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Phylogenetic Relationship Between Chinese and Western Old World Hipparionines (Equidae, Perissodactyla)

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Abstract

The Late Miocene Chinese hipparions that are morphologically similar to those from the western Old World were studied. Two monophyletic groups of the Late Miocene Eurasian hipparions were recognized in the forms from northern China, which were commonly distributed in the western and eastern Old World. It is likely that *Hipparion fossatum* and *H. hippidiodus* from northern China are respectively related to *H. moldavicum* and *H. urmiense* from the Turolian in the western Old World. *Hipparion fossatum* (China) and *H. moldavicum* (northern shore of the Black Sea and Iran) share the following characters: sub-rhomboid to sub-triangular POF situated close to the orbit, and small and slender third metapodials. *Hipparion hippidiodus* (China), *H. platygenys* (northern shore of the Black Sea), and *H. urmiense* (Iran) show following shared characters: reduced POF situated high on the face and moderately far from the orbit; small protocones, simple enamel plications, slender snout region, and large and slender to semi-robust third metapodials. *H. fossatum* and *H. hippidiodus* are associated with the "dorcadoides" (open-land living) and "mixed" faunas of northern China. The hipparionines from northern China that show affinities with the forms from the western Old World are chronologically older than those associated with the "gaudryi" (forest living) fauna based on the faunal composition. The hipparionines in the "gaudryi" fauna are similar to North American genus: *Hipparion* s.s. (*H. tehonense* and *H. forcei*). The hipparionines from the Late Miocene of northern China exhibit affinities to those from both the western Old World and North America. The hipparionine assemblages in northern China during the Late Miocene and the earliest Pliocene are result of mixture of immigrated forms from North America and from western part of Eurasia, especially, Black Sea and Sub-Paratethys regions.

Key words: *Hipparion*, Perissodactyla, Mammalia, Late Miocene, Vallesian, Turolian, China, biogeography.

Introduction

Chinese hipparionines have not been studied as wide as those of western Old World. That was partly because the accessibility to specimens and fossil localities in China were limited for vertebrate paleontologists. Hipparionine horses in western Old World have been reexamined for recognition of monophyletic groups based on comparison of differently named taxa that are widely distributed. The Chinese hipparionine horses have been studied by several researchers: Forstén (1985), Qiu *et al.* (1987) and Bernor *et al.* (1990).

In spite of those studies, the comparative studies of Chinese hipparionines with those of western Old World and North America have not been presented. It is important in biogeography and biochronology of hipparion fauna to make clear the phylogenetic relationship of Chinese hipparionines with the western Old World's and North American forms.

Here, I present phylogenetic closeness of some species of Late Miocene Chinese hipparionines to those from the western Old World, especially the northern shore region

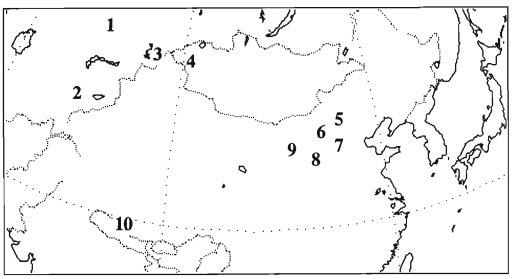

Fig. 1. Location map of North China and Inner Asia. 1: Pavlodar, Kazakh S.S.R. (Turolian-Ruscinian), 2: Sor, Tadzhik S.S.R. (Turolian-Ruscinian), 3: Kalmakpai, Kazakh S.S.R. (Pliocene), 4: Altan-Teli; & Khirgis-Nur, Mongolia (Mio-Pliocene), 5: Zhunger, Inner Mongolia (Baodean = Turolian), 6: Baode, Shanxi (early Baodean = early Turolian), 7: Xin'an, Henan; Yushe & Wuxiang, Shanxi (latest Baodean = latest Turolian), 8: Lantian, Shaanxi (latest Bahean), 9: Qingyang, Gansu (Bahean), 10: Biru (Bahean); Guizhong (Baodean), Tibet.

of the Black Sea and the Sub-Paratethys region (Fig. 1). This means that there are some monophyletic groups of hipparionines in the Late Miocene that include forms from both China and western Old World. The recognition of monophyletic groups widely distributed in Eurasia is important for biogeographic researches on well diversified Late Miocene "*Hipparion*" fauna and biostratigraphic work on the continental Miocene based on the mammalian fossil remains.

Previous Stduies

The previous studies on Chinese hipparionines can be divided into classic (Koken, 1885; Schlosser, 1924; Sefve, 1927) and modern works (Forstén, 1968, 1985; Qiu *et al.* 1987). In the classic studies, Koken's and Schlosser's works are based on fragmentary specimens such as teeth and limb bones. The classic species *Hipparion richthofeni* Koken 1885 was established based on poor materials (isolated cheek teeth) and consider taxonomically invalid by Gromova (1952).

Sefve (1927) studied the materials collected during the 1920's from northern China by Sino-Swedish Expedition directed by J. G. Anderson, and described 11 new species of *Hipparion* and one new genus (*Proboscidipparion*). Forstén (1968) examined Lagrelius collection and delimited the number of species of Chinese hipparionines as 5 species of *Hipparion* and 1 species of *Proboscidipparion*.

Forstén (1985) revised the Lagrelius Collection and the materials stored in American Museum of Natural History and synonymized some Sefve's species. But, she did not give detailed consideration to phylogenetic relationship between the Chinese hipparionines and western Old World forms.

Qiu *et al.* (1987) extensively examined specimens from northern China especially from the Plio-Pleistocene hipparionines at the Yushe and Wuxiang Basins in the south eastern Shanxi, and erected sub-generic combinations of a single genus *Hipparion* for Chinese Late Miocene-Pleistocene hipparionines.

Bernor *et al.* (1990) reexamined specimens described by Sefve (1927) and additional materials stored in Frick collection of AMNH. They presented phylogenetic hypothesis on Chinese hipparionine taxa that were similar in their assignment to that by Qiu *et al.* (1987).

Abbreviations and Method

1. Abbreviations

AMNH: American Museum of Natural His-

tory, New York.
PIN: Paleontological Institute, Moscow.
PUZ: Department of Zoology Collection, Punjab University, Lahore.
MG: Muzei Gruzii, Tbilisi.
IVPP.V: Institute of Vertebrate Paleontology and Paleoanthropology, Beijing.
PMU.M: Paleontological Institute of Uppsala University, Uppsala.
MC Ⅲ: The third metacarpal.
MT Ⅲ: The third metatarsal.
POF: Preorbital fossa.
POB: Preorbital bar.
TRNW: Transverse width of cheek tooth on the occlusal surface.
PRTL: Protocone length of cheek tooth on the occlusal surface.
DAW: Distal articular width of the MC Ⅲ and MT Ⅲ.
TL: Total length of MC Ⅲ and MT Ⅲ, excluding the sagittal keel. See Eisenmann *et al.* (1988) for the method of measurements.
D/d: upper/lower deciduous.
I/i: upper/lower incisor.
C/c: upper/lower canine.
P/p: upper/lower premolar, P4 is an upper fourth premolar.
M/m: upper/lower molar, m2 is a lower second molar.
P3-4, p3-4, M1-2, m1-2: collective term for indistinguishable isolated teeth (e.g., P3-4 refers to upper third and fourth premolars).

2. Taxonomic Characters

The characters for hipparionine taxonomy have been widely discussed by many authors (Forstén, 1968; Eisenmann, 1979; Woodburne and Bernor, 1980; Qiu *et al.*, 1987; Bernor *et al.*, 1990). There are still debates among these authors concerning the taxonomic validity of cranial and post-cranial characters. Here, I used following characters: 1) the relative location of POF to the orbit and to the facial crest; 2) the shape of POF; 3) the relative size of the protocone in upper cheek teeth; 4) the degree of the enamel plications of the upper cheek teeth; 5) the relative width of the upper snout in relation to the snout length; and 6) the proportions of the third metacarpal (MC Ⅲ) and the third metatarsal (MT Ⅲ) (Fig. 2).

All characters concerning with dentition are affected by difference of the wear stage in a single individual.

The relative location of POF to the orbit is represented by scatter diagram of the preorbital bar (POB) width plotted against the P2-orbit distance. The preorbital bar width is the distance between the posterior rim of the POF and the anterior rim of the orbit. The P2-orbit distance is measured from the anterior edge of the P2 at the alveolus to the anterior rim of the orbit. The P2 orbit distance is roughly considered as the skull (therefore, body) size of the animals.

The distance between the ventral rim of the POF and the facial rest (FC) shows the relative dorsoventral location of the POF. When the distance is small compared with the dorsoventral diameter of the POF, the POF is situated ventrally on the facial region.

The relative length of the protocone in the upper cheek teeth is represented by scatter diagram of the protocone length plotted against the transverse width of the teeth. As the anteroposterior length of a cheek tooth in hipparionines greatly decreases through wear process and the transverse width does not, the latter measurements are good estimate for size of a single tooth. As the protocone length and the transverse width of the tooth decrease in the severely worn tooth, the comparison should be performed for the

moderately worn teeth (= adult age).

