than the type *H. moldavicum* (Figs. 3—5, Table 10). The metapodials are longer than, but within the range of variation of type *H. mediterraneum*; phalanx 2 is relatively narrower (Figs. 3—5, Table 10).

The teeth resemble those of the type *H. moldavicum,* except that in the sample from Cimişlia the plication count is lower and the tooth crowns slightly less hypsodont (Tables 3, 6—9).

Barbu (1959:30—31) compared the skulls from Cimişlia with a specimen from Taraklia (Dept. Pal., Bucharest 522). She noticed that in the former the preorbital fossa is situated farther in front of the eye, being also shorter and less clearly defined, than in the latter. This is true of some skulls from Cimişlia (e.g. Dept. Pal., Bucharest 378a, ?423a, no no., Kichinev Museum 4040/84), but not of others (e.g. Dept. Pal., Bucharest 378(?), 378(64), 378e, 378g). In one of the former skulls (Dept. Pal., Bucharest, no no.) the fossa is barely visible, thus resembling that of *H. platygenys* Gromova from Taraklia. The species *H. praeginganteum* Tarabukin is described on the skull Kichinev Museum no. 4040/84.

In two skull fragments from Novaja Emetovka (Pal. Mus. Kiev, no no.) and in the single skull fragment from Kuijalnik (OGUM 1041) the preorbital fossa is triangular, wide and well defined all round, as in *H. moldavicum.* The fossa is situated close in front of the eye (Fig. 6).

3.4. Hadji Bey

The material from the Meotian of Hadji Bey consists chiefly of isolated teeth (material in OGUM). Although the upper teeth seem to fall into two size groups, the lower do not, but span the range of the uppers without any clear grouping, nor are the teeth differentiated in morphology. Since the limb bones are few, not much can be said about this sample.

Gabunia (1961:125—132) discussed a "large" and a "small" hipparion from Hadji Bey. He compared the former to *H. giganteum,* but commented on the relatively low plication count of the teeth. The smaller form he thought to be related to *H. tudorovence,* since in his opinion the teeth showed similar traits, e.g. strong develop-

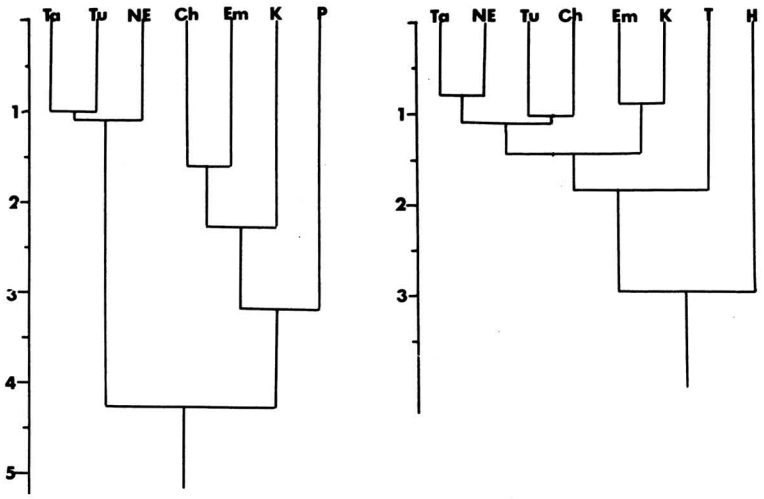

Fig. 7. Phenogram of UPGMA clustering constructed from the sample means of 14 limb bone (left) and 10 tooth (right) measurements. Distance scale in standard deviations.

ment of cingular stylids around the protoconal base. The teeth are larger than those of the medium-sized hipparions discussed above (probably partly because of mixing with those of a larger form), but the few limb bones are similar (Tables 6—10). The mean plication count of the uppers from Hadji Bey is low as compared with the teeth from those sites, but resembles the plication count of the teeth of type *H. mediterraneum* (Tables 8 and 9).

4. Discussion

The hipparions of southwestern USSR discussed resemble type *H. mediterraneum* from Pikermi in many morphological traits, the most important being general size, gracile build, and a mostly well-defined, triangular preorbital fossa. As a group these hipparions differ from *H. mediterraneum* in the higher mean plication count of the upper cheek teeth (Table 9), in the higher frequency of MT III lacking a facet for the cuneiform (Table 10), and in having a slenderer phalanx 2 (Fig. 5). They are especially close-knit in tooth morphology (Fig. 7).

