HORS-SÉRIE Numéro 2-2005 ISSN 1771-1150

QUATERNAIRE

International Journal of the French Quaternary Association

LES ONGULÉS HOLARCTIQUES DU PLIOCÈNE ET DU PLÉISTOCÈNE

sous la direction d'Évelyne Crégut-Bonnoure

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

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

AFEQ

Maison de la Géologie
79, rue Claude Bernard
75005 PARIS

EQUUS QINGYANGENSIS (EQUIDAE, PERISSODACTYLA) OF THE UPPER PLIOCENE OF BAJIAZUI, CHINA : EVIDENCE FOR THE NORTH AMERICAN ORIGIN OF AN OLD WORLD LINEAGE DISTINCT FROM *E. STENONIS*

■

Vera EISENMANN* and DENG Tao**

ABSTRACT

Skulls and limb bones of the Chinese Upper Pliocene *E. qingyangensis* (Bajiazui, Gansu) are astonishly similar to those of the Middle Pliocene North American *E. shoshonensis* (Hagerman, Idaho) and different from the usual villafranchian *E. stenonis*. Biometrical data support the existence of two distinct lineages of primitive *Equus* in the Old and New World.

Key words: China, North America, Europe, Plio-Pleistocene, *Equus*, biometry, phylogeny.

RÉSUMÉ

EQUUS QINGYANGENSIS (EQUIDAE, PERISSODACTYLA) DU PLIOCÈNE SUPÉRIEUR DE BAJIAZUI, CHINE : ÉLÉMENTS EN FAVEUR D'UNE ORIGINE NORD-AMÉRICAINE D'UNE LIGNÉE DE L'ANCIEN MONDE DISTINCTE D'*E. STENONIS*

Une espèce primitive d'*Equus*, *E. qingyangensis*, provenant du Pliocène supérieur de Bajiazui, Comté de Qingyang, Province de Gansu, est représentée par des crânes et des os des membres. Leur comparaison biométrique avec divers *Equus* montre une grande ressemblance avec une forme nord-américaine du Pliocène moyen, *E. shoshonensis* d'Hagerman (Idaho) et d'importantes différences avec les *E. stenonis* villafranchiens de l'Ancien et du Nouveau Monde. Ces données sont en faveur de l'existence de deux lignées différentes d'*Equus* primitifs au Plio-Pléistocène.

Mots-clés : Chine, Amérique du Nord, Europe, Plio-Pléistocène, *Equus*, biométrie, phylogénie.

INTRODUCTION

Everybody agrees that the main evolution of Equidae was a North American affair, and that various migrations brought various equids from the New World to the Old (Forsten, 1989). When it comes, however, to really recognize the same species, or even the same sub-genus or genus, the matter may lead to long controversies. For example, the discussions on whether the North American tridactyl *Cormohipparion* (Skinner & MacFadden, 1977) is, or is not, a genus (or subgenus) and has, or has not, migrated into the Old World were going on for twenty years (Bernor *et al*., 1990; Forsten & Krakhmalnaya, 1997) and the answer is not yet clear. Even when it comes to relatively recent taxa, opinions may differ. Eisenmann (1992) considers that the North American Irvingtonian *Equus scotti* is the first caballine horse and that it is distinct from *E. excelsus*, opinion contradicted by Azzaroli (1995). In the present paper, we trust to bring conclusive arguments in favour of a very close relation between two primitive *Equus*: *E. qingyangensis* (Deng & Xue, 1999a) from the Upper Pliocene of China and *E. shoshonensis* from the Middle Pliocene of North America.

EQUUS SHOSHONENSIS

One of the best samples of monodactyl horses in North America was found at the Hagerman Quarry, Idaho, and dated to about 3.4 Ma (Lundelius *et al*., 1987). This *E. shoshonensis* (sometimes synonymized with *E. simplicidens*) was currently believed to be the ancestor of all extant *Equus* (Azzaroli & Voorhies, 1993). It is represented by entire skulls and mandibles and numerous well preserved teeth and limb bones. Skulls and teeth were well illustrated, in particular by

* UMR 5143 et UMR 5197 du CNRS, Département Histoire de la Terre, CP 38, 8 rue Buffon, 75005 Paris, France.
** Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, P.O.Box 643, Beijing 100044, China.

While the present paper was in press, another Chinese *Plesippus* was discovered and described. It cannot be discussed here but the reference of the publication is :
Qiu Zhanxiang, Deng Tao, Wang Banyue, 2004 – Early Pleistocene Mammalian Fauna from Longdan, Dongxiang, Gansu, China. *Palaeontologica Sinica*, New Series C, 121 (27)1-198.

Manuscrit reçu le 07/02/2001, accepté le 17/04/2003

Measurements (mm.)		*E. shoshonensis,*	Hagerman				*E. qingyangensis,*	Bajiazui	
	n	x	min	max	s	v	M 63043	B 61249	B 61001
16. Supraoccipital crest B.	25	65,5	57	74	3,98	6,08			
23. Anterior ocular line	25	428,8	390	455	16,35	3,81			
3. Vomerine length	19	146,0	130	160	7,64	5,23	140	136,8	
4. Postvomerine length	20	106,5	92	117	6,76	6,35		97,6	
2-5. Palatal length, sensu stricto	24	145,3	135	160	6,69	4,61	137,3	132,3	150
5. Muzzle length	25	142,0	126	161	7,76	5,47			150
17. Muzzle breadth	26	64,5	57	71	4,12	6,38		[68]	[66]
17bis. Minimal Muzzle B.	24	39,9	30	46	4,22	10,57			
13. Frontal breadth	24	221,3	200	244	12,03	5,44	230		
10. Choanal maximal B.	10	48,9	43	56	4,41	9,03	52,3		
25. Facial height	19	109,3	100	126	7,36	6,74			
28. Cranial height	15	88,5	80	100	6,70	7,56	111,3		
9. Choanal length	17	88,0	72	108	7,81	8,88	[90]		
20. Meatus auditivus externus H.	17	14,9	12	18	1,83	12,30			
31. Nasoincisival notch L.	24	190,8	171	201	6,88	3,61			[190]
32. Cheek length	26	195,5	170	211	9,45	4,83		177	
1. Basilar length	24	525,4	495	550	15,17	2,89			
8. Upper cheek teeth length	25	187,2	167	199	6,81	3,64	170	180	182
		E. hemionus onager					*E.sanmeniensis*	*E.yunnanensis*	*E.cf.yunn.*
Measurements (mm.)			Iran				Nihowan	Madahai	Loc 32
	n	x	min	max	s	v	NIH 002	V 4250-1	M 1324-25
16. Supraoccipital crest B.	33	56,6	47	66,5	4,68	8,27			
23. Anterior ocular line	33	347	323	368	11,75	3,39	480	412	419
3. Vomerine length	33	116,8	100	137	9,07	7,77	[152]	124,5	127,7
4. Postvomerine length	33	101,9	88	114	5,67	5,56	126	106	107,1
2-5. Palatal length, sensu stricto	33	115,7	96	132	7,83	6,77	160	140	148
5. Muzzle length	33	103,7	82	120	8,23	7,94	155	132	140
17. Muzzle breadth	32	54,9	48	66,5	4,24	7,72	70	70,7	63,8
17bis. Minimal Muzzle B.	33	40,7	33	47,5	3,27	8,03	53	39	36
13. Frontal breadth	33	195,8	182	217	7,42	3,79		201	210
10. Choanal maximal B.	33	47,5	42	52	2,67	5,62		48	44
25. Facial height	33	102	90	118	6,03	5,91	130	82	
28. Cranial height	33	90,1	80	98	4,17	4,63		100	
9. Choanal length	33	63	53	71	4,54	7,21	[80]		72
20. Meatus auditivus externus H.	32	14,4	11,4	16,5	0,96	6,67			
31. Nasoincisival notch L.	22	142,9	130	159	7,03	4,92	225		[182]
32. Cheek length	21	160	143	174	7,67	4,79	193		[177]
1. Basilar length	36	435,2	410	463	14,4	3,31	[580]	496	522
8. Upper cheek teeth length	34	158,7	137	190	10,8	6,81	[200]		178