The enamel plications of the upper cheek teeth consist of plications of the anterior and the posterior borders of the prefossette and the postfossette, and the number of the pli caballins that is located lingually facing against the protocone. The enamel plications decrease through the wear process. The measurements of upper dental characters on Chinese and some Eurasian hip-

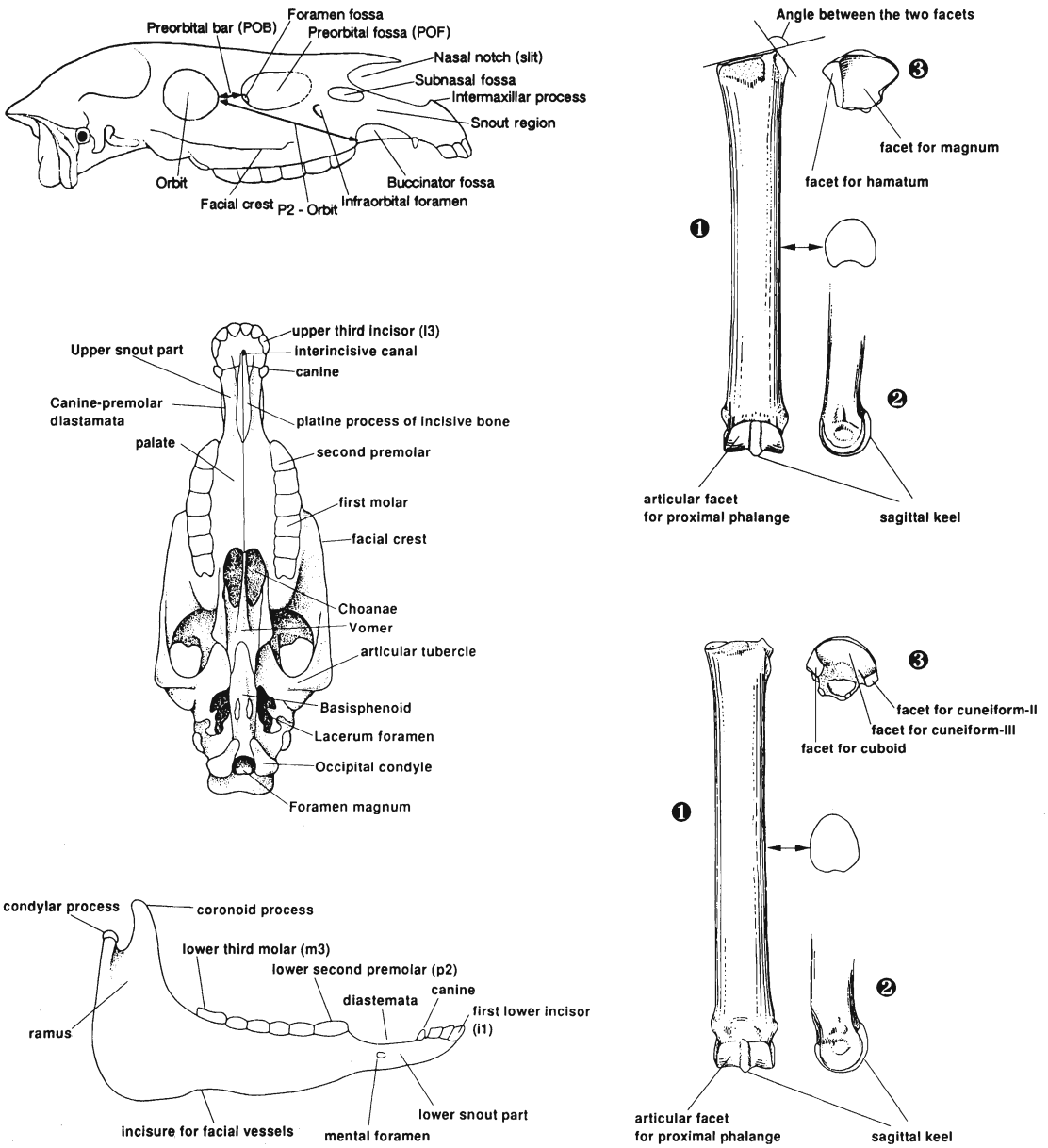

Fig. 2. Skull and MC, MT Ⅲ morphology. A. Lateral view of skull; B. Ventral view of skull; C. lateral view of mandible; D. MC Ⅲ; E. MT Ⅲ. 1: frontal view, 2: lateral view of distal part, 3: proximal view.

parions are shown in Table 1.

The relative snout width is represented by scatter diagram of the snout width that is measured in the distal edge of both I3s' plotted against the snout length that is the distance between the distal edge of the I3 and the anterior rim of the P2.

The proportions of the MC Ⅲ and MT Ⅲ are represented by scatter diagram of the distal articular width against the total length of the bones. The distal articular width of these bones is measured on the articular trochlea. The total length does not include the sagittal keel, because the keel is often abraded by weathering.

The measurement data are transformed into the logarithmic scale and plotted on the bi-variates plots. These plots can show the allometric relationship among those measurements.

The other anatomical characters such as depth of the nasal notch and the development of the articular facets on the third metapodials that have been traditionally used for hipparionine taxonomy are also mentioned and used for the taxonomy of Chinese and western Old World hipparionines. Detailed explanation of the characters for hipparionine taxonomy is presented by Eisenmann *et al.* (1988).

Table 1. Size and other character in the first upper molar of some Eurasian hipparions.

M1TRNW

Taxa	Mean	STDEV	Range	N
H. weihoense	23.0	0.702	22.3-23.7	4
H. xizangense	22.0	-	-	1
H. guizhongensis	23.95	1.169	22.6-24.6	3
H. hippidiodus (43, 44)	23.34	0.744	22.3-24.2	7
H. hippidiodus (115, Gansu)	22.08	0.327	21.7-22.4	5
H. fossatum (30)	20.11	0.822	19.0-21.6	16
H. cf. *fossatum* (31)	19.1/19.4	-	-	2
H. cf. *fossatum* (52)	21.87	0.611	21.2-22.4	3
H. cf. *fossatum* (108)	21.5	-	-	1
H. cf. *fossatum* (109)	20.8/20.9	-	-	2
H. cf. *fossatum* (110)	19.8/20.2	-	-	2
H. urmiense (Maragheh)	22.2/21.5	-	-	2
H. urmiense (Gabunia)	23.5	-	22.1-26.0	9
H. platygenys (Gromova)	23.0	-	-	1

M1PRTL

Taxa	Mean	STDEV	Range	N
H. weihoense	8.03	1.153	7.0-9.3	4
H. xizangense	7.0@	-	-	1
H. guizhongensis	7.2	0.173	7.0-7.3	3
H. hippidiodus (43, 44)	6.13	0.427	5.7-6.8	7
H. hippidiodus (115, Gansu)	6.84	0.607	5.8-7.4	5
H. fossatum (30)	6.49	0.851	5.7-8.4	15
H. cf. *fossatum* (31)	7.5/8.4	-	-	2
H. cf. *fossatum* (52)	7.03	0.635	6.3-7.4	3
H. cf. *fossatum* (108)	7	-	-	1
H. cf. *fossatum* (109)	6.3/6.3	-	-	2
H. cf. *fossatum* (110)	6.7/7.3	-	-	2
H. urmiense (Maragheh)	6.3/7.0	-	-	2
H. urmiense (Gabunia)	8.1	-	7.2-9.5	9
H. platygenys (Gromova)	6.3	-	-	1

@: proximal value

M1PLIC

Taxa	Mean	STDEV	Range	N
H. weihoense	22.75	5.058	17-27	4
H. xizangense	23.0	-	-	1
H. guizhongensis	17.0/17.0	-	-	2
H. hippidiodus (43, 44)	12.14	2.478	9-16	7
H. hippidiodus (115, Gansu)	9.67	1.155	9-11	3
H. fossatum (30)	12.8	4.459	7-21	15
H. cf. *fossatum* (31)	16.0	7.81	7-21	3
H. cf. *fossatum* (52)	9.33	5.859	5-16	3
H. cf. *fossatum* (108)	16.0	-	-	1
H. cf. *fossatum* (109)	13.0/15.0	-	-	2
H. cf. *fossatum* (110)	8.0/9.0	-	-	2
H. urmiense (Maragheh)	10.0/11.0	-	-	2
H. urmiense (Gabunia)	7.3	-	2-14	9
H. platygenys (Gromova)	7.0	-	-	1

Comparisions of Chinese Hipparions

1. Hipparion weihoense *Liu* et al. *(1978)*

(1) Holotype

IVPP.V 3113.1, well preserved skull with L and R P2-M3.

(2) Locality and Age

Lantian, Shaanxi; Late Miocene (Bahean = Baodean).

(3) Distribution

Lantian, Shaanxi.

(4) Referred materials

See Ji, *et al.* (1980).