An internal grouping in limb bone size, probably reflecting stratigraphic differences, is clearly reflected in the phenogram (Fig. 7). The rather small hipparions from Taraklia, Novo Elisavetovka, and Tudorovo belong to the species *H. moldavicum*. The larger forms from Ciobruci, Cimişlia, Novaja Emetovka, and Kuijalnik are differentiated in size from *H. moldavicum*. On limb bone size they may be grouped with type *H. mediterraneum*. I refer these forms to *H.*cf. *moldavicum* in spite of the difference in size, because of the similarity in tooth and limb morphology and limb proportions. The status of the medium-sized hipparion from Hadji Bey is not clear. In its teeth it differs from the rest of the hipparions of the southwestern USSR, but resembles *H. mediterraneum*.

I regard the hipparions discussed as belonging to the *mediterraneum* group. The origin of the group may be sought in *H. verae* Gabunia from the Upper. Sarmatian of Grebeniki. *Hipparion verae* (formerly *H. gromovae* Gabunia, younger homonym of *H. gromovae* Villalta & Crusafont) is a medium-sized to large hipparion with moderately plicated teeth. The preorbital fossa is oval to triangular, but more faintly defined and situated slightly farther in front of the orbit than in the hipparions discussed.

The hipparions of the *mediterraneum* group arose in the Turolian/Upper Sarmatian-Meotian through adaptive radiation, which heralded the peak of *Hipparion* evolution in the Old World. In contrast to earlier (Vallesian/Middle Sarmatian) hipparions, which were mainly woodland forms, the newly evolved forms were found in grassland or mixed grassland-woodland faunal associations.

The mammal faunas of southwestern USSR were correlated with West European ones by Mein (1974), but their internal order has since been slightly altered by Korotkevič (1976). If the fauna from Pikermi is Upper Sarmatian, as Korotkevič (1978 pers.comm.) thinks, the stratigraphically closest faunas in this region

would be the Upper Sarmatian/Meotian faunas of Kuijalnik and Novaja Emetovka and probably Ciobruci, Cimişlia, and Hadji Bey (Korotkevič 1976, 1978 pers.comm.), i.e. sites where rather large, slender-built forms of *Hipparion* predominated. The smaller hipparions, e.g. *H. moldavicum* from Taraklia, Novo Elisavetovka, and Tudorovo, are Meotian/Upper Meotian and thus younger (Fig. 2).

The *Hipparion* fauna of Kuijalnik is rather similar to that of Samos Quarry 5, which is considered younger than Pikermi (Van Couvering & Miller 1971). In both faunas there are several *Hipparion* species, including the dwarf form, *H. matthewi*. The fauna of Kuijalnik may thus be younger than Pikermi, closer in age to Samos Quarry 5 (e.g. Middle Turolian), in which case the Meotian faunas of southwestern USSR would be Upper Turolian.

Table 1. 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
Novo Elisavetovka	37/66	13/146	2/171	6/55
Taraklia	72/105	52/240	1/248	4/81
Tudorovo	16/24	7/54	2/72	1/17
Ciobruci	17/25	5/57	1/53	1/18
Kuijalnik	21/30	6/94	3/127	5/37
Novaja Emetovka		9/43	1/66	
Cimişlia	25/38	12/96	2/97	2/32

Table 2. Frequency of protostylid and ectostylid in relation to total number of teeth investigated.

	P_{3-4}		M_{1-2}	
	protost.	ectost.	protost.	ectost.
Novo Elisavetovka	93/125	16/125	88/104	4/104
Taraklia	81/123	21/123	122/139	20/139
Tudorovo	50/62	5/62	54/61	4/61
Ciobruci	2/2	—/2	3/3	—/3
Kuijalnik	54/64	4/64	63/63	5/63
Novaja Emetovka	81/91	11/91	63/69	2/69
Cimişlia	19/33	3/33	17/21	—/21

Table 3. Mean index of hypsodonty. In parenthese total number of teeth used for calculations.