Table 1: Skull dimensions of extant and fossil *Equus*. n=number of specimens, x=mean, min=minimal observed value, max=maximal observed value, s=standard deviation, v=coefficient of variation (v=100s/x). B.=breadth, H.=height, L.=length.
Tableau 1 : Dimensions craniennes d'Equus actuels et fossiles. n=nombre de spécimens, x=moyenne,
Min et max = valeurs minimales et maximales observées, s=écart-type, v=coefficient de variation. B.= largeur, H.=hauteur, L.=longueur.

Azzaroli & Voorhies (1993) but no comprehensive biometrical description was ever published. The present paper contributes to a better description and interpretation of this material.

The limb bones of *E. shoshonensis* have broadly the same relative lengths as the modern Grevy's zebra (Eisenmann, 1999, tabl. 5), at least down to the first phalanges (fig. 1). It is thus possible to estimate its wither's height by applying the 'indices' calculated for this zebra (Eisenmann, 2000, tabl. 2). The results vary from 148,9cm (based on the third metatarsal, MT III) to 155,7cm (based on the tibia). The approximative weight, estimated by using the combination of distal width and depth of third metacarpals (Eisenmann, 2000) is about 330 kg. The general body built is that of a rather cursorial species. In contrast to most other *Equus*, and like in extant Hemiones, the posterior phalanges are short relative to the MT III (fig. 2). The skull has been likened to the skull of the Grevy's zebra and *E. shoshonensis* has often been referred to the same subgenus – *Dolichohippus* – following the suggestion of Skinner & Hibbard (1972). The basicranial proportions, however, are quite different (Samson, 1975; Forsten & Eisenmann, 1995). The skulls of *E. shoshonensis* (as well as of *E. stenonis*) differ from any modern species of *Equus* (Eisenmann & Baylac, 2000).

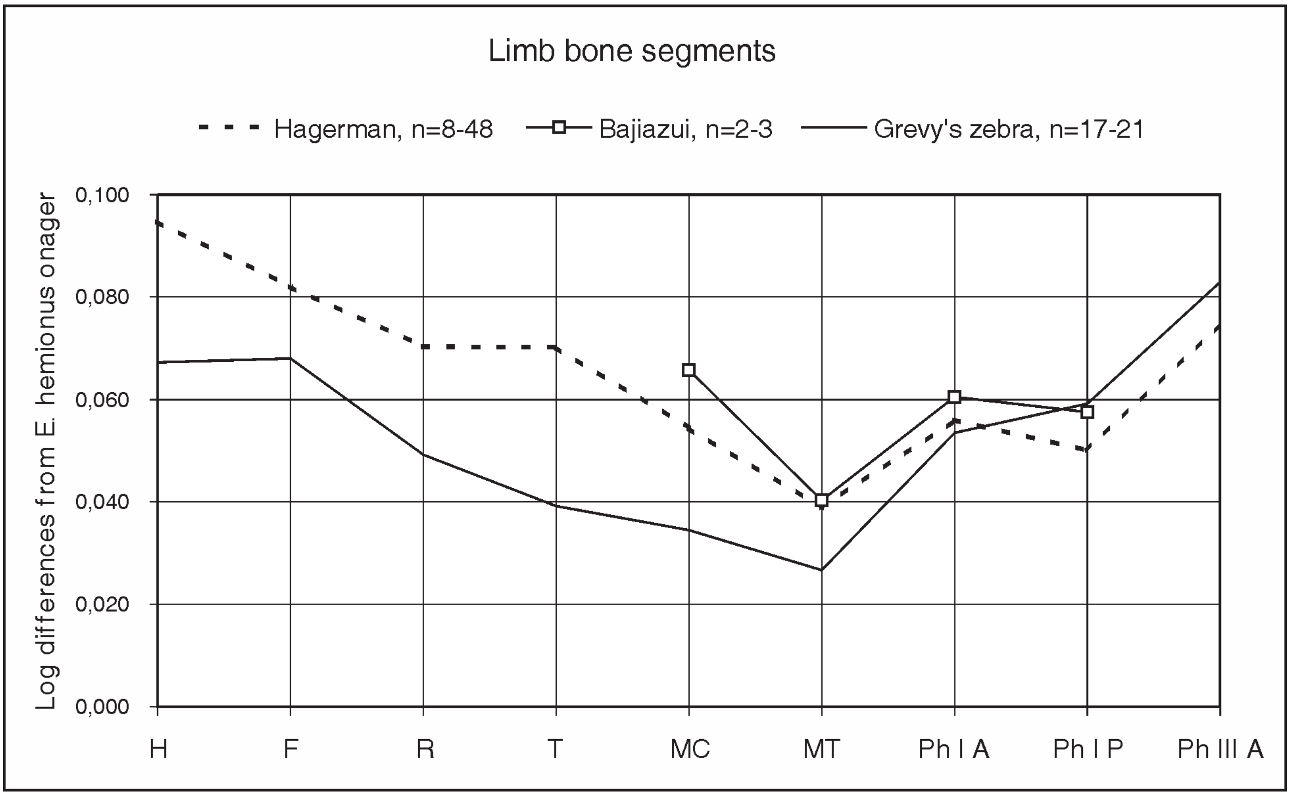

Figure 1: Ratio diagrams of limb dimensions of *E. shoshonensis* (Hagerman), *E. qingyangensis* (Bajiazui), and of the extant *E. Dolichohippus grevyi* compared to the extant Onager. Maximal lengths of humerus (H), femur (F), radius (R), tibia (T), third metacarpal (MC), third metatarsal (MT), first anterior phalanx (Ph I A), first posterior phalanx (Ph I P) and maximal width of third anterior phalanx (Ph III A), n = number of specimens.

Figure 1 : Diagrammes de Simpson des longueurs maximales d'humérus, fémur, radius, tibia, troisièmes métacarpiens et métatarsiens, premières phalanges antérieures et postérieures et largeur maximale de la troisième phalange antérieure d'*E. shoshonensis* (Hagerman), *E. qingyangensis* (Bajiazui) et de l'*E. Dolichohippus grevyi* actuel en comparaison avec l' Onagre actuel. n = nombre de spécimens.