(5) Diagnosis

Large size; protocone oval and not elongated; moderate enamel plication; the nasal notch situated above P2; the outline of POF subrhomboid and well defined in all rims; the long axis of POF oriented antero-ventrally; POB short relative to the P2-orbit

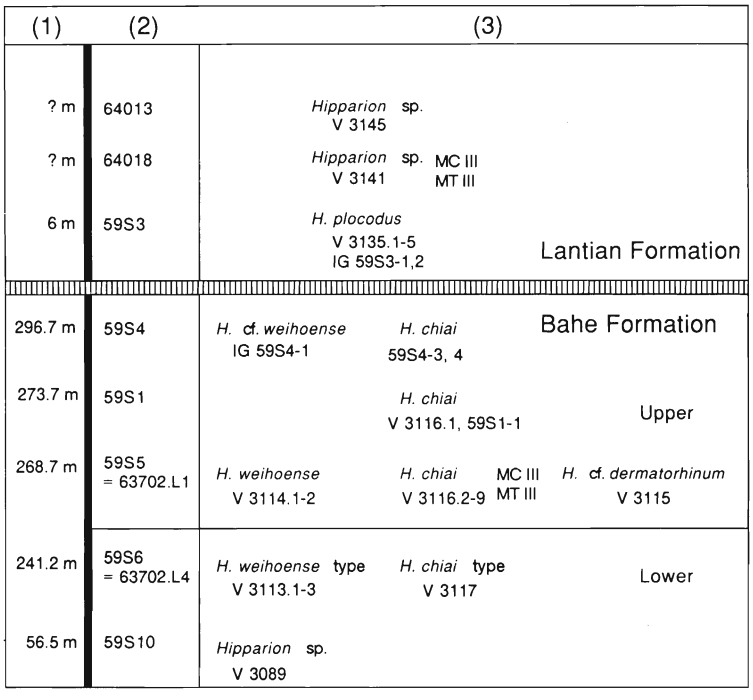

Fig. 3. Occurrence of hipparions in the Lantian Section, Shaanxi. (1) Height above the base of each formation; (2) Sub-localities; (3) Hipparionine fossils with registered number, metapodial specimens indicated.

distance; the lacrimal bone touches the posterior part of POF.

(6) Discussion

Hipparion weihoense was discovered from the Bahe Formation in the Lantian district of the Shaanxi province. The mammalian fauna from the Formation was considered as the Vallesian (Liu *et al.*, 1978) (Fig. 3).

The type specimen of *Hipparion chiai* was discovered from the same horizon of the Bahe Formation with that of the type of *H. weihoense*. *H. chiai* is similar to *H. weihoense* in its facial and dental morphology and size, although Liu *et al.* (1978) distinguished them.

The occlusal morphology of the upper cheek teeth of *H. chiai* (IVPP.V 3117.0) cannot be distinguished from that of *H. weihoense*. The size of the upper dentitions (width of M1 and cheek tooth row length) of *H. weihoense* and *H. chiai* are similar to one another. Although the lingually located pli hypostyle in the premolars was considered to be a diagnostic character of *H. chiai* by Liu *et al.* (1978), this tendency can be also observed in the premolars of *H. weihoense*. The mean M1TRNW of *H. chiai* is 21.3 mm (N= 8), and it is not greatly different from that of *H. weihoense* (IVPP.V 3113.1, type: 22.3 mm) (Table 1). The P2-M3 length of the type is 146.1 mm.

Materials of hipparionine were discovered from the Lantian Formation overlying the Bahe Formation. They were assigned to *H. plocodus* by Liu *et al.* (1978). The hipparionine from the Lantian Formation has medium length of P2-M3 (134 mm in IVPP. V3115.1; 131.5 mm in IVPP.V 3115.2: old individual), and small and slender third metapodials.

Their M1TRNW is similar to that of *H. chiai*, and the protocones are oval and not elongated. The plication count of M1 is 17 (in IVPP.V 3135.1 ?). The dental morphology of the Lantian *H. plocodus* is comparable with that of *H. coelophyes* from Loc. 43

and 44 in the Baode district of Shanxi province.

The POF of *H. weihoense* is oval to subrhomboid with well defined peripheral rims. The POF is moderately situated from the orbit (Fig. 4). The nasal slit is shallow and its posterior edge is at the level anterior to P2. The upper cheek teeth have rich enamel plications and large and oval protocone. The

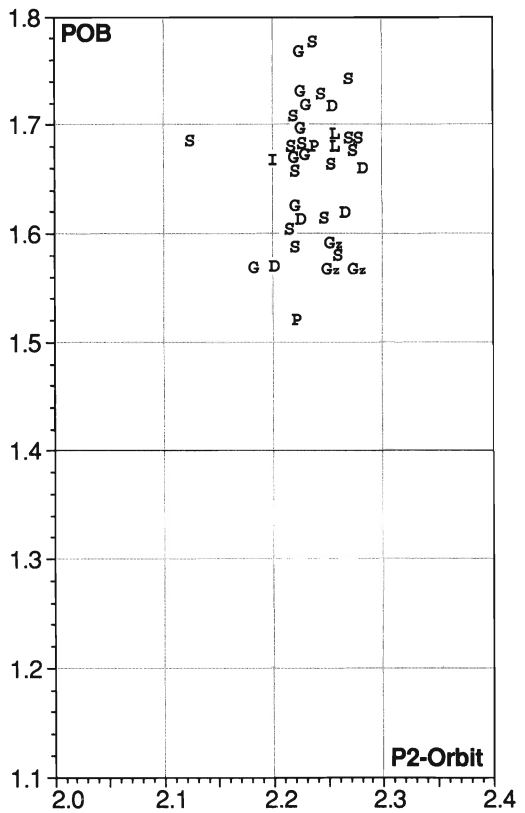

Fig. 4. POB/P2-Orbit diagram of large hipparions from China and some western Old World forms. G: H. *giganteum* from Grebeniki (Turolian, Ukraina); I: *H. primigenium* from Inzersdorf (Vallesian, Austria); L: *H. weihoense* from Lantian (Bahean, Shaanxi); S: *Hipparion* large species from Samos (Turolian, Greece); Pr: *H. brachypus* from Pikermi (Turolian, Greece); D: *H. dermatorhinum* from Loc. 30, Baode (Baodean, Shanxi); Gz: *H. guizhongensis* from Guizhong (Turolian, Tibet).

MC Ⅲ and MT Ⅲ of this taxon were not discovered. MC Ⅲ and MT Ⅲ were discovered from the horizon about 27 m above the horizon where the type specimen of *H. weihoense* was found. They show slender proportions that are different from those of Vallesian *H. primigenium*.

Hipparion weihoense is characterized by the primitive features of skull and cheek teeth shown by Early Vallesian western Old World hipparionines. Those characters are: well defined rim of POF; oval outline of POF; location of POF moderately far from the orbit and close to the facial crest; elongate protocones; rich enamel plications and pli caballins.

(7) Comparison

Liu *et al.* (1978) pointed out that *H. weihoense* was similar in facial and dental morphology and their size to *H. giganteum* from Grebeniki (Upper Sarmatian) in Ukraina. They suggested that the mammalian fauna from the Bahe Formation was earlier than that of the "*Hipparion*" fauna in northern China, such as Gansu, Shanxi and Henan. Li *et al.* (1984) considered the fauna from the Bahe Formation to be of Vallesian age based on existence of this hipparionine species, large hyaenid and spiral-horned bovids.

Large-sized hipparionines with well defined oval POF situated far from the orbit are widely distributed in the western Old World during the Turolian period. Such taxa are, for example: *Hipparion brachypus* from Pikermi, Greece, an unnamed large-sized *Hipparion* from Samos, Greece and *H. giganteum* from Grebeniki.

Hipparion brachypus was described by Hensel (1862). Its cheek tooth row length is 154.86 mm and TRNW of M1 is 24.11 mm (middle wear stage) in average (Koufos, 1987). The enamel plication is moderate to

complicated (average counts = 16.9 in middle-worn M1). The pli caballin is with 1-4 plis. The POF is well defined and deep, situated far from the orbit (Fig. 4). The POF is sub-rhomboid in outline. The MC Ⅲ and MT Ⅲ are robust in proportions that are similar to those of *H. primigenium* from Inzersdorf (Vallesian), Austria (Figs. 5 and 6).

An unnamed large-sized *Hipparion* from Samos was mentioned by Wehrli (1941). This form has large size (P2-M3 length = 147.7-161.4 mm : Woodburne and Bernor, 1980). The protocone is oval and short (M1PRTL = 6.3 mm and M1TRNW = 23 mm in Tafel 18, fig. 8 by Wehrli, 1941). The enamel plication is moderate (ca. 16) and the pli caballin is single. The POF is oval and moderately defined. It is situated far from the orbit (width of POB = 38.8-53.5 mm : Woodburne and Bernor, 1980) (Fig. 4). The nasal slit is deep and its posterior edge is at the level of P2-P3 boundary. The snout portion is elongated.

Hipparion giganteum is a large-sized form that co-occur with *H. verae* in Grebeniki (Ukraina: Late Sarmatian by Korotkevitch, 1988), northern shore region of the Black Sea (Gabunia, 1959). The P2-M3 length is 147-161 mm. The protocone is oval and short. The enamel plication is complex (about 18 plis in average, at medium worn M1-2), and the pli caballin is single. The POF is well defined and oval in outline, and is far from the orbit and the facial crest. The posterior edge of the nasal slit is at the level anterior to P2. The third metapodials are robust in proportions.