	P^4	M^{1-2}	P_4	M_{1-2}
Novo Elisavetovka	22.4(7)	25.4(7)	21.3(2)	26.2(4)
Taraklia	22.1(22)	25.1(22)	23.7(7)	26.6(6)
Tudorovo	22.1(6)	26.1(10)	23.4(4)	23.9(5)
Ciobruci		24.7(2)	20.8(1)	25.5(1)
Kuijalnik	22.3(12)	25.9(22)	21.4(12)	24.9(13)
Novaja Emetovka	22.2(10)	25.8(13)	22.3(10)	24.6(5)
Cimişlia	22.7(4)	24.5(7)	22.1(2)	23.2(3)

Table 4. 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. (Yates' correction for small samples, *= $P < 0.05$, **= $P < 0.02$, ***= $P < 0.01$).

		P^2					
	NE	Ta	Tu	T	K	Em	Ch
NE	—	2.33	0.82	1.07	1.68	—	0.95
Ta	10.55***	—	0.01	0.00	0.06	—	0.10
Tu	0.72	2.08	—	0.01	0.07	—	0.01
P^{3-4} T	0.00	4.94*	0.51	—	0.03	—	0.03
K	0.50	10.99***	1.85	0.30	—	—	0.14
Em	4.67*	0.01	1.10	3.01	6.40**	—	—
Ch	0.81	3.21	0.01	0.50	2.07	1.65	—
			M^{1-2}				
	NE	Ta	Tu	T	K	Em	Ch
NE	—	0.11	0.12	0.08	0.11	0.19	0.00
Ta	2.66	—	1.31	0.08	1.48	0.02	0.72
Tu	1.86	0.20	—	0.07	0.42	1.19	0.66
M^3 T	0.35	0.24	0.47	—	0.13	0.76	0.29
K	0.02	1.57	0.13	0.18	—	0.85	0.95
Em	—	—	—	—	—	—	0.72
Ch	1.23	0.00	0.33	0.27	1.95	—	—

Table 5. Table of χ^2 comparing frequencies of protostylid and ectostylid in P_{3-4} and M_{1-2} in local samples. (Yates' correction for small samples, significance levels as in Table 4).

P_{3-4}			Protostylid			
Ectostylid	NE	Ta	Tu	K	Em	Ch
NE	—	2.16	0.89	2.44	7.18***	3.93*
Ta	0.89	—	4.36*	7.19***	15.25***	0.78
Tu	0.93	2.77	—	0.30	2.10	5.77**
K	1.07	3.02	0.00	—	0.72	8.40***
Em	0.02	1.02	0.64	0.74	—	15.33***
Ch	0.34	1.96	0.05	0.95	0.62	—

M_{1-2}			Protostylid			
Ectostylid	NE	Ta	Tu	K	Em	Ch
NE	—	0.50	0.49	9.02***	1.67	0.01
Ta	8.66***	—	0.03	6.90***	0.59	1.39
Tu	0.17	3.26	—	5.66**	0.28	1.56
K	1.35	0.92	0.08	—	7.92***	17.15***
Em	0.57	7.71***	1.99	3.84	—	2.95
Ch	0.05	2.26	3.21	3.83	2.67	—

Table 6. Table of *t* for statistics on tooth dimensions (cm). (l = length, br = breadth, significance levels as in Table 4).

			P^{3-4}							
			NE	Ta	Tu	T	K	H	Em	Ch
P_{3-4}	NE	l.	—	0.0	1.71	0.29	3.52	1.10	2.58**	2.44**
		br.	—	1.50	0.09	1.55	2.23*	0.73	0.43	2.79***
	Ta	l.	0.38	—	1.89	0.31	4.38***	1.37	2.99***	2.78***
		br.	3.06***	—	0.45	2.50**	3.61***	1.23	1.35	4.22***
	Tu	l.	1.71	1.97	—	0.79	1.39	0.31	0.50	0.48
		br.	0.28	2.16*	—	1.57	1.98	0.89	0.68	2.37**
	T	l.	1.72	1.52	1.19	—	1.69	0.45	1.19	1.16
		br.	0.21	0.64	0.26	—	0.14	0.14	0.89	0.53
	KK	l.	7.22***	7.33***	3.92***	0.89	—	1.45	1.05	1.0
		br.	1.99	4.64***	1.94	0.06	—	0.24	1.20	0.50
	H	l.	6.79***	6.88***	5.35***	0.19	3.29***	—	0.82	0.79
		br.	4.08***	6.08***	3.97***	0.64	2.43**	—	0.45	0.47
	Em	l.	3.09***	3.37***	0.93	1.05	3.35***	5.02***	—	0.0
		br.	0.88	3.59***	0.99	0.06	0.77	3.37***	—	1.58
	Ch	l.	0.98	1.21	0.36	1.39	3.63***	5.27***	1.16	—
		br.	1.36	0.19	1.08	0.49	2.31**	4.14***	1.82	—