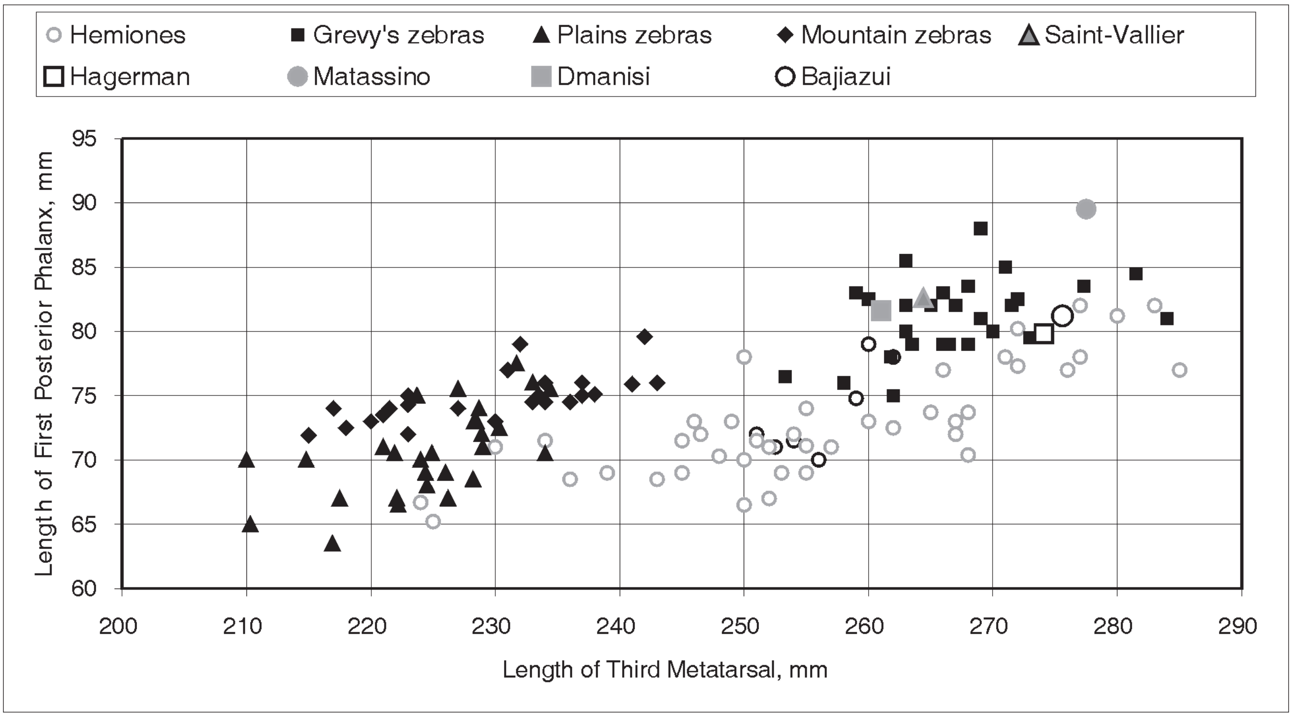

Figure 2: Scatter diagram of maximal length of first posterior phalanges versus maximal length of third metatarsals in extant equids and in *E. stenonis* (Saint-Vallier, Matassino, Dmanisi), *E. shoshonensis* (Hagerman), and *E. qingyangensis* (Bajiazui).

Figure 2 : Diagramme de dispersion des longueurs maximales des troisièmes métatarsiens et des premières phalanges postérieures d'*Equus* actuels et d' *E. stenonis* (Saint-Vallier, Matassino, Dmanisi), *E. shoshonensis* (Hagerman) et *E. qingyangensis* (Bajiazui).

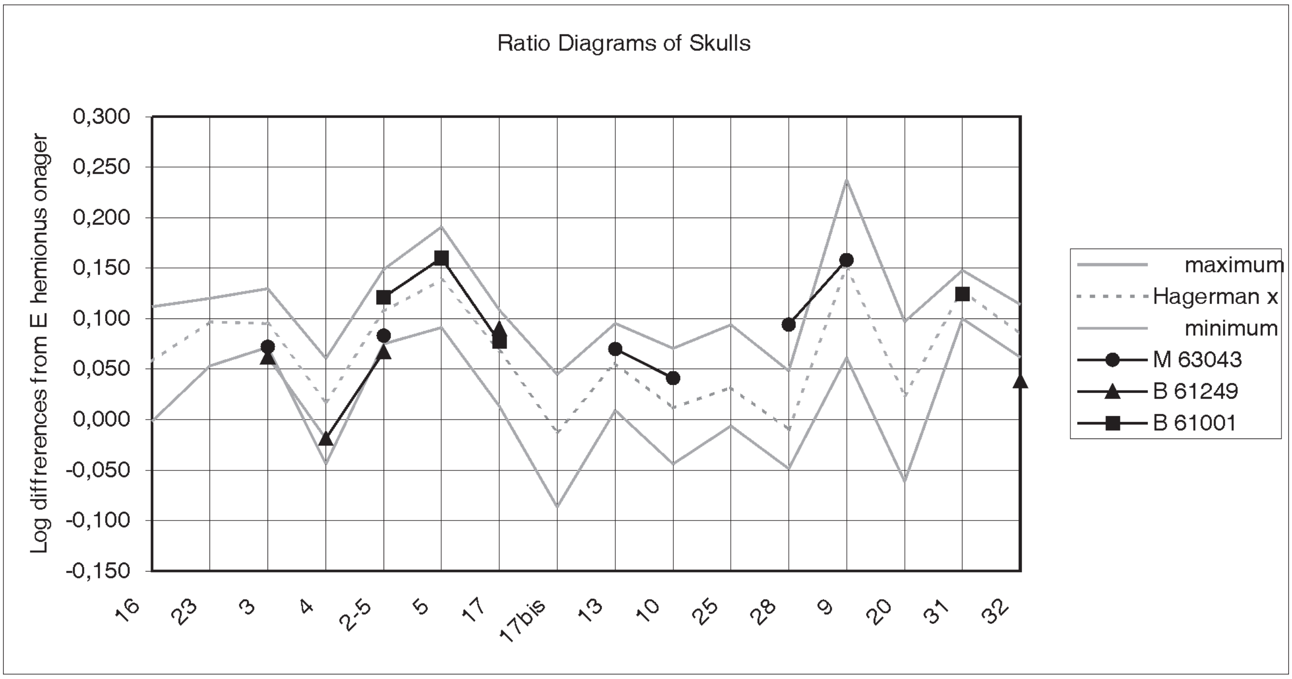

Figure 3: Ratio diagram of skull dimensions in the fossil equids of Bajiazui (*E. qingyangensis*) and Hagerman (*E. shoshonensis*) compared to the extant Onager, *E. hemionus onager*. Measurements are defined in Table 1.
Figure 3 : Diagrammes de Simpson des dimensions craniennes d'*E. shoshonensis* (Hagerman)et d'*E. qingyangensis* (Bajiazui) en comparaison avec l' Onagre actuel. Les mesures sont définies dans le tableau 1.