Hipparion sarmaticum (Lungu, 1973) from Kalfa (Middle Sarmatian = Vallesian) in Moldavian is a large form (P2-M3 = 165-176 mm) with well developed POF. The enamel plication is complicated, and the protocone is oval. The POF is located far from the orbit, and its rims are well defined. The proportions of the third metapodials in this taxon are robust. Forstén (1978) considered this taxon to be very close

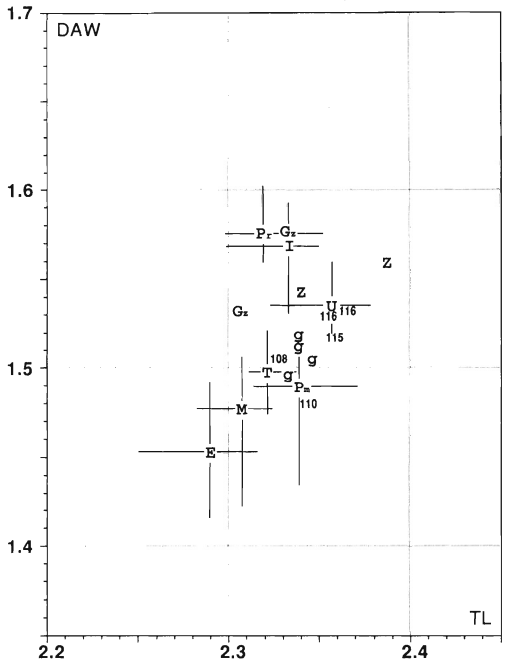

Fig. 5. Distal articular width (DAW) plotted against total length (TL) in MC Ⅲ for Chinese and other forms. Pm: *H. mediterraneum* from Pikermi; M: *H. moldavicum* from Maragheh (Turolian, Iran); I: *H. primigenium* from Inzersdorf and other Austrian Vallesian localities, and Eppelsheim and Höwenegg (Vallesian Germany); T: *H. moldavicum* from Taraklia (Turolian, Moldavia); E: *H. elegans* from Pavlodar (Turolian, Kazakhstan); U: *H. urmiense* from Maragheh; g: MC Ⅲs from Qingyang (Baodean, Gansu) (= *H. hippidiodus*); 115 and 116: MC Ⅲs from Loc. 115 and 116, Qingyang, each other (Baodean, Gansu) (= *H. hippidiodus*); 108 and 110: MC Ⅲs from Loc. 108 and 110, Baode, each other (Baodean, Shaanxi); Z: MC Ⅲs from Zhunger (Turolian, Inner Mongolia). Other abbreviations for specimens are same as in Fig. 4. The vertical and horizontal lines are range of each variables. The points with the ranges are mean values.

to Vallesian *H. primigenium* from central Europe.

A large hipparionine with primitive characters was described from the Late Miocene in Tibet (Baodean, by Li *et al.* 1984). *Hipparion xizangense* from Biru, Tibet (Zheng, 1980) exhibits primitive dental characters similar to those of *H. weihoense*. The skull of *H. xizangense* is medium in size (P2-M3 length = 142 mm and TRNW of M1 = 22 mm in IVPP.V 5190.1). The enamel plication is complex (average of counts in all cheek teeth = 22; pli caballins are double or multiple). The protocone is lenticular in shape.

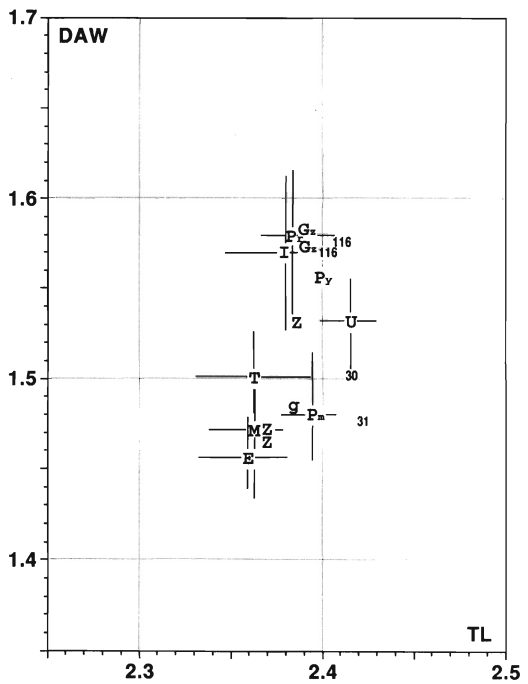

Fig. 6. Distal articular width (DAW) plotted against Total length (TL) in MT Ⅲ for Chinese and other forms. Py: *H. platygenys* from Taraklia (Turolian, Moldavia); 30 & 31: MT Ⅲs from Loc. 30 and 31, Baode, each other, (Baodean, Shanxi) (= *H. fossatum*). Other abbreviations for specimens are same as in Figs. 4 and 5. Ranges and means for some forms are also shown.

The protostylids in lower cheek teeth are developed in p3-m3. The proportions of MC Ⅲ and MT Ⅲ are robust and similar to those of *H. primigenium* from the Vallesian in central Europe (Germany and Austria). Zheng (1980) and Qiu *et al.* (1987) believed that this taxon was closely related to Vallesian *H. primigenium*.

Hipparion theobaldi is a large-sized hipparionine from the Late Miocene beds (the Dhok Pathan zone: 5-8 Ma) in the Siwalik Hills (India and Pakistan). Hussain (1971), MacFadden and Bakr (1979), MacFadden and Woodburne (1982), and Bernor and Hussain (1985) studied this taxon, paying attention to the morphology of POF. Those authors (except Hussain) assigned this species to the genus *Cormohipparion* that was established for hipparionines from the Middle to Late Miocene in North America. This species is large (P2-M3 length = 160-173 mm). The POF is oval and well defined, and far from the orbit (POB width = 55; 59 mm). The enamel plication is complex (18 plis in M1 of PUZ 69/371) and the protocone is oval (MacFadden and Woodburne, 1982). The third metapodials that were assigned to this taxon by Hussain (1971) have large distal articular width and thus very robust proportions. Their proportions are more robust than those of Vallesian *H. primigenium*.

The facial (well defined and deep POF; its sub-rhomboid shape) and dental morphology (complex enamel plication; elongate protocone) of *H. weihoense* are similar to those of Vallesian *H. primigenium* from central Europe. Large-sized hipparionines also appear in the Turolian localities (9-5 Ma) of the western Old World, which show similar facial and dental morphology to those of the Vallesian forms (e.g. *H. brachypus* from Pikermi, unnamed large-

sized *Hipparion* from Samos, *H. giganteum* from Grebeniki, *H. theobaldi* from Siwaliks). It is likely that the geological age of *H. weihoense* from Lantian is not Vallesian as suggested by Chinese paleontologists but Turolian, because of lack of radiometric and/or magnetostratigraphic dating for the continental beds in Lantian.

2. Hipparion fossatum *Sefve (1927) emended by Forstén (1985)*

(1) Synonymy

1927 – *Hipparion richthofeni* (part), Sefve
1927 – *Hipparion fossatum* (part), Sefve
1927 – *Hipparion kreugeri* (part), Sefve
1968 – *Hipparion plocodus* (part), Forstén
1971 – *Hipparion forstenae*, Zhegallo
1978 – *Hipparion plocodus* (part), Zhegallo
1985 – *Hipparion fossatum*, Forstén
1987 – *Hipparion forstenae*, Qiu *et al.*
1990 – *Hipparion forstenae*, Bernor *et al* .

(2) Lectotype

PMU.M 3821 a+b, a skull and mandibles of old individual with snout region, from Loc. 30 housed in the Paleontological Institute of the Uppsala University, Sweden.

(3) Locality and Age

Loc. 30, Loc. 31, Loc. 52, Loc. 108, Loc. 109, Loc. 110; Late Miocene (Early Baodean = Early Turolian).

(4) Distribution

Northern China, Mongolia, central Asia (?).

(5) Referred specimens

Loc. 30: PMU.M 267, younger adult skull with L and R P2-M3; PMU.M 268, adult skull with L and R P2-M3 ; PMU.M 269, very old skull with L and R P2-M3; PMU.M 303, adult skull fragment with R P4-M3; PMU.M 585, younger adult skull with pathological L cheek teeth row; PMU.M 586, old skull with L and R P4-M3, from sub-locality 30(6); PMU.M 591, old adult skull with L P2-M2; PMU.M 592, very old skull with L and R P2-M3, from sub-locality 30(5); PMU.M 3820, adult skull with L and R P2-M3; PMU.M 3821a+b, very old skull with L and R P2-M3; PMU.M 3873, old skull with L and R P2-M3, from sub-locality 30(2); PMU.M 7357, very old skull with L P2-M3; PMU.M 7362, old (?) skull with R M3 (middle part of skull); PMU.M 7988, old maxilla with L P4-M3; PMU.M 8285, adult palate with L P2-M1; PMU.M 8295, distal portion of MC Ⅲ; PMU.M 285, MT Ⅲ distal portion; PMU.M 307, R MT Ⅲ distal portion; PMU.M 582, MT Ⅲ distal portion; PMU.M 8270, MT Ⅲ distal portion; Loc. 52: PMU.M 315, skull fragment with L P3-M3; PMU.M 3685, skull of old individual; PMU.M 327, R mandible with incisor part of snout; PMU.M 328, L mandible with P3-M3 PMU.M 8520, R MC Ⅲ proximal part; PMU.M 339, MT Ⅲ distal portion; Loc. 109: PMU.M 584, skull fragment with complete cheek teeth rows; IVPP Baode: IVPP.V 8245, old skull with L and R cheek teeth rows; IVPP.V-unnumbered specimen (no-3), juvenile skull fragment with L and R DP2-DP4; C/125, adult palate with L and R P2-M3, labelled as "Jijiagou, 1929."