Table 7. Table of t for statistics on tooth dimensions (cm). (l = length, br = breadth, significance levels as in Table 4).

M_{1-2}		M^{1-2} NE	Ta	Tu	T	K	H	Em	Ch
NE	l.	—	0.99	3.09***	0.93	3.91***	4.71***	3.52***	1.05
	br.	—	1.66	0.10	0.49	3.85***	2.27*	3.28***	2.28*
Ta	l.	2.41**	—	3.78***	0.48	5.09***	5.35***	4.48***	2.61**
	br.	2.99***	—	1.10	1.34	5.59***	3.18***	4.45***	3.58***
Tu	l.	0.50	1.34	—	2.95***	0.31	1.66	0.29	1.21
	br.	2.63***	0.43	—	0.51	3.07***	2.11*	2.9***	1.99
T	l.	2.38**	3.14***	2.52**	—	3.13***	4.25***	3.27***	2.05
	br.	0.43	0.75	0.08	—	1.69	1.34	1.82	1.02
K	l.	4.74***	7.67***	4.47***	0.69	—	2.21*	0.0	1.16
	br.	2.72***	5.38***	4.49***	0.0	—	0.04	0.5	0.8
H	l.	7.27***	8.78***	7.13***	1.85	4.42***	—	2.14*	2.88***
	br.	4.63***	6.54***	5.81***	0.60	2.99***	—	0.36	0.52
Em	l.	1.38	3.60***	1.64	1.82	2.94***	6.23***	—	1.09
	br.	0.85	2.90***	2.75***	0.20	1.37	6.63***	—	1.06
Ch	l.	0.53	2.17*	0.87	2.02	2.95***	6.09***	0.54	—
	br.	1.30	0.0	0.24	0.65	2.54**	4.46***	1.60	—

Table 8. Table of t for statistics on tooth dimensions. Significance levels as in Table 4.

Plication count		Protoconal lenght NE	Ta	Tu	T	K	H	Em	Ch	P
	NE	—	1.63	3.49***	1.04	0.29	2.31*	0.45	0.60	2.91***
	Ta	3.36***	—	2.68***	2.81***	2.20*	3.28***	0.95	2.38**	4.26***
	Tu	0.97	1.46	—	4.32***	3.87***	4.38***	2.61***	4.01***	5.31***
	T	0.65	3.27***	1.39	—	0.84	1.68	1.42	0.45	2.09
	K	0.36	2.18*	0.54	0.71	—	2.20*	0.75	0.36	2.81***
	H	4.42***	7.84***	4.83***	3.41***	4.32***	—	2.58**	1.96	0.0
	Em	0.55	1.77	0.32	1.02	0.19	4.25***	—	1.01	3.14***
	Ch	1.92	4.83***	2.50**	1.07	1.97	2.31*	2.06*	—	2.48**
	P	3.99***	6.37***	4.30***	3.09***	3.86***	0.17	3.90***	2.24*	—

Table 9. Statistics on tooth dimensions (cm). In order: range observed, number of observations, mean with standard error, standard deviation.