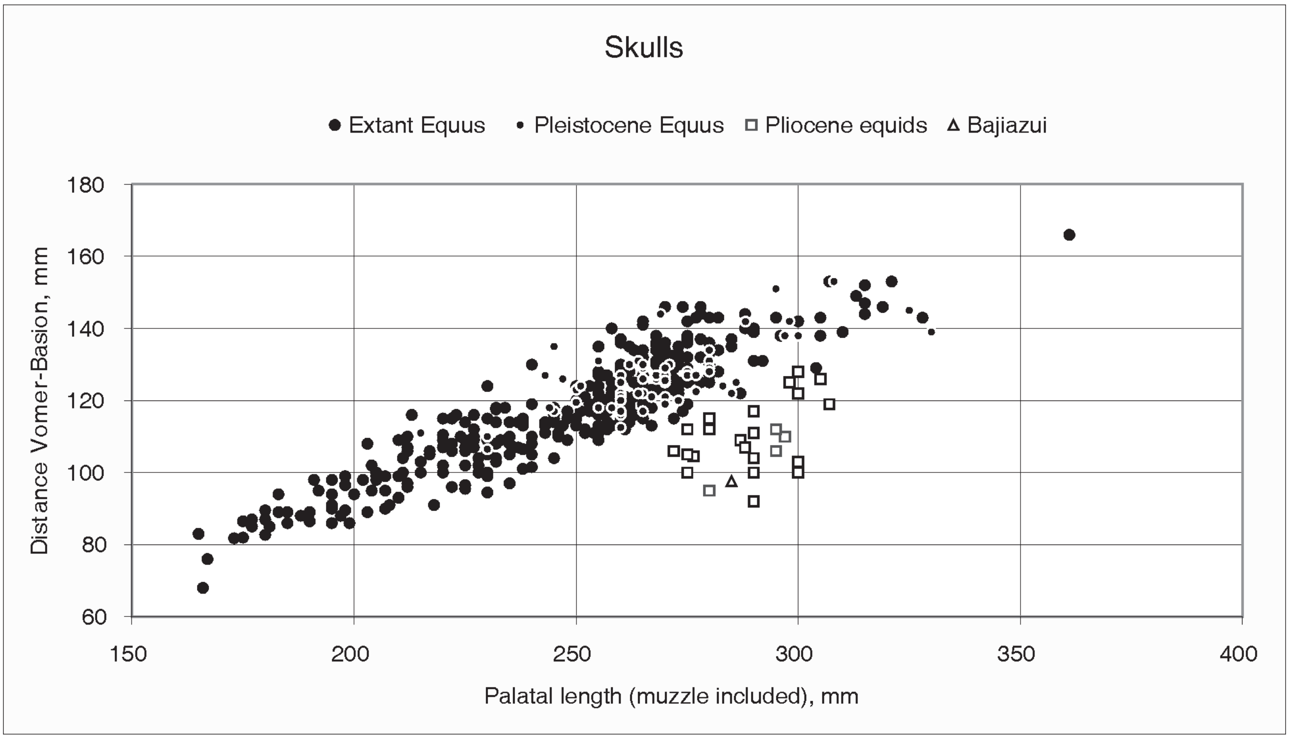

Figure 4: Scatter diagram of basicranial dimensions in extant and Pleistocene *Equus* and in *E. shoshonensis* (Hagerman), *E. sanmeniensis* (Nihowan), *E. yunnanensis* (Madahai), *E.* cf. *yunnanensis* (Locality 32), and *E. qingyangensis* (Bajiazui). The palatal length includes the length of the muzzle.
Figure 4 : Diagramme de dispersion de longueurs basicraniennes d'*Equus* actuels et pléistocènes et d'*E. shoshonensis* (Hagerman), *E. sanmeniensis* (Nihowan), *E. yunnanensis* (Madahai), *E.* cf. *yunnanensis* (Locality 32) et *E. qingyangensis* (Bajiazui). La longueur du palais inclut la longueur du museau.

THIRD METACARPALS				*E. qingyangensis*			
		n	x	min	max	s	v
Greatest length	1	3	249,3	240,0	255,0	8,14	3,27
Mid-shaft breadth (DT)	3	8	33,8	32,0	35,9	1,26	3,74
Mid-shaft depth (DAP)	4	9	27,5	26,0	29,0	1,05	3,83
DT proximal	5	4	51,9	49,5	54,0	2,19	4,22
DAP proximal	6	4	35,7	34,0	37,0	1,29	3,61
DT articular facet for carpale II	7	4	47,3	42,7	54,3	5,02	10,62
DT articular facet for carpale IV	8	4	14,9	11,4	16,7	2,39	16,04
DT distal maximal	10	19	48,4	43,8	51,0	1,92	3,97
DT distal articular	11	17	47,2	44,6	49,0	1,33	2,82
DAP distal maximal	12	20	36,1	34,4	39,5	1,12	3,10
Medial condyle DAP minimal	13	21	28,1	26,4	30,0	1,05	3,73
Medial condyle DAP maximal	14	17	31,7	30,3	32,9	0,78	2,45
THIRD METATARSALS		n	x	min	max	s	v
Greatest length	1	3	275,0	267	281	7,21	2,62
Mid-shaft breadth (DT)	3	7	33,6	32	34,9	0,96	2,84
Mid-shaft depth (DAP)	4	5	30,4	29,5	31,2	0,73	2,39
DT proximal	5	6	48,0	46,5	49,7	1,22	2,55
DAP proximal	6	6	35,8	33,4	38,5	1,89	5,27
DT articular facet for tarsale II	7	6	42,7	41	44,6	1,59	3,73
DT articular facet for tarsale IV	8	6	12,1	11,3	13,3	0,73	6,04
DT distal maximal	10	15	46,2	42	51,4	2,43	5,27
DT distal articular	11	13	45,6	42,8	50,2	2,07	4,53
DAP distal maximal	12	17	35,8	33,7	38	1,12	3,12
Medial condyle DAP minimal	13	16	26,7	24,7	28,6	1,12	4,21
Medial condyle DAP maximal	14	17	30,2	27,1	33,2	1,33	4,41

Table 2: Metapodial dimensions in millimeters of *E. qingyangensis*. See abbreviations in Table 1.
Tableau 2 : Dimensions en millimètres des troisièmes métapodes d'*E. qingyangensis.* Mêmes abréviations que dans le Tableau 1.

EQUUS QINGYANGENSIS

In the North-Western China, Xue and Wang collected at Bajiazui a good sample of a fossil *Equus*. Bajiazui is located in Qingyang County, Gansu Province. At the bottom of the section, a sandy-clay layer yielded numerous mammals including *Proboscidipparion sinense* and *Equus qingyangensis*. According to paleomagnetic data, the fossils come from above the Gauss-Matuyama boundary, and are believed to be of Lower Nihowanian age. The fossils are well preserved, without any evidence of transport and the remains of *Equus* and *Hipparion* were at times found in the same blocks of sediment.

