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ORIGINS, DISPERSALS, AND MIGRATIONS OF EQUUS

(MAMMALIA, PERISSODACTYLA)

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Abstract

Caballine horses may be known from as early as the Early Irvingtonian in North America and as early as 1.3 Ma in Europe. Good evidence is much younger, however: around 0.7 Ma in North America, Asia, and Europe. The oldest European true horse, *E. mosbachensis*, has much larger limb bones than *E. scotti* from Siberia and North America. There is good evidence for hemione-like equids from around 0.7 Ma in Texas and Kansas, but not before the Late Pleistocene in the Old World. An Asiatic origin cannot, however, be ruled out, since hemiones are said to occur in the Middle Pleistocene of Asia. *E. hydruntinus* seems to 'appear' in Europe around 0.3 Ma ago, or possibly earlier. It may have originated there, from *E. stenonis* through *E. altidens*, and migrated to China and North America, but its hemione affinities and a gigantic MC III from the Itantsian complex raise the question of a possible American or Asiatic origin. Ass-like fossils exist in North and East Africa from around 2 Ma , and possibly even earlier in Europe (Huelago). A Pleistocene North African species, *E. melkiensis*, presently extinct, may have developed locally from *E. numidicus* through *E. tabeti*. A related form was probably present at 'Ubeidiya, around 1.5 Ma. Asses are also known in the Upper Pleistocene and Holocene of the Middle East. *E. burchelli* - like zebras are poorly known from around 1.7 Ma (Sub-KF unit of the Koobi Fora Formation), and much better from 0.7 Ma (Algeria). *E. grevyi* - like zebras are poorly known from before 1.9 Ma at the FLK NI site of Olduvai, and in Shungura G7. The *E. stenonis* complex is composed of at least five forms (including the typical one). It is not immediately related to the much older and more primitive *E. simplicidens* of Hagerman. The latter, and not *E. stenonis*, may be at the origin of asses and zebras.

Résumé

De vrais chevaux pourraient dater de l'Irvingtonien ancien en Amérique du Nord et de 1,3 Ma en Europe; mais les chevaux ne sont bien représentés que beaucoup plus tard: il y a 0,7 Ma en Amérique du Nord, Asie et

Europe. Parmi ces derniers, le cheval européen, *E. mosbachensis*, présente des membres beaucoup plus grands que les chevaux de Sibérie et Amérique du Nord, *E. scotti*. Des equidés ressemblant aux hémiones sont bien connus depuis 0,7 Ma au Texas et au Kansas, mais pas avant le Pléistocène supérieur dans l'Ancien Monde; une origine asiatique ne peut être exclue car des hémiones ont été signalés dans le Pléistocène moyen d'Asie. *E. hydruntinus* semble apparaître en Europe il y a 0,3 Ma. Il dérive peut-être d'un *E. stenonis*, à travers *E. altidens*, et peut avoir migré d'Europe en Chine et Amérique du Nord. Toutefois ses affinités hémioniennes et l'existence d'un métapode de proportions voisines (malgré sa grande taille) dans le complexe d'Itantsa, témoignent peut-être d'une origine asiatique ou américaine. Des equidés asiniformes existent en Afrique du Nord et de l'Est depuis 2 Ma environ, et peut-être même plus tôt en Europe (Huelago, Espagne). Une espèce maghrébine pléistocène actuellement éteinte, *E. melkiensis*, peut s'être développée localement à partir d'*E. numidicus*, à travers *E. tabeti*. Une forme apparentée est connue en Israel à Ubeidiyeh, il y a 1,5 Ma. Des ânes existent aussi dans le Pléistocène supérieur et l'Holocène du Moyen Orient. Des zèbres ressemblant à *E. burchelli* existent peut-être depuis 1,7 Ma en Afrique de l'Est (unité sub-KF de la formation de Koobi Fora), certainement depuis 0,7 Ma en Afrique du Nord (Tighenif). Des zèbres ressemblant à *E. grevyi* sont peut-être présents il y a 1,9 Ma en Afrique de l'Est (Shungura G et Olduvai FLK NI). Le complexe sténonien comprend au moins cinq formes (y compris la forme typique). Aucune ne semble spécialement proche d'*E. simplicidens* d'Hagerman, beaucoup plus ancien et plus primitif. Cette espèce américaine, et non *E. stenonis*, pourrait être à l'origine des zèbres et des ânes.