M^1-M^2 length									
K	1.63—2.07	122	1.82±0.01	0.11	Em	1.63—2.04	67	1.82±0.01	0.10
Ch	1.62—2.06	65	1.80±0.01	0.11	T	1.73—1.84	5	1.75±0.02	0.04
Ta	1.61—2.03	159	1.76±0.01	0.08	NE	1.57—2.01	140	1.77±0.01	0.08
Tu	1.58—2.07	54	1.83±0.02	0.12	H	1.67—2.06	23	1.87±0.02	0.09
M^1-M^2 breadth									
K	1.87—1.45	97	2.11±0.01	0.11	Em	1.78—2.43	66	2.12±0.02	0.15
Ch	1.86—2.34	57	2.09±0.02	0.12	T	2.03—2.12	5	2.06±0.02	0.05
Ta	1.72—2.30	158	2.03±0.01	0.11	NE	1.83—2.27	132	2.05±0.01	0.10
Tu	1.84—2.33	44	2.05±0.02	0.11	H	1.87—2.26	20	2.11±0.02	0.11
P^3-P^4 length									
K	1.84—2.35	83	2.07±0.01	0.12	Em	1.79—2.22	44	2.05±0.01	0.09
Ch	1.86—2.26	64	2.05±0.02	0.12	T	1.92—2.08	6	2.01±0.03	0.08
Ta	1.74—2.35	150	2.00±0.01	0.11	NE	1.74—2.35	117	2.00±0.01	0.14
Tu	1.87—2.26	41	2.04±0.02	0.12	H	1.82—2.24	29	2.03±0.02	0.12
P^3-P^4 breadth									
K	1.93—1.44	80	2.24±0.01	0.13	Em	1.84—2.42	39	2.21±0.02	0.13
Ch	2.03—2.55	62	2.25±0.01	0.11	T	2.15—2.31	6	2.24±0.02	0.05
Ta	1.96—2.40	145	2.18±0.01	0.10	NE	1.93—2.46	108	2.20±0.01	0.11
Tu	1.97—2.47	35	2.19±0.02	0.12	H	2.03—2.50	23	2.23±0.04	0.17
M_1-M_2 length									
K	1.73—2.12	66	1.90±0.01	0.09	Em	1.64—2.07	66	1.85±0.01	0.11
Ch	1.68—2.03	19	1.84±0.02	0.08	T	1.84—2.03	4	1.93±0.04	0.08
Ta	1.66—2.11	135	1.80±0.01	0.09	NE	1.67—2.20	103	1.83±0.01	0.11
Tu	1.67—2.12	60	1.82±0.01	0.11	H	1.76—2.26	29	2.02±0.02	0.13
M_1-M_2 breadth									
K	1.04—1.35	69	1.21±0.01	0.07	Em	1.02—1.43	69	1.19±0.01	0.10
Ch	0.98—1.33	17	1.15±0.02	0.09	T	1.17—1.24	3	1.20±0.02	0.03
Ta	1.03—1.36	134	1.15±0.01	0.08	NE	1.03—1.36	105	1.18±0.01	0.07
Tu	0.98—1.33	54	1.14±0.01	0.09	H	1.12—1.45	30	1.28±0.02	0.10
P_3-P_4 length									
K	1.93—2.32	61	2.14±0.01	0.09	Em	1.82—2.36	88	2.08±0.01	0.13
Ch	1.87—2.30	28	2.05±0.02	0.12	T	2.19 , 2.24	2	2.21±0.02	
Ta	1.76—2.37	123	2.02±0.01	0.13	NE	1.84—2.26	124	2.03±0.01	0.11
Tu	1.83—2.40	60	2.06±0.02	0.13	H	1.96—2.47	25	2.25±0.03	0.16
P_3-P_4 breadth									
K	1.23—1.54	55	1.36±0.01	0.07	Em	1.13—1.52	89	1.35±0.01	0.09
Ch	1.17—1.51	22	1.32±0.02	0.08	T	1.31 , 1.40	2	1.35±0.04	
Ta	1.16—1.52	121	1.31±0.01	0.07	NE	1.22—1.53	99	1.34±0.01	0.07
Tu	1.18—1.50	51	1.34±0.01	0.07	H	1.27—1.55	25	1.41±0.01	0.07
Protoconal length									
P	0.55—0.81	52	0.65±0.01	0.06	K	0.47—0.81	195	0.62±0.01	0.06
Em	0.49—0.81	111	0.62±0.01	0.07	Ch	0.44—0.78	154	0.62±0.01	0.07
T	0.52—0.76	107	0.63±0.01	0.06	Ta	0.45—0.81	432	0.61±0.003	0.07
NE	0.49—0.76	296	0.62±0.01	0.06	Tu	0.44—0.83	107	0.59±0.01	0.07
H	0.51—0.84	46	0.65±0.01	0.08					
Plication count									
P	7—31	33	18.8±1.13	6.47	K	3—51	133	24.33±0.87	10.09
Em	7—42	64	24.6±0.96	7.71	Ch	3—41	97	21.95±0.84	8.24
T	6—46	85	23.3±0.89	8.16	Ta	7—46	297	26.40±0.40	6.92
NE	7—43	180	23.9±0.62	6.40	Tu	7—42	94	25.00±0.89	8.64
H	8—32	34	19.06±0.85	4.94					