1. Skull

Three adult fragments (Deng & Xue, 1999b, plates I-III) give a good idea of the general skull size (about 520mm in basilar length) and shape. Nearly all skull dimensions fall inside the *E. shoshonensis* variation (table 1, fig. 3). The basicranial proportions (fig. 4) indicate that this species did not belong to modern *Equus*. It plots inside the scatter of the North American *E. shoshonensis* and close to all primitive *Equus*, in particular to the Chinese (table 1) *E. yunnanensis* of Madahai, Yuanmou County, Yunnan Province (Liu & Yu, 1974) and specimen M 1321 from locality 32, Qixian County, Shanxi Province which was referred by Zdansky (1935) to *E.* cf. *sanmeniensis*. The type skull of *E. sanmeniensis* of Nihowan is, however, larger and the specimen from Loc 32 may be tentatively referred to *E. yunnanensis*. The naso-incisival notch of *E. qingyangensis*, although longer than in *E. shoshonensis*, is not as long relative to the cheek length as in *E. stenonis* (fig. 5).

The vomerine length is very long relative to the post-vomerine length, like in *E. shoshonensis*, and more so than in most *E. stenonis* (fig. 6). It is also long relative to the palatal length *sensu stricto* (length of the palate excluding the muzzle length). There again (fig. 7), *E. qingyangensis* and *E. shoshonensis* plot apart from most *E. stenonis*.

2. Teeth

In contrast to *E. teilhardi* (Eisenmann, 1975), and like in *E. shoshonensis*, the lower incisors do have cups (Deng & Xue, 1999a, plate I). On the other hand, the cheek teeth are clearly different from *E. shoshonensis*. The upper (Deng & Xue, 1999b, plate V) are smaller and have longer protocones (fig. 8). On the lower cheek teeth, instead of the usual round pattern and rather deep linguaflexids (or lingual grooves) of *E. shoshonensis* (Azzaroli & Voorhies, 1993, Pl. 1c), the double knots of the lower P3-P4 of *E. qingyangensis* (Deng & Xue, 1999b, plate VI-2) tend to have more elongated and dropping metaconids and shallow linguaflexids. The

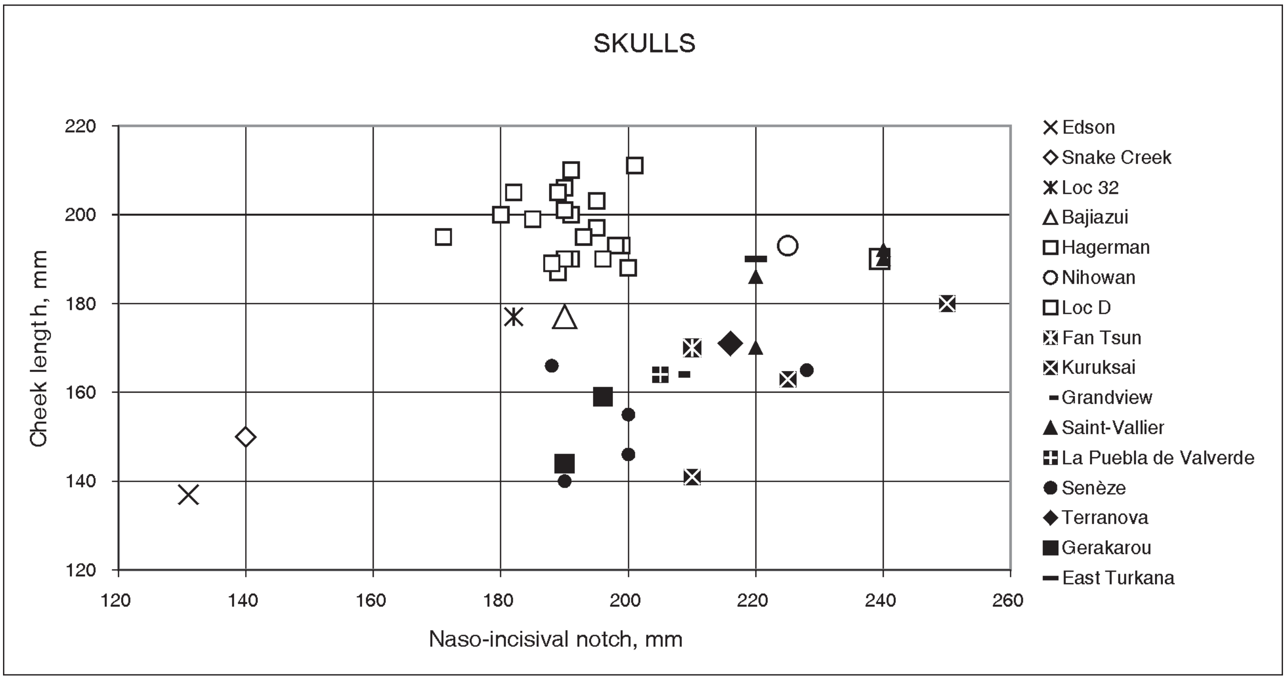

Figure 5: Scatter diagram of facial dimensions in *Dinohippus* (Edson and Snake Creek), *E.* cf. *yunnanensis* (Locality 32), *E. stenonis sensu lato* (Locality D, Fan Tsun, Kuruksai, Grandview, Saint-Vallier, La Puebla de Valverde, Senèze, Terranova, Gerakarou), *E. qingyangensis* (Bajiazui), *E. shoshonensis* (Hagerman), *E. sanmeniensis* (Nihowan), and *E. koobiforensis* (East Turkana).
Figure 5 : Diagramme de dispersion de longueurs faciales de *Dinohippus* (Edson and Snake Creek), *E.* cf. *yunnanensis* (Locality 32), *E. stenonis sensu lato* (Locality D, Fan Tsun, Kuruksai, Grandview, Saint-Vallier, La Puebla de Valverde, Senèze, Terranova, Gerakarou), *E. qingyangensis* (Bajiazui), *E. shoshonensis* (Hagerman), *E. sanmeniensis* (Nihowan), et *E. koobiforensis* (East Turkana).