(6) Diagnosis

Medium sized; snout with medium to slender proportions; nasal bone rolled in ventrally; preorbital fossa sub-rhomboid situated close to the orbit, its depth shallow to deep; anterior and dorsal rims poorly defined; posterior pocket absent, or deep; faint subnasal fossa exists; deep nasal notch, its posterior end located above the P2 anterior half; medium sized cheek teeth; enamel plications low to moderate; protocone oval to rounded; pli caballin single; medium sized metapodials.

(7) Discussion

Hipparion fossatum is originally des-

cribed by Sefve (1927) based on the specimens heterogeneous in their facial morphology. Classical name for Chinese *Hipparion*, *Hipparion richthofeni* was established by Koken (1885) based on poorly preserved specimens with unknown provenance, which were purchased from the drug stores in China. The validity of the taxonomic name was strongly questioned by Gromova (1952), Forstén (1968, 1985), and Zhegallo (1978).

Zhegallo (1971) proposed the new specific name *H. forstenae* with lectotype M3873 for morphotype called *H. richthofeni* by Sefve (1927).

Forstén (1985) reviewed Chinese hipparionines and assigned the skulls with narrow preorbital bar to *H. fossatum*. She used the nomen: *H. plocodus* for the specimens with wide preorbital bar and the POF located dorsally on the facial region.

Qiu *et al.* (1987), following the nomenclature by Zhegallo (1971), named *H. forstenae* those specimens with similar facial characters to one another that were described under the name of *H. richthofeni* by Sefve (1927). Their nomen was followed by Bernor *et al.* (1990).

Sefve (1927) assigned skulls from Loc. 30, 31 and 44 to his *H. fossatum*. If the nomen: *H. richthofeni* is abandoned because of its poor taxonomic background, the nomen: *H. fossatum* might be appropriate, as proposed by Forstén (1985), for the specific name for a group of skulls from Loc. 30 which were called *H. forstenae* by Zhegallo (1971), Qiu *et al.* (1987) and Bernor *et al.* (1990). The contents of specimens in *H. fossatum* by Sefve (1927) should be emended. Figure 7 shows synonymy of Chinese hipparionines by previous authors.

Hipparion fossatum has sub-triangular POF located close to the orbit and to the facial crest (Fig.8). The POF is posteriorly pocketed and well defined in ventral and posterior rims. The dorsal and anterior rims of the POF are variably defined. The nasal slit is deep and its posterior edge is at the level of P2. Lateral edges of the nasal bones are ventrally rolled in. The width of the upper snout of this taxon is narrow and similar to that of *H. mediterraneum* Pikermi. The snout of *H. fossatum* and *H. mediterraneum* is narrower than that of *H. prostylum* and *H. dietrichi* from southern France and the Greco-Iranian province. The protocone is oval and moderate in size. The enamel plication is more simple than that of

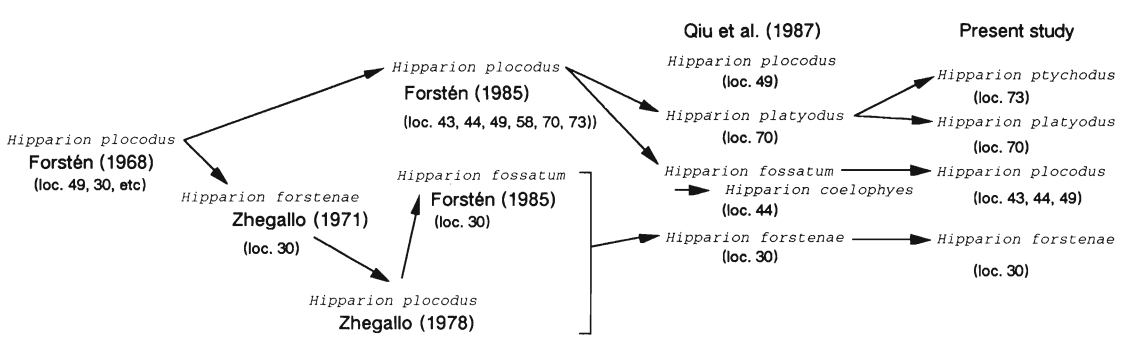

Fig. 7. Synonymy diagram of Chinese hipparions.

the Vallesian *H. primigenium* from central Europe. The third metapodials with small size from Loc. 30 exhibit slender proportions similar to those of *H. mediterraneum* from Pikermi, Greece (Fig. 6). *H. fossatum* is discovered from Loc. 30, Baode, Shanxi, and there are several skulls probably assigned to this taxon in Loc. 31, 52, 108, 109 and 110 in the Baode district of Shanxi province.

Hipparion moldavicum is described by Gromova (1952) from the Meotian beds in Taraklia, Moldavia. The taxon has narrow POB and subrhomboid to subtriangular outline of POF. The proportions of third metapodials in this species are slender and similar to those of *H. mediterraneum* from Pikermi (Figs. 5 and 6). *Hipparion moldavicum* is distributed in the Meotian localities of the northern shore region of the Black Sea and in Maragheh, Iran. In Taraklia, this species co-occurs with another form: *Hipparion platygenys* with reduced POF and larger size. As discussed in later, *H. platygenys* is closely related to Turolian *H. urmiense* and *H. hippidiodus* from Iran and northern China, respectively.

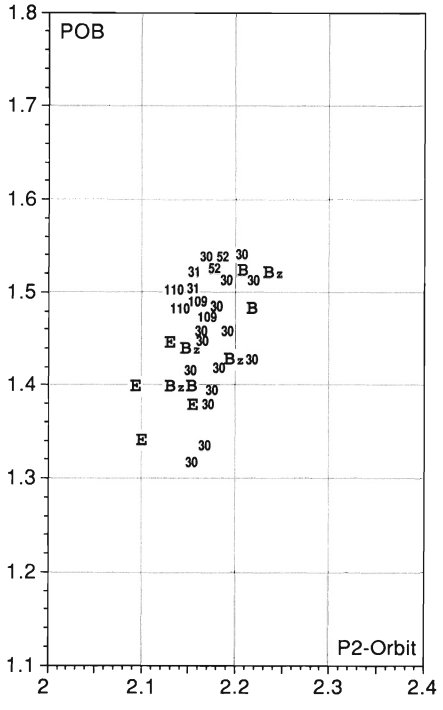

Fig. 8. POB/P2-Orbit diagram of hipparions from Baode district, northern Shanxi and some localities in USSR. 30: *H. forstenae* from Loc. 30, 31, 52, 108, 109and 110: *H.* cf. *forstenae* from Loc. 31, 52, 108, 109 and 110; Bz: *H. garedzicum* from Bazalethi, Georgia; E: *H. elegans* from Pavlodar, Kazakhstan.

Hipparion guizhongensis from the Woma Formation in the Guizhong Basin of Tibet (Ji *et al.* 1980) was assigned to *H. fossatum* by Qiu *et al.* (1987). However, the large size and rich enamel plications of *H. guizhongensis* distinguish it from *H. fossatum* (Figs. 4 and 8). Although the dental morphology of the Tibetan hipparionine is similar to that of *H. primigenium*, their facial morphologies are different from one another. The large size and rich enamel plications are plesiomorphic characters for Eurasian Turolian hipparionines. The Woma Formation was correlated with Baodean interval (= Turolian) by Li *et al.* (1984). The MC III and MT III of *H. guizhongensis* are robust in proportions (Figs. 5 and 6), being similar to those of *H. primigenium* from central Europe.

Meladze (1967) described skulls of hipparionine from Bazalethi (Late Turolian to Early Ruscinian by Alberdi and Gabunia, 1985), Gruzia and assigned them to *H. garedzicum* (Gabunia, 1959). Four skulls of adult age (IP B-50, 51, 52 and 53) show well preserved facial region. The facial morphology of these specimens was heterogeneous: B-50 and 53 had small POF located far from the orbit; and B-51 and 52 have well defined large POF located close to the orbit and the subnasal fossa (Fig. 8). He believed this difference of facial morphology was due to sexual dimorphism. The third metapodials

are also heterogeneous in their size and proportions. There is the metapodials that have slender proportions similar to those of *H. moldavicum* from Taraklia, Moldavia.

A part of the specimens of *Hipparion garedzicum* described from Bazalethi are similar to the *H. moldavicum* in facial morphology. The large and well defined POF located close to the orbit and subnasal fossa that are observed in B-51 and 52 are features common to *H. moldavicum* and *H. fossatum*. Qiu *et al.* (1987) suggested close relationship of *H. garedzicum* from Bazalethi with the group of *H. fossatum* (their subgenus *Cremohipparion*).