Table 10. Statistics on dimensions of limb bones (cm). In order: range observed, number of observations, mean with standard error, standard deviation.

MC III length										
P	19.2—23.6	34	21.36±0.15	0.93	K	21.3—23.0	3	21.9±0.55	0.95
Em	21.4—21.9	6	21.63±0.08	0.19	Ch	20.5—23.5	11	21.4±0.25	0.83
T	20.3, 20.4	2	20.4 ±0.07		Ta	19.6—22.8	28	21.04±0.13	0.71
NE	17.9—21.8	48	20.44±0.11	0.77	Tu	19.9—21.9	17	20.79±0.16	0.66
MC III proximal breadth									
P	3.33—4.05	44	3.67±0.02	0.16	K	3.10—3.71	6	3.39±0.08	0.21
Em	3.19—3.97	29	3.57±0.03	0.19	Ch	3.45—3.97	11	3.62±0.04	0.13
T	3.55—3.73	4	3.61±0.03	0.07	Ta	3.11—3.85	46	3.46±0.02	0.15
NE	2.98—3.86	49	3.39±0.02	0.16	Tu	3.16—3.89	20	3.45±0.04	0.20
MC III distal articular breadth									
P	2.87—3.65	41	3.16±0.02	0.18	K	3.12—3.69	12	3.28±0.04	0.16
Em	2.92—3.68	46	3.26±0.02	0.17	Ch	2.96—3.67	19	3.31±0.04	0.21
T	3.12—3.62	5	3.27±0.07	0.17	Ta	2.82—3.44	54	3.11±0.01	0.10
NE	2.86—3.43	67	3.10±0.01	0.12	Tu	2.93—3.38	21	3.12±0.02	0.12
MT III length									
P	23.4—27.1	41	24.96±0.12	0.81	K	24.7—25.9	6	25.16±0.19	0.48
Em	23.0—26.1	10	24.6 ±0.30	0.95	Ch	22.3—26.5	22	24.15±0.22	1.06
T	24.1—25.3	6	24.48±0.17	0.42	Ta	21.6—25.9	62	23.32±0.09	0.76
NE	21.9—25.5	75	23.48±0.09	0.82	Tu	22.7—25.1	29	23.56±0.11	0.60
MT III proximal breadth									
P	3.40—4.08	54	3.77±0.02	0.16	K	3.42—4.19	14	3.85±0.04	0.17
Em	3.44—4.11	59	3.78±0.02	0.16	Ch	3.45—4.15	22	3.81±0.04	0.20
T	3.53—4.16	11	3.84±0.05	0.19	Ta	3.28—4.03	121	3.64±0.01	0.14
Ne	3.31—4.06	73	3.63±0.01	0.15	Tu	3.31—4.02	30	3.65±0.03	0.17
MT III distal articular breadth									
P	2.85—3.68	45	3.16±0.02	0.19	K	3.12—3.61	13	3.35±0.04	0.17
Em	2.94—3.58	61	3.26±0.01	0.13	Ch	3.03—3.47	27	3.21±0.02	0.13
T	3.08—3.31	6	3.23±0.03	0.07	Ta	2.88—3.45	88	3.10±0.01	0.10
NE	2.91—3.52	105	3.11±0.01	0.12	Tu	2.88—3.33	35	3.11±0.01	0.10
H	3.77	1							

Proportions of MT III examined lacking a facet for the cuneiform
P: 3/39 K: 2/24 Em: 11/75 Ch: 7/22 T: 1/16 Ta: 28/36 NE: 23/84 Tu: 10/31