Introduction

This paper deals with the possible migrations of some monodactyl equids (genus *Equus*) between 3.5 Ma and the present. The scope of this paper does not allow an extensive discussion of the anatomical characters on which the taxonomic determinations are based, nor a comprehensive review of all species and all sites. Although necessarily incomplete, vague, and more or less incorrect, the three tables showing the spatio-temporal distribution of different *Equus* species are essential to any further discussion about migrations. The first table is devoted to *E. simplicidens* (SI), typical *E. stenonis* (bold characters), and less typical forms (ST?, ST1, ST2, ST3). In the second table appear asses (A) and zebras (G for *E. grevyi*, B for *E. burchelli* and its probable ancestor *E. mauritanicus*). The third table concerns caballine horses (C) (including *E. scotti* (S)), hemiones (H), *E. hydruntinus* (HY), and its possible ancestor *E. altidens* (A). In most cases, the age of a site is taken as published, even if it does not seem to fit with the *Equus* determination. The discrepancies will be noted in the text. In most cases the fossils were studied by myself; exceptions to this will be noted.

Stenonine forms

Since the first discoveries of 'stenonine' fossils (Table 1) in Europe and North America, scientists have stressed their resemblances to each other and to African zebras, especially Grevy's zebra. More precise comparisons must be made, however, before discussing the migrations of *E. simplicidens* (Hagerman Quarry, Idaho) to Europe and Africa, which, according to REPENNING (1987) took place about 3.4 Ma ago. Comparing the beautiful collections of Hagerman fossils with the richest European collections (skulls, teeth and limb bones from both La Puebla de Valverde and Saint-Vallier) and African fossil and extant *Equus* shows that only *E. stenonis* from Saint-Vallier and La Puebla, and possibly *E. koobiforensis* from East Turkana, may be related, and that they differ strikingly from modern zebras and *E. simplicidens* in having a deeper, more derived narial notch. The differences between *E. stenonis* and *E. simplicidens* are in good accord with a large difference in age: *E. koobiforensis* is about 1.9 Ma old and *E. stenonis* from Saint-Vallier and La Puebla may be of roughly the same age, i.e. 1 or 1.5 Ma younger than *E. simplicidens*.

Around 2.5 Ma ago there were larger forms (Montopoli, Loubières de Pardines, El Rincon, Upper Sinap) whose skulls are unknown, or have deep narial notches, like those from Nihowan and Livenzovka (*fide* AZZAROLI 1990). Some metapodials from Nihowan are rather *E. simplicidens* -like, while others evoke the stenonine form ST1; those of Livenzovka (according to the data of Baigusheva) are very slender. The typical (and very well documented) *E. simplicidens* of Hagerman is not to be found anywhere, and there is no clear evidence for a rapid dispersal of *E. simplicidens* to the Old World around 3.4 Ma ago.

At Huelago, which is supposed to be of the same age as Rincon (ALBERDI et al. 1989), an evolved, possibly asinine, form is found (ST3), which usually is present at younger sites (Dmanissi, according to data published by GABUNIA & VEKUA 1989; 'Ubeidiya?, EISENMANN 1986; Pirro and Selvella, GIULI et al. 1987; GIULI

It is *E. simplicidens* which is 3 4 Ma old , according to Repenning, not its migration. VE

Table 1:

Region	Site	3.5	3.35	3	2.5	2.36	2.33	1.9	1.6	1.4	1.25	0.9
Magnetism				K	GAUSS		R1,R2	OLD				J
Millions Years		3.5	3.35	3	2.5	2.36	2.33	1.9	1.6	1.4	1.25	0.9
Shungura Tuffs			B			F	G	H2	J7	L		
East Turk. Tuffs			TB					KBS	KF	CH	UNT	
Olduvai-Laetoli		T8							Bed I	Lem L II	Upper II	III
E Africa	Shungura				NO EQUUS			G4-13				
	K.Fora							KBS-				
	Olduvai								cf SI	ST1		
Israel	Oubeidiyeh										ST3 ?	
Syria												
Turkey	Sinap sup				ST?							
Spain	El Rincon 1				ST?							
	Huelago				ST3							
	La Puebla de Valv.							LPDV				
France	Loubières de Pardines				ST?			SV				
	Ceyssaguet									ST1		
Italy	Montopoli				ST?							
	Olivola								OLIV			
	Pirro, Selvella											ST3
Greece	Pyrgos, Gerak.									ST2		
S. USSR	Livenzovka				ST?							
	Kuruksaj							KURUK				
	Morskaja, Khapry									ST1		
	Psekups							ST2				
	Dmanissi								ST3			
China	Nihowan				Big SI ?					ST1?		
Idaho	Hagerman		SI									

Table 1: Spatio-temporal distribution of primitive *Equus*. SI = *E. simpicidens*; bold characters: occurrences of typical *E. stenonis*, (LPDV = La Puebla de Valverde, SV = Saint-Vallier, KURUK)= Kuruksaj, OLIV = Olivola); ST?, ST1, ST2, ST3 = less typical stenonine forms.