Zhegallo (1978) described *H. garedzicum magianense* from the Guzar Formation at Sor in Magian basin of Tadzhik. The facial morphology of the taxon is similar to that of *H. moldavicum* and *H. mediterraneum*. The age of the Guzar Formation was considered to be Early Pliocene and it was correlated with the Neogene deposits in Pavlodar by Zhegallo (1978). PIN 3544-1 from Sor assigned to *H. garedzicum magianense* has sub-triangular POF close to the orbit and the facial crest (Zhegallo, 1978; Fig. 72). The specimen, PIN 3544-2 from Sor, a snout portion, shows well developed subnasal fossa and deep nasal slit with its posterior edge situated at the level of the mid of P2. The transverse width of M1 is 23.7 mm in PIN 3544-1 and 21 mm in PIN 354-2. The wear of cheek tooth row is more advanced in PIN 3544-1 than in PIN 3544-2. The enamel plications in M1 count 16 in the both specimens. The pli caballins are single in a most cheek tooth.

Hipparion garedzicum was erected by Gabunia (1959) based on specimens from Udabno (Late Sarmatian-Meotian, by Gabunia, 1959), the Sagaredzhoi district of Gurzia (type MG 156/13). According to Gabunia's description, the POF of the taxon is very small and located far from the orbit (POB width = 53 mm) and far from the facial crest. The nasal notch of this taxon from Udabno is shallow and its posterior edge is at the level anterior to P2. The cheek tooth row length is 145 mm in MG 156/13. This value is smaller than that of *H. garedzicum magianense* from Sor (157 mm in PIN 3544-1). *Hipparion garedzicum magianenese* described from Sor has different facial morphology from that of type specimen of the species from Caucasia. The type specimen is similar to hipparionines from Siwaliks in India and *H. ptychodus* from Loc. 73 in northern China that have oval POF situated far from the orbit and the facial crest. *Hipparion garedzicum magianenese* is close to *H. fossatum* from Loc. 30.

Hipparion elegans was described by Gromova (1952) from Pavlodar (Kazakhstan). This taxon shows small skull size (cheek tooth row length = 133-137 mm) and slender third metapodials. The age of Pavlodar was inferred as the Late Turolian to earliest Ruscinian by Tleuberdina (1988). The POF of this taxon is sub-rhomboid in outline and well defined in all rims. There is a posterior pocket. The POF morphology is similar to that of *H. moldavicum* (Gromova, 1952) (Fig. 8). The protocone is rounded and the enamel plication is simple. The TRNW of medially worn M1 is 20.2 mm in average. The proportions of MC Ⅲ and MT Ⅲ of *H. elegans* are similar to those of *H. moldavicum* from Maragheh (Watabe and Nakaya, 1991a) and Taraklia (Gromova, 1952; Forstén, 1980) (Figs. 5 and 6).

The hipparionine fossils were collected from several localities in Inner Mongolia by Sino-Soviet Paleontological Expedition (1959-1960). The major collections came from Huade and Zhunger in the region.

There are two forms in specimens from Zhunger: larger and smaller. The larger form (IVPP V 5645.1: P3-M3) has M1TRNW of 24.5 mm; M1PRTL of 10 mm; and M1-M3 occlusal length of 67 mm. This specimen is at the late wear stage, showing small amplitude of enamel plications. The pli caballins are single in all teeth, and plication count on M1 is 1/6/7/1 (15). The smaller form (IVPP V 5644.2: right P3-M2) has M1TRNW of 20 mm and M1PRTL of 6.3 mm. The protocone is oval and the pli caballins are single. The plication count on P4 is 3/5/4/2 (14).

There are two forms in MC Ⅲs and MT Ⅲs from Zhunger. One form is large and slender, and another one is small and slender that is similar to that of *H. moldavicum* from Maragheh (Figs. 5 and 6).

Qiu (1979) designated the larger form to *H.* cf. *dermatorhinum* and the smaller form to *H. plocodus*. On the basis of dental morphology, those two taxa cannot be distinguished. The term "*Hipparion plocodus*" has been used as wide inclusive concepts for Chinese Turolian medial to small sized hipparions as done by Forstén (1968).

(8) Comparison

Bernor *et al.* (1990) included this taxon (*H. fossatum* = their *H. forstenae*) into the supra-specific "Group 2" proposed by Woodburne and Bernor (1980).

Hipparion fossatum from northern China is morphologically similar to *H. mediterraneum* and *H. moldavicum* from the northern shore region of the Black Sea and the sub-Paratethys region (or the Greco-Iranian region by DeBonis *et al.*, 1986). They are all comprised in a single monophyletic group.

The synapomorphies of this monophyletic groups are: sub-triangular dorsoventrally high POF; narrow POB width; sub-nasal fossa (not shown by all individuals); deep nasal slit; relatively narrow upper snout; and slender and small MC Ⅲ and MT Ⅲ. The deep and ventrally expanded POF with the ventral rim close to the facial rest of this monophyletic group is similar to the morphology seen in *H. primigenium* from the Vallesian in central Europe, but other above-mentioned features are not seen in *H. primigenium*.

The hipparionines with similar facial morphology to *H. fossatum* are widely distributed in Eurasia (Greece, northern shore of the Black Sea, Turkey?, Iran, Caucasus, Tadzhikistan and Kazakhstan). But, they are not reported from the Iberian Peninsula. Although Alberdi (1974) considered the hipparionine from Piera, the Penedes region, to be *H. mediterraneum*, the facial and postcranial morphology of the form is different from that of *H. mediterraneum* from Pikermi (type locality) (Watabe, personal observation).

3. Hipparion hippidiodus *Sefve* (1927) *emended by Forstén* (1985)

(1) Synonymy

1927 – *Hipparion hippidiodus* (part), Sefve
1927 – *Hipparion dermatorhinum* (in part), Sefve
1968 – *Hipparion hippidiodus*, Forstén
1978 – *Hipparion hippidiodus*, Zhegallo
1985 – *Hipparion hippidiodus*, Forstén
1987 – *Hipparion hippidiodus*, Qiu *et al.*
1990 – *Hipparion hippidiodus*, Bernor *et al*.

(2) Lectotype

PMU.M 3819 adult skull, from Loc. 115, Qingyang district, Gansu province of northern China. Stored in the Paleontological Institute of the Uppsala University.

(3) Locality and Age

Loc. 43, Loc. 44, Loc. 115, Loc. 116, Qingyang localities by IVPP; Late Miocene (Baodean = Turolian).

(4) Distribution

Northern China, Inner Mongolia (?), eastern Kazakhstan.

(5) Referred specimens from the Qingyang district, Gansu province

a. Skulls: Loc. 115: PMU.M 3819, old skull with L and R complete cheek teeth row; PMU.M 252, R maxilla with P2-M1, old; PMU.M 8756, L P3-M3, old; IVPP Qingyang: F 72078, adult skull lacking snout region; IVPP.V 8216, incomplete adult skull with L M2-M3 and R P3-M3 was collected from Loc. 115; IVPP.V 8208, old maxilla with L P2-M3, lacking facial region; IVPP. V 8211, juvenile maxilla with L DP2-DP4; IVPP.V 8215, upper snout with L and R I1-I2.

b. Mandibles: Loc. 115: PMU.M 8770, juvenile mandible with L dP2-dp4; PMU.M 8783. young mandible with R P4-M3; PMU. M 8678, adult mandible with R P3-M3; Loc. 116: PMU.M 330, R mandibles with p2-m3; PMU.M 331, L mandible with p2-m2, those two specimens belong to the same individual; IVPP Qingyang: IVPP.V 8210(430), L old mandible with p2-m2; IVPP.V 8209 (411), adult mandible with R p2-m3; IVPP. V 8210, adult mandible with L p2-m3; IVPP.V 8214, L juvenile mandible with dp2-dp4; IVPP.V 8212, R juvenile mandible with dp2-dp4 slightly worn; IVPP.V 8213, L juvenile mandible with dp2-dp4 slightly worn, IVPP.V 8212 and IVPP.V 8213 probably belong to the same individual.

c. Metacarpal Ⅲ: PMU.M 257 from Loc. 115; PMU.M 338 from Loc. 116; IVPP.V 8217 from Qingyang; IVPP.V 8218 from Qingyang; IVPP.V 8219 from Qingyang; IVPP. V 8220 from Qingyang.

(6) Diagnosis

Medium to large size; slender snout proportions; large cheek tooth (M1TRNW: 22.3-24.2·mm, 23.3 mm as an average for the Loc. 43 and 44 forms) (Table 1), especially the premolars; nasal notch above P2; no subnasal fossa; shallow and very poorly defined POF; posterior rim of POF defined by small "pit"; protocones relatively small compared to tooth size; protocone rounded to oval (M1PRTL: 5.7-6.8, 6.1 as average for medium worn teeth); plication count low to medium (maximum counts: 16, 12.1 in average); pli caballins single; metapodials slender and similar to those of *H. mediterraneum* (Figs. 5 and 6).