Astragalus distal breadth										
P	3.50—4.10	24	3.87±0.03	0.17	K	3.66—4.19	26	3.92±0.02	0.13
Em	3.64—4.23	15	3.89±0.04	0.18	Ch	3.51—4.10	22	3.81±0.03	0.16
T	3.56—3.76	3	3.66±0.04	0.08	Ta	3.15—4.15	216	3.71±0.01	0.15
Ne	3.28—4.05	33	3.69±0.02	0.16	Tu	3.43—3.96	23	3.70±0.03	0.15
H	3.74	1							
Astralagus height									
P	4.88—5.41	24	5.14±0.03	0.15	K	4.67—5.49	26	5.12±0.03	0.18
Em	4.84—5.43	15	5.09±0.04	0.15	Ch	4.58—5.32	15	5.01±0.05	0.22
T	4.81—5.11	3	4.93±0.07	0.12	Ta	4.29—5.59	193	4.88±0.01	0.21
Ne	4.44—5.28	32	4.77±0.03	0.19	Tu	4.48—5.07	22	4.80±0.03	0.15
H	4.86	1							
Calcaneum height									
P	9.43—10.7	12	10.01±0.11	0.40	K	9.97—10.4	4	10.09±0.08	0.17
Em	9.73—11.2	8	10.12±0.16	0.45	Ch	9.53—11.2	10	10.27±0.15	0.48
T	9.63	1			Ta	8.84—10.5	55	9.56±0.05	0.37
Ne	9.14—10.6	18	9.59±0.11	0.47	Tu	9.26—9.93	10	9.60±0.06	0.21
H	10.27	1							
Calcaneum tuber antero-posterior diameter									
P	3.52—4.00	14	3.77±0.04	0.15	K	3.82—4.21	11	4.03±0.03	0.12
Em	3.76—4.09	9	3.95±0.03	0.09	Ch	3.97—4.36	17	4.12±0.03	0.14
T	3.85	1			Ta	3.17—4.16	85	3.85±0.01	0.18
Ne	3.72—4.13	25	3.85±0.02	0.11	Tu	3.63—4.20	12	3.83±0.05	0.20
H	3.81	1							
Phalanx 2 volar length									
P	3.20—3.63	10	3,38±0.03	0.12	K	3.43—4.04	36	3.63±0.02	0.14
Em	3.34—3.95	28	3.58±0.02	0.14	Ch	3.37—3.90	18	3.65±0.03	0.14
Ta	3.18—3.84	138	3.45±0.01	0.13	NE	3.19—3.70	46	3.40±0.01	0.13
Tu	3.18—3.83	29	3.47±0.02	0.14					
Phalanx 2 breadth									
P	2.50—2.88	17	2.72±0.02	0.12	K	2.58—3.06	36	2.81±0.02	0.12
Em	2.50—3.05	30	2.76±0.02	0.14	Ch	2.61—3.04	19	2.78±0.02	0.11
Ta	2.22—3.02	138	2.62±0.01	0.11	NE	2.34—2.93	51	2.60±0.01	0.11
Tu	2.49—2.96	29	2.65±0.02	0.12					
Phalanx 1 volar length									
P	4.89—5.97	12	5.32±0.09	0.34	K	4.93—6.02	30	5.46±0.04	0.27
Em	4.77—5.96	31	5.35±0.05	0.30	Ch	4.86—5.52	9	5.27±0.08	0.24
Ta	4.57—5.91	64	5.26±0.03	0.28	NE	4.71—5.75	45	5.20±0.03	0.23
Tu	4.90—5.59	13	5.25±0.05	0.19	H	5.83	1		
Phalanx 1 breadth									
P	2.15—2.67	21	2.40±0.02	0.12	K	2.22—3.51	31	2.56±0.04	0.24
Em	2.00—2.69	30	2.46±0.02	0.14	Ch	2.29—2.74	10	2.48±0.04	0.14
Ta	2.09—2.88	73	2.34±0.01	0.11	NE	2.07—2.71	49	2.32±0.01	0.13
Tu	2.15—2.97	13	2.45±0.06	0.23	H	2.60	1		

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