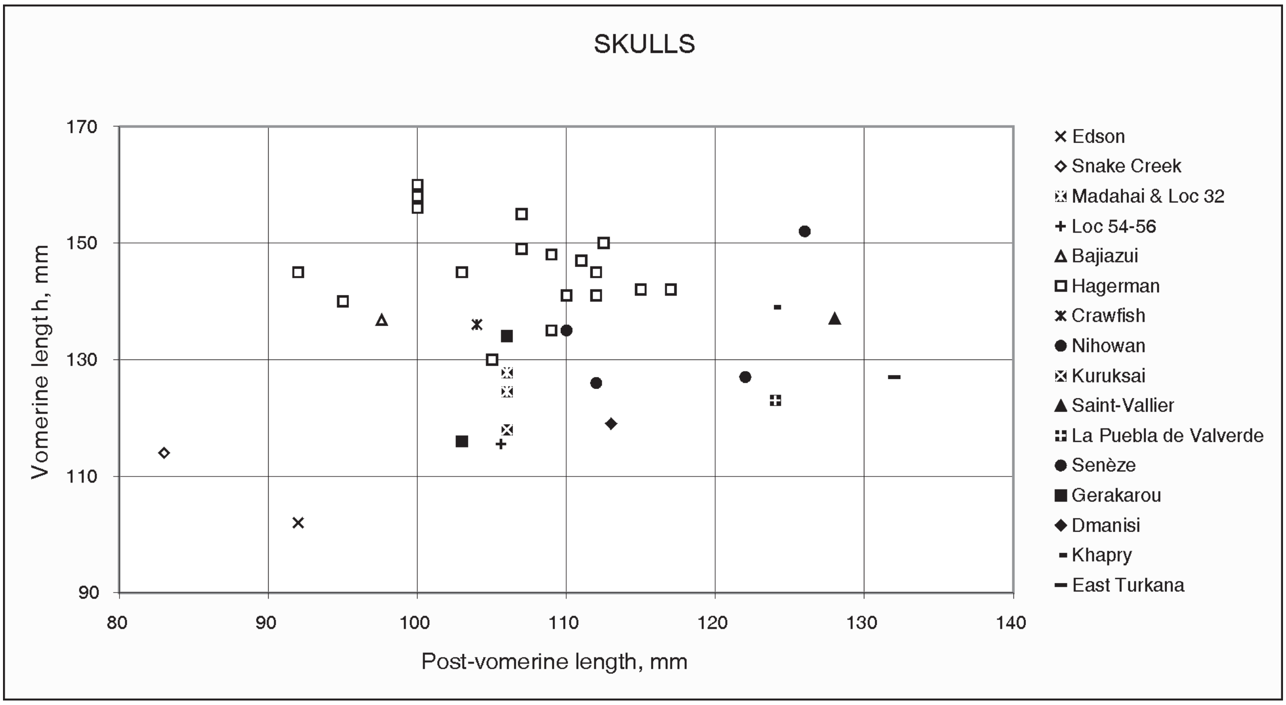

Figure 6: Scatter diagram of basicranial dimensions in *Dinohippus* (Edson and Snake Creek), *E. yunnanensis* (Madahai and Locality 32), *E. stenonis sensu lato* (Locality 54-56, Kuruksai, Saint-Vallier, La Puebla de Valverde, Senèze, Gerakarou, Dmanisi, Khapry), *E. qingyangensis* (Bajiazui), *E. shoshonensis* (Hagerman), *E. simplicidens* (Crawfish), *E. sanmeniensis* (Nihowan), and *E. koobiforensis* (East Turkana).
Figure 6 : Diagramme de dispersion de longueurs basicraniennes de *Dinohippus* (Edson and Snake Creek), *E. yunnanensis* (Madahai and Locality 32), *E. stenonis sensu lato* (Locality 54-56, Kuruksai, Saint-Vallier, La Puebla de Valverde, Senèze, Gerakarou, Dmanisi, Khapry), *E. qingyangensis* (Bajiazui), *E. shoshonensis* (Hagerman), *E. simplicidens* (Crawfish), *E. sanmeniensis* (Nihowan) et *E. koobiforensis* (East Turkana).

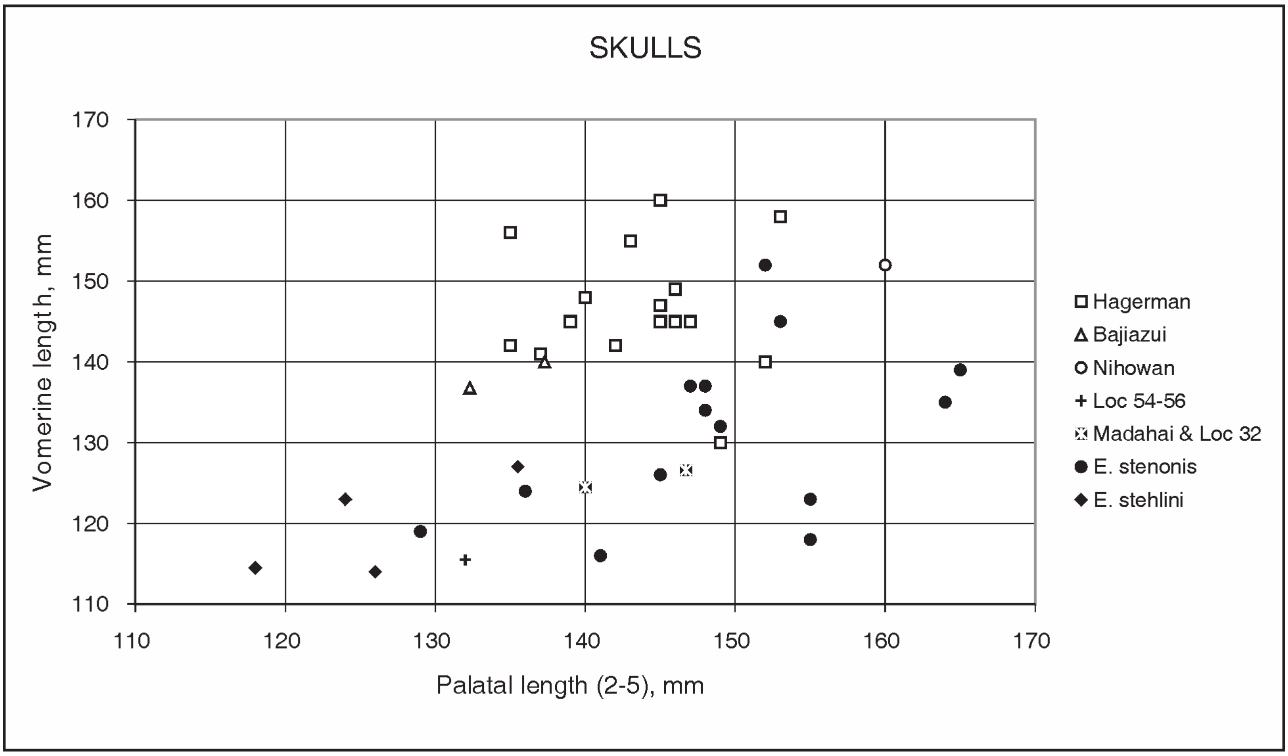

Figure 7: Scatter diagram of basicranial dimensions in *E. shoshonensis* (Hagerman), *E. qingyangensis* (Bajiazui), *E. sanmeniensis* (Nihowan), *E.* cf. *stenonis* (Locality 54-56), *E. yunnanensis* (Madahai and Locality 32), various *E. stenonis* and *E. stehlini*. The palatal length does not include the muzzle length.
Figure 7 : Diagramme de dispersion de longueurs basicraniennes d'*E. shoshonensis* (Hagerman), *E. qingyangensis* (Bajiazui), *E. sanmeniensis* (Nihowan), *E.* cf. *stenonis* (Locality 54-56), *E. yunnanensis* (Madahai and Locality 32), de divers *E. stenonis* et d'*E. stehlini*. La longueur du palais *sensu stricto* n'inclut pas la longueur du museau.