(7) Discussion

This taxon has reduced POF lacking anterior, dorsal and ventral rims. The posterior rim of the POF is also poorly defined and only small pit exists as the remnant of the rim. The posterior rim of the POF is

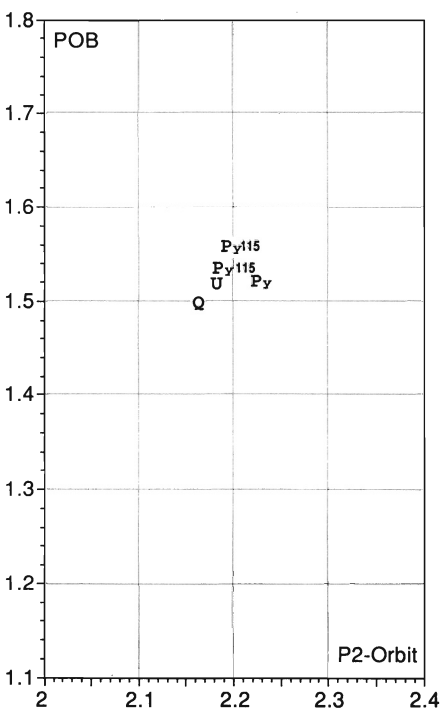

Fig. 9. POB/P2-Orbit diagram of hipparions from Qingyang district, Gansu and some Eurasian localities. 115: *H. hippidiodus* from Loc. 115; U: *H. urmiense* from Maragheh, Iran; Py: *H. platygenys* from Taraklia, Moldavia.

close to the orbit (Fig. 9). The upper snout is very narrow and the nasal slit is deep and incised to the level of P2. The protocone is oval to rounded and small in relation to entire tooth. The enamel plication in the upper cheek teeth is simple. The MC Ⅲ and MT Ⅲ from Loc. 115 and other localities in the Qingyang district, Gansu, are slender in proportions (Figs. 5 and 6).

Hipparion hippidiodus is distributed in Loc. 115 and 116, Qingyang, Gansu; and Loc. 43 and 44, Baode, Shanxi. This species co-exists with *H. coelophyes* in those localities. The small skulls of *H. coelophyes* with oval and dorsally located POF situated far from the orbit are distinguished from those of *H. hippidiodus*. The age of localities in Gansu that yielded this form has been regarded as Turolian (= Baodean) (Forstén, 1985 ; Qiu *et al.*, 1987).

Hipparion urmiense was erected by Gabunia (1959) based on the specimens from Maragheh (Turolian: northwest Iran) stored in State Museum of Gruzia (Muzei Gruzii). The skull of this taxon is medium-sized and narrow (Gabunia, ibid.). The length of the upper cheek tooth row is 147-155 mm. The POF is rudimentary and located anterodorsally on the facial region as a shallow depression (MG 148/191 and 148/159). The nasal slit is deep and its posterior edge is at the level of the boundary between P2 and P3. The enamel plications on upper cheek teeth are simple (mean = 7.3 in moderately worn M1). The pli caballin is single. The TRNW is 23.5 mm and the PRTL is 8.1 in moderately worn M1. Although Gabunia (1959) stressed that his specimens were collected from a single horizon, there is still possibility that the teeth from plural taxa were included there. This form is reported from Maragheh (Watabe and Nakaya, 1991a, b). The facial morphology in the Maragheh form is similar to that in the type specimens by Gabunia (Fig. 9). The third metapodials from Maragheh assigned to this taxon are slender in proportions (Figs. 5 and 6).

Large sized hipparionine, *H. platygenys*, was mentioned in the specimens from Taraklia (age: Meotian = Turolian), Moldavia by Gromova (1952). *Hipparion platygenys* differs from sympatric species *H. moldavicum* in its large size and reduced POF. The cheek tooth row is medium to large (150 mm in PIN 1256-2883, type). The POF is rudimentary and poorly defined in peripherals. The POF is located moderately far from the orbit (POB = 32 mm) and its posterior rim is slit-like (Fig. 9). The protocone is oval (PRTL in middle worn M1 = 6.3 mm and the enamel plications are simple (maximum counts in M1 = 7.5). The mean of the TRNW is 23 mm in middle worn M1. Those facial features are similar to those of *H. hippidiodus*. Gromova (1952) found that there were large-sized postcranial bones in Taraklia, which differed from those of *H. moldavicum*. Although she did not assign those postcranial elements to *H. platygenys*, she considered it to be possible. The large-sized MT Ⅲ from Taraklia show large and semi-robust proportions that are similar to those of MT Ⅲs from Loc. 116 in Gansu (Fig. 6).

Zhegallo (1978) reported *Hipparion hippidiodus* from eastern Kazakhstan (Kalmakpai, the Zaisan Basin: Pliocene) that had large skull size and reduced POF. The adult specimen has not POF, and the juvenile skull (PIN 2433-450) has shallow POF that opens anteriorly and has flat bottom. The nasal slit is deep and its posterior edge reaches to the level of the boundary between P2 and P3. The cheek tooth row and skull are large (M2-M3 = 143-174 mm). The upper cheek teeth from Kalmakpai show small

protocone. The enamel plications are simple (4-8 in moderately worn M1). The third metapodials are slender, and their size and proportions are similar to those of the bones from Qingyang, Gansu. *Hipparion hippidiodus* was reported from Altan-Teli in western Mongolia by Zhegallo (1978).

A skull specimen that was named *Hipparion* sp. by Korotkevitch (1988) from Cherevichnoe, Ukraina (Terminal Miocene), is similar in the facial morphology to *H. urmiense* from Maragheh. The POF of the hipparionine from Cherevichnoe has very unclear rims. The nasal slit is deep and its posterior edge is at the level of P3. The posterior edge of the nasal slit is above the posterior half of P2 in MMTT 13/1342 (*H. campbelli* = *H. urmiense*) from Maragheh.

(8) Comparison

There are hipparionines of the Turolian age are characterized by reduced POF, large skull size (larger than *H. moldavicum*) and simple upper dentition (simple enamel plication, and small and rounded to oval protocone). When the well preserved skulls are known, they show narrow skull width. The POF is situated far from the orbit, but not as far as in *H. prostylum* from Maragheh and Saloniki (Watabe and Nakaya, 1991b). Their third metapodials are long and slender. The reduced POF and the slender third metapodials are not observed in the Vallesian hipparionines in Eurasia, and those characters are synapomorphies for them (*H. hippidiodus* - *platygenys-urmiense group*). However, the reduction of POF is also shown by Pliocene hipparionines in Africa (*H. turkanense*: Eisenmann, 1979) and Eurasia (*H. rocinantis* in Spain: Alberdi, 1974; *H. houfenense* in northern China: Qiu *et al.* 1987). Hooijer (1975) and Eisenmann (1980) compared *H. hippidiodus* with *H. turkanense* from the Lothagam Formation (terminal Miocene to Early Pliocene), Kenya in Sub-Saharan Africa mentioning their reduction of POF. The phylogenetic relationship between Late Miocene hipparionines with reduced POF in Eurasia (*H. hippidiodus, H. platygenys* and *H. urmiense*) and Africa (*H. turkanense*) has not yet been documented.

The Late Miocene hipparionines with reduced POF are distributed in the northern shore region of the Black Sea (Taraklia: *H. platygenys*), northwest Iran (Maragheh: *H. urmiense*), Kazakhstan (Kalmakpai: *H. hippidiodus*) and northern China (Loc. 43, 44 and 115: *H. hippidiodus*). This distribution is similar to that of a monophyletic lineage: *H. mediterraneum-fossatum-moldavicum* group.

Bernor *et al.* (1990) proposed phylogenetic hypothesis, namely, *H. weihonense-H. platyodus-H. coelophyes-H. hippidiodus* lineage with tendency of reduction of POF; However, they did not compare *H. hippidiodus* with other Eurasian forms with reduced POF. They considered this lineage not to be a chronostratigraphically gradual, because *H. coelophyes* and *H. hippidiodus* co-occurred in a single locality.

Bernor *et al.* (1990b) removed *H. platyodus* from the evolutionary lineage from *H. weihoense* to *H. hippidiodus*. They selected 40 cranial and dental characters for classification of Old World and North American hipparionines horses. They considered *H. weihoense* to be similar to *H. primigenium* from Central Europe of Vallesian age. The character state that is uniquely shared by large and primitive hipparions in Eurasia and Northern Africa including *H. primigenium* and *H. weihoense* is: long POB with the anterior edge of the lacrimal placed more than 1/2 the distance from the anterior orbital rim to the posterior rim of the fossa.

However, *H. hippidiodus* has POF more closely located to the orbit than *H. coelophyes* (Qiu *et al.*, 1987; Watabe, personal observation).

H. hippidiodus and *H. coelophyes* share only 16 among 26 total characters proposed by Bernor *et al.* (1990b) (thus, the ratio of shared characters against total character is: 16/26 = 0.615). *H. coelophyes* and *H. weihoense* share 20 characters (thus the index is: 0.769). *H. hippidiodus* and *H. campbelli* from Maragheh (= *H. urmiense* by Watabe and Nakaya, 1991b) share 22 characters (the index is: 0.826. *H. hippidiodus* and *H. weihoense* share only 15 characters (the index is: 0.577). This phenetical assessment of similarity among those taxa does not necessarily show close similarity between *H. hippidiodus* and *H. coelophyes*. There is no shared derived character and important overall similarity between *H. coelophyes* and *H. hippidiodus*.

Hipparion mediterraneum from Pikermi, *H. proboscideum* from Samos, and *H. moldavicum* from Taraklia and Maragheh share derived facial characters, and they form a monophyletic groups (Forstén, 1980; Woodburne and Bernor, 1990; Watabe and Nakaya, 1991b). They exhibit close overall similarity one another in Bernor *et al.*'s character matrix: the average of the number of shared characters is 21.7 among 26, thus the ratio of shared characters becomes 0.83. This is an example of phenetic similarity based on Bernor *et al.*'s character matrix for a monophyletic group defined by shared derived characters.

General Discussion

Kurtén (1952) divided mammalian fossil faunas from northern China into the "gaudryi" fauna and the "dorcadoides" fauna (Table 2). He also recognized the mixed fauna whose composition is mixture of those from the "gaudryi" and the "dorcadoides" faunas. The "gaudryi" fauna is typically defined by the presence of brachydont *Gazella gaudry* (Bovidae, Artiodactyla), and the "dorcadoides" fauna is defined by the presence of hypsodont *Gazella dorcadoides*.

The localities yielding the "dorcadoides" fauna are distributed in the Gansu and the northwestern region of the Shanxi provinces. The localities of the "gaudryi" fauna are distributed in the southeastern region of the Shanxi province and the Henan provinces. The "mixed" fauna is observed in the northwestern region of the Shanxi province.

Table 2. Classification of localities in Northern China by Kurten (1952).

Dorcadoides Fauna
(Open land - Steppe)

Loc. 30 (Taijiagou, Baode, Shanxi)
Loc. 31 (Liuwangou, Yuejiali, Baode, Shanxi)
Loc. 108 (Zhenjiamaogou, Jijiagou, Baode, Shanxi)
Loc. 110 (Wangjialianggou, Jijiagou, Baode, Shanxi)
Loc. 114 (Mahuatan, Nanshawa, Hechu, Shanxi)
Loc. 115 (Mujiazuigou, Qiaozizhuan, Qingyang, Gansu)

Mixed Fauna
(Mixed)

Loc. 43 (Sanjialianggou, Jijiagou, Baode, Shanxi)
Loc. 44 (Shenshuzui, Yuejiali, Baode, Shanxi)
Loc. 49 (Yangmugou, Jijiagou, Baode, Shanxi)
Loc. 52 (Linwangou, Yuejiali, Baode, Shanxi)
Loc. 109 (Huanglugou, Jijiagou, Baode, Shanxi)
Loc. 51 (Beihougou, Wulangou, Fugu, Shaanxi)

Gaudryi Fauna
(Forest)

Loc. 11 (Zhengouwan, Xinan, Henan)
Loc. 12 (Shangyingou, Xinan, Henan)
Loc. 70 (Jinggou, Xigouzun, Wuxiang, Shanxi)
Loc. 73 (Douqiaogou, Dongzun, Wuxiang, Shanxi)
Hsi-Liang (Yuchiaotun, Hsiliang, Yushe, Shanxi)
Tan-Tsun (Chiao-chia-kou, Tantsun, Yushe, Shanxi)

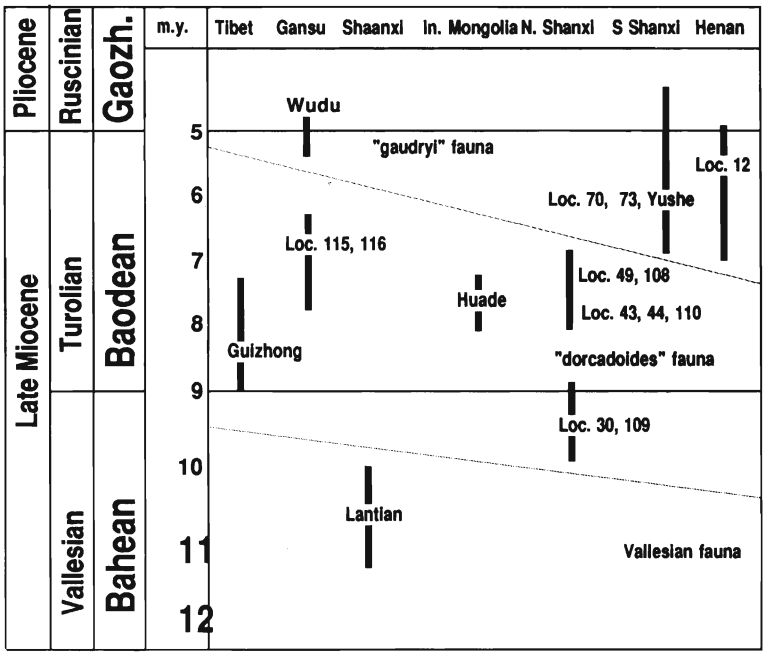

Fig.10. Correlation of mammalian localities in Northern China. Compiled from Zhegallo (1978), Kurtén (1985), Qiu (1985), and Qiu *et al.* (1987). This correlation is based on comparison of faunal composition.

The mammalian faunas containing *Hipparion* in the Gansu and Shanxi provinces are correlated with the Turolian interval by Li *et al.* (1984) and Forstén (1985). The chronological ordering of the localities has not been proposed until Kurtén (1985) and Qiu (1985). More summarized correlations of those localities was proposed by Qiu *et al.* (1987) (Fig. 10). They used the evolutionary lineages of fossil hyaenids (Carnivora) for the ordering of the localities.

The ungulate taxa in both faunas are different from each other. The "gaudryi" fauna is characterized by the presence of rhinoceros genus *Dicerorhinus* and giraffid genus *Honanotherium*. The "dorcadoides" fauna contains *Chilotherium* and *Samotherium* – *Palaeotragus* respectively.

The heterogeneity in the faunal compositions from the localities in northern China that are totally correlated with the Turolian interval might be due to both differences in geologic age and ecological habitat (Kurtén, 1952; Qiu *et al.*, 1987). As the works on magnetostratigraphy and micromammal fossils have not been done, the detailed correlation of Turolian localities in northern China with the land mammalian stages constructed in the western Old World.

Solounias and Dawson-Saunders (1988) studied the masticatory morphology of the ruminants (cervids, giraffids and bovids) from Samos and Pikermi, Greece. The most species of the giraffids and bovids in the *Hipparion* fauna were considered as grazer adapted to the open-land savanna environment. Contrary to this previous idea, they proposed that these ruminant species were browser or intermediate feeders that were adapted to the woodland-forest habitats.

The giraffid genera that are widely distributed the localities in northern China such as *Samotherium, Palaeotragus* and *Honanotherium* are assumed as browser by Solounias and Dawson-Saunders (1988.). However, the genera of bovids such as *Urmia-*

therium and *Plesiaddax* are assumed to be grazers, and *Protoryx* and *Palaeoryx* are intermediate feeders. These grazer and intermediate feeders are more abundant in the "dorcadoides" fauna in northern China than in the "gaudryi" fauna. According to their study, all three species of *Gazella* (*G. capricornis, G. mytilinii* and *G. dorcadoides)* from Samos and Pikermi are considered as browser. The study on feeding habits of the Late Miocene rhinocerotids has not yet been made (see Fortelius, 1982 for those of Quaternary rhinocerotids).

According to Kurtén (1985) and Qiu (1985), the "gaudryi" fauna is generally younger than the "dorcadoides" fauna (Table 2). The hipparionines from the "dorcadoides" fauna are *H. fossatum* and *H. hippidiodus* that show close relationship with the western Old World forms. A large form: *Hipparion dermatorhinum* that might be related to Turolian large hipparionines in western Old World such as *H. giganteum* in Grebeniki and *H. brachypus* in Pikermi co-occurs with *H. fossatum* in Loc. 30, Baode, northern Shanxi. On the other hand, the hipparionines from the "gaudryi" fauna (localities in Yushe, Wuxiang, and Xin'an districts) such as *H. platyodus, H. ptychodus, H. tylodus* and *H. sefvei* and *H. coelophyes* from the "mixed" fauna (some of Baode localities, Shanxi) are similar to the North American genus, *Hipparion* sensu stricto (MacFadden, 1984), in their facial morphology (Watabe, in press).

The North American genus *Hipparion* (sensu MacFadden, 1984): *H. tehonense* and *H. forcei* are chronologically distributed in the duration from 11 to 9 Ma in the western coast of North America (Hulbert, 1988). As the age for Chinese localities such as Yushe, Wuxiang, and Xin'an is estimated as 7 to 5 Ma, there is a gap in age between the North American Hipparion and northern Chinese hipparionines.

Tedford *et al.* (1987) suggested that there was a faunal turnover in the Hemphillian interval, which occurred at 6 Ma and subdivided the fauna into two: Early and Late. According to them, the Early Hemphillian fauna is characterized by many elements of the continuing Clarendonian fauna that contains *Hipparion* and *Cormohipparion* as equine members, and this diversity of horses is dropped in the Late Hemphillian fauna. The immigrants from Eurasia to North America in 7 and 6 Ma consist of taxa of Carnivora, Rodentia, Lagomorpha, and Artiodactyla (Tedford *et al.* 1987).

The interchanges of mammalian fauna between Eurasia and North America were suggested by the studies on Chinese Proboscidea by Tobien *et al.* (1984) as was done by Tedford *et al.* (1989).

The hipparionine assemblages in the Late Miocene to Pliocene (?) mammalian fauna from northern China are characterized by the mixture of the taxa migrated from the western Old World and from North America during the Late Miocene to Early Pliocene periods.

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