				E. shoshonensis			
FIRST ANTERIOR PHALANGES		n	x	min	max	s	v
Greatest length	1	19	86,9	84	90	1,97	2,27
Mid-shaft breadth (DT)	3	19	32,6	30,5	34,5	1,09	3,33
DT proximal	4	19	50,3	48	54	1,65	3,28
Proximal depth (DAP)	5	19	35,9	34	38,5	1,23	3,42
DT distal maximal	6	19	44,2	42,5	45,1	0,91	2,05
Greatest length of trigonum phalangis	7	19	53,8	47	62	3,84	7,14
Supratuberosital length	10	19	64,5	60	69	2,01	3,12
Infratuberosital length	12	19	14,1	11	17	1,39	9,92
DT distal articular	14	19	42,0	40	44	0,91	2,16
FIRST POSTERIOR PHALANGES		n	x	min	max	s	v
Greatest length	1	15	79,8	77	83	1,98	2,49
Mid-shaft breadth (DT)	3	15	31,0	29	33,5	1,54	4,97
DT proximal	4	15	50,3	47	53	1,76	3,50
Proximal depth (DAP)	5	15	37,1	35	39	1,21	3,27
DT distal maximal	6	15	41,3	39	44	1,46	3,53
Greatest length of trigonum phalangis	7	15	45,1	42	48	2,02	4,48
Supratuberosital length	10	15	55,3	52	59	1,99	3,59
Infratuberosital length	12	15	16,3	14	19	1,50	9,16
DT distal articular	14	15	39,1	37	41	1,31	3,35

Table 3: First phalanges dimensions in millimeters of *E. shoshonensis*. See abbreviations in Table 1.
Tableau 3 : Dimensions en millimètres des premières phalanges d'*E. shoshonensis.* Mêmes abréviations que dans le Tableau 1.

	E. shoshonensis	*E. stenonis*
	E. qingyangensis	
Length of Naso-incisival notch		
relative to Cheek length	shorter	longer
Post-vomerine length		
relative to Vomerine length	shorter	longer
Palatal length (muzzle excluded)		
relative to Vomerine length	shorter	longer
Length of First posterior phalanges		
relative to length of Third Metatarsals	shorter	longer

Table 4: Skull and limb bones differences between *E. shoshonensis*-like and *E. stenonis*-like equids.
Tableau 4 : Différences entre les crânes et les os des membres des lignées d'*E. shoshonensis* et d'*E. stenonis*.

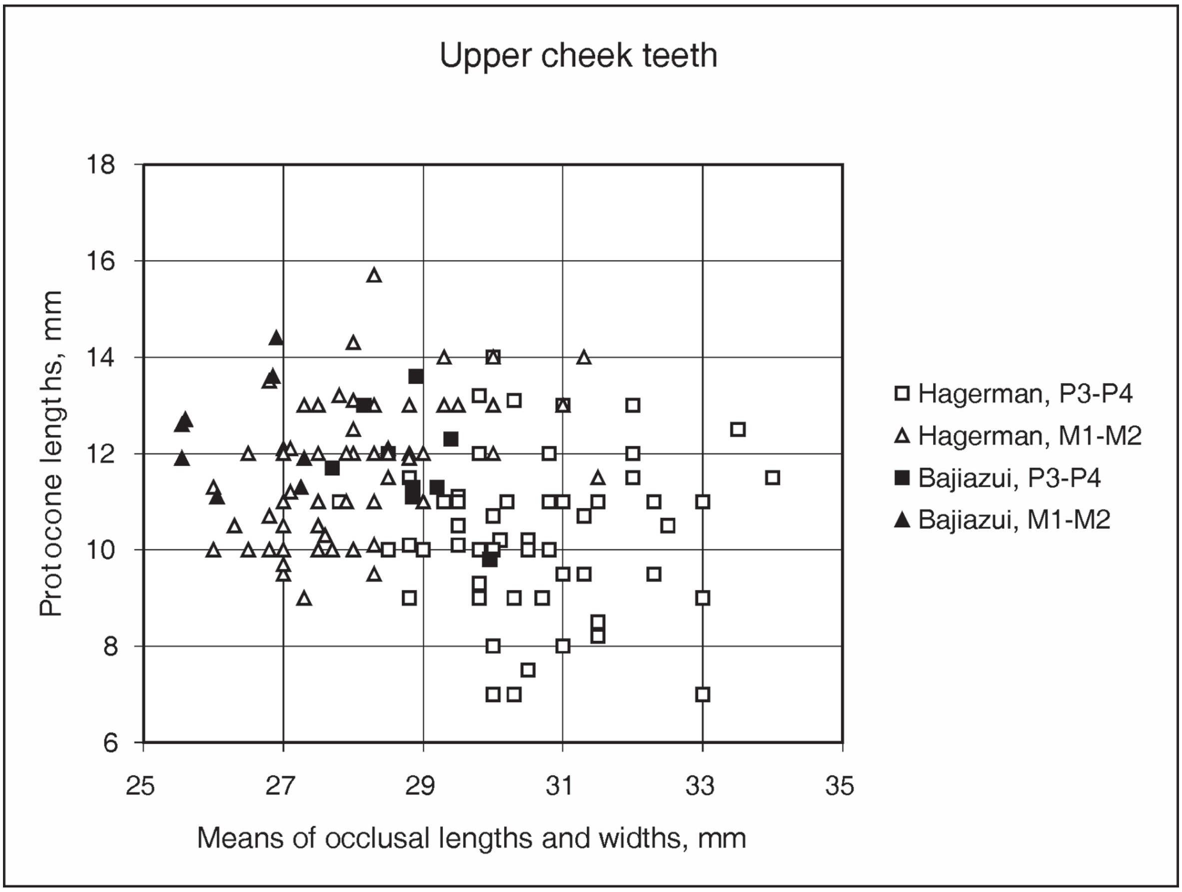

Figure 8: Scatter diagram of upper cheek teeth dimensions in *E. shoshonensis* (Hagerman) and *E. qingyangensis* (Bajiazui).
Figure 8 : Diagramme de dispersion des dimensions de dents jugales supérieures d'*E. shoshonensis* (Hagerman) et *E. qingyangensis* (Bajiazui).

overall pattern is reminescent of modern Hemiones and of *E. calobatus* as illustrated by Skinner, Hibbard, et al. (1972, fig. 58). Contrary to the latters, however, the ectoflexid (or vestibular groove) is deep on the molars.

3. Limb bones

Figure 1 shows that the metapodials and first phalanges of *E. qingyangensis* are slightly longer than those of *E. shoshonensis* but have similar relative lengths. The average metatarsal and first posterior phalanx lengths of *E. qingyangensis* and *E. shoshonensis* plot close to each other (fig. 2). The metapodials of *E. qingyangensis* (table 2) are not very different from those of *E. shoshonensis* (Eisenmann & Karchoud, 1982) even if the metacarpals seem a little longer, slenderer, and deeper while the metatarsals are about the same length but a little more robust. The first phalanges (Deng & Xue, 1999b, table 12) are also similar in size and proportions to those of *E. shoshonensis* (table 3).

DISCUSSION AND CONCLUSION

Although the age of Bajiazui is not precisely known, it is certainly younger, possibly about 1 Ma younger, than the age of Hagerman. Moreover, the localities are separated by thousands of kilometers. Thus, the conspecificity of the two taxa is not probable and, indeed, the morphologies of the teeth show that they are different. But given their separation in time and distance, the resemblances between them is astonishing : similar size, similar limb bone proportions, similar morphology of the skull.

These resemblances put both *E. shoshonensis* and *E. qingyangensis* apart from the ubiquitous (Forsten, 1999) *E. stenonis*. As already discussed previously (Eisenmann, 1999), not all Plio-Pleistocene *Equus* of the Old World should be referred to *E. stenonis*. Some taxa seem to resemble more the North-American *E. shoshonensis* (or *E. simplicidens*) but they are not documented enough : the skulls of the African *E. numidicus* and *E. tabeti* are not known (the skull of *E. koobiforensis* resembles more *E. stenonis* than *E. shoshonensis* : the palate is long and the choanae short). The skull of the European *E. granatensis* (sometimes synonymised with *E. altidens*) is not known, and very scarce fossils represent the probably-not-stenonine *Equus* of Huelago and Tegelen. The material referred to *E. qingyangensis* is the first evidence complete enough to support the presence of a primitive lineage different from *E. stenonis* in the Old World.

Most primitive *Equus* skulls from China resemble *E. stenonis* (Forsten, 1986), by their long naso-incisival notch (*E. sanmeniensis* from Nihowan, and specimens M 1418 from Loc. D and FAM 60-B 719 from Fan Tsun, Taigu District) and/or by their relatively short vomerine length (M 1467/68 from Loc. 54/56). The type specimen of *E. yunnanensis* seems to have a short vomerine length as well as the specimen M 1324-25 from Loc. 32 (fig. 6 and 7). The later has also a short naso-incisival notch (fig. 5). Unfortunately, both specimens are not perfectly preserved. If our observations are confirmed, *E. yunnanensis* would be another example of the 'mosaic' of characters frequently evidenced by equids.

In the present state of our knowledge, it is not probable that any extant species of *Equus* has either *E. stenonis* or *E. shoshonensis* for a direct ancestor. All extant *Equus* probably share an apomorphy in their basicranial proportions and may be considered as monophyletic (Eisenmann & Baylac, 2000). Although some of the extant *Equus* species are rather *E. stenonis*-like in their body proportions (Plains zebras) while others (Hemiones) are rather *E. shoshonensis*-like, these resemblances very probably result from homoplasies. Indeed, because of frequent homoplasies, the present 'phylogenies' of primitive *Equus sensu lato* can only be very tentative, as is also the list of diagnostic characters presented here (table 4). We believe, however, that *E. shoshonensis* may be the direct ancestor of *E. qingyangensis* and that both are part of a lineage distinct from *Equus stenonis*.

LITERATURE CITED

AZZAROLI A., & VOORHIES M., 1993 – The Genus *Equus* in North America. The Blancan species. *Palaeontographia Italica*, **80**, 175-198.

AZZAROLI A., 1995 – A synopsis of the Quaternary species of *Equus* in North America. *Bolletino della Societa Paleontologica Italiana*, **34**(**2**), 205-221.

BERNOR R.L., TOBIEN H., & WOODBURNE M.O., 1990 – Patterns of Old World Hipparionine Evolutionary Diversification and Biogeographic Extension. *In* E.H. Lindsay et al. (eds), *European Neogene Mammal Chronology*, Plenum Press, New York, 263-319.

DENG T., & XUE X., 1999a – *Equus qingyangensis* sp. nov. (Perissodactyla, Equidae) from the Early Pleistocene of Qingyang, Gansu, China. *Vertebrata Palasiatica*, **37** (**1**), 62-74.

DENG T., & XUE X., 1999b – *Chinese Fossil Horses of* Equus *and Their Environment*. China Ocean Press, in Chinese, 158p. English abstract, 129-153.

EISENMANN V., 1975 – Nouvelles interprétations des restes d'Equidés (Mammalia, Perissodactyla) de Nihowan (Pléistocène inférieur de la Chine du Nord) : *Equus teilhardi* nov. sp. *Géobios*, **8** (**2**),125-134.

EISENMANN V., & KARCHOUD A., 1982 – Analyses multidimensionnelles des métapodes d'*Equus sensu lato* (Mammalia, Perissodactyla). *Bulletin du Muséum national d'Histoire naturelle*, C, **4** (**1-2**), 75-103.

EISENMANN V., 1992 – Origins, dispersals, and migrations of *Equus* (Mammalia, Perissodactyla). *Courier Forschungsinstitut Senckenberg*, 153, 161-170.

EISENMANN V., 1999 – *Equus granatensis* of Venta Micena and evidence for primitive non-stenonid horses in the Lower Pleistocene. Proceedings of the International Conference of Human Palaeontology "*The hominids and their environment during the Lower and Middle Pleistocene of Eurasia*"Orce 1995, 175-189.

EISENMANN V., 2000 – *Equus capensis* (Mammalia, Perissodactyla) from Elandsfontein. *Palaeontologia africana*, **36**, 91-96.

EISENMANN V., & BAYLAC M., 2000 – Extant and fossil *Equus* (Mammalia, Perissodactyla) skulls : a morphometric definition of the subgenus *Equus*. *Zoologica Scripta*, **29** (**2**), 89-100.

FORSTEN A., 1986 – Chinese fossil horses of the genus *Equus*. *Acta Zoologica Fennica*, **181**, 1-40.

FORSTEN A., 1989 – Horse diversity through ages. *Biological Review*, **64**, 279-304.

FORSTEN A., & EISENMANN V., 1995 – *Equus* (*Plesippus*) *simplicidens* (Cope), not *Dolichohippus*. *Mammalia*, **59** (**1**), 85-89.

FORSTEN A., & KRAKHMALNAYA T., 1997 – The hipparions (Mammalia, Equidae) from the late Miocene of Cherevichnoe on the northern Black Sea coast, Ukraine. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte*, **1997** (**8**), 489-499

FORSTEN A., 1999 – A review of *Equus stenonis* Cocchi (Perissodactyla, Equidae) and related forms. *Quaternary Science Reviews*, **18**, 1373-1408.

LIU H., & YU Y., 1974 – New materials of *E. yunnanensis* in Yanmou, Yunnan. On diagnosis of *E. yunnanensis* and phylogeny of *Equus* in Asia. *Vertebrata Palasiatica*, **12** (**2**), 126-134.

LUNDELIUS E.L. Jr., CHURCHER C.R., DOWNS T., HARINGTON C.R., LINDSAY E.H., SCHULTZ G.E., SEMKEN H.A., WEBB S.D., & ZAKRZEWSKI R.J., 1987 – The North American Quaternary sequence, *In* M.O. Woodburne (ed.), *Cenozoic Mammals of North America, Geochronology and Biostratigraphy*, 211-235.

SAMSON P., 1975 – Les Equidés fossiles de Roumanie. *Geologica Romana,* **14**, 165-352.

SKINNER M.F., & HIBBARD C.W. (ed.), 1972 – Early Pleistocene preglacial and glacial rocks and faunas of North-Central Nebraska. *Bulletin of the American Museum of Natural History*, **148** (**1**), 1-148.

SKINNER M.F., & MacFADDEN B.J., 1977 – *Cormohipparion* n.gen. (Mammalia, Equidae) from the North American Miocene (Barstovian-Clarendonian). *Journal of Paleontology*, **51** (**5**), 912-926.

ZDANSKY O., 1935 – *Equus* und andere Perissodactyla. *Palaeontologia Sinica*, Series C, **6** (**5**), 1-54.