Table 2:

Region	Site	2.36	2.33	1.9	1.6	1.4	1.25	0.9	0.8	0.7	0.6	0.5	0.4	0.3	0.2	0.1
Magnetism				OLD				J		B	R	U	N	H	E	S
Millions Years		2.36	2.33	1.9	1.6	1.4	1.25	0.9	0.8	0.7	0.6	0.5	0.4	0.3	0.2	0.1
Shungura Tuffs		F	G	H2	J7	L										
East Turk. Tuffs				KBS	KF	CH	UNT			SIL						
Olduvai				I	Lem	L II	Upp II	III								
S Africa	Black Earth Cave															Z
E Africa	Shungura		N	A?,G												
	K.Fora		O	B ?	A?B/G	A?B,G	G									B,G
	Olduvai			A?,G			B									
	Anna Bokoma				B											
N Africa	Ain Boucherit			A?												
	Ain Hanech					A?										
	Tighenif		E									B				
	Salé		Q											A		
	Rabat		U												A	
	Allobroges, etc.		U													A
Israel	Oubeidiyeh		S			A?										
	Qafzeh															A?
Syria	Mureybit															A
Arabia	Oman, etc.															A

Table 2: Spatio - temporal distribution of Asses (A) and Zebras (G for *E. grevyi*, B for *E. burchelli* and *E. mauritanicus*).

1987). Another age discrepancy concerns ST2, a form present at Mygdonia (KOUFOS in press) and Pyrgos, around 1.3 Ma ago (MEULEN & KOLFSCHOTEN 1986:209) and also in the Psekups mammal complex, the lower boundary of which is supposed to be between 1.97 and 2.5 Ma (VANGENGEIM et al. 1990). ST2 and ST3 are middle-sized or small forms. ST1, present in the Upper Bed II of Olduvai, at Ceyssaguet (old collections), and possibly at Morskaya, Khapry, and Nihowan, which are all tentatively placed at the same age, is very large.

Equus grevyi

E. grevyi (Table 2) is a mixture of primitive and not very characteristic teeth, larger and more robust but otherwise *E. africanus* - like metacarpals, larger and more robust but otherwise hemione-like metatarsals, and very elongated skulls with a moderate narial notch. Grevy's zebras are definitely different from Eurasian *E. stenonis*, from *E. koobiforensis*, and from the large equids from Upper Bed II of Olduvai (ST 2). To derive *E. grevyi* from *E. stenonis* or *E. koobiforensis*, one would have to admit the regressive evolution of the narial notch, overdeveloped in both fossil species, and clearly a derived character in equids.

The fossil skulls and limb bones most similar to *E. grevyi* belong to *E. simplicidens*, but their skulls differ in one of the most important characters in *Equus* systematics: the relationship between vomerine and post-vomerine length. No *Equus* as old as *E. simplicidens* is known from Africa. The first *Equus* in East Africa are all younger than 2.33 Ma; the precise age of North African sites (Ain Boucherit, Ain Jourdel) is not known.

Some *E. grevyi* - like metacarpals are found in member G of the Shungura Formation, Omo (Ethiopia) and possibly at site FLK NI (Olduvai, Tanzania). *E. grevyi* may also be present in Kenya below the Chari Tuff and in the Guomde Formation (EISENMANN 1983).

Plains zebras: *Equus burchelli*

The rich material (skulls, teeth, limb bones) from the Middle Pleistocene of Tighenif (= Ternifine = Palikao, Algeria), described as *E. mauritanicus* is definitely related to this group (Table 2), although some characters evoke *E. grevyi* (EISENMANN 1979).

Tighenif is believed to be around 0.7 Ma in age (GERAADS et al. 1986). Older fossils from East Africa (below KBS Tuff, below KF Tuff, below Chari Tuff in Kenya, and at site JK2 B, Olduvai Bed III), may also be referred to *E. burchelli*. This species is also present at Anna Bokoma, Djibouti (BONIS et al. 1988), but the age of this site may be either Lower or Middle Pleistocene.

Mountain zebra: *Equus zebra*

The skulls resemble those of Grevy's zebras, but are relatively wider (especially across the muzzle) and have a large external auditory meatus, like in the asses. The teeth are primitive, and are not diagnostic. The metapodials are relatively short, and the hooves narrow and flat in accordance with an adaptation to a mountain biotope. Some Late Pleistocene material from Black Earth Caves (South Africa) preserved in the Paleontological Museum, Berkeley, may belong to *E. zebra*.

Asses

On the whole, asses (Table 2) are difficult to identify from paleontological materials because they share many characters with zebras, hemiones, *E. hydruntinus*, and Plio-Pleistocene equids. For example, the lower cheek teeth have a primitive 'stenonine' pattern, but have evolved shallow vestibular grooves on molars, like in hemiones.

At present, wild asses are restricted to Africa and are represented by only one species with two subspecies: *E. africanus africanus* and *E. africanus somaliensis*. From various art depictions, however, 'there is ample evidence for a wild ass... living in the Maghreb until Roman times' (GROVES 1986:34). GROVES (1986:33) stated that there is no definite osteological basis for such an ass, but he was probably unaware of several fossils from the Late Pleistocene of North Africa (Filfila, Allobroges) that may belong to wild asses and were described as *E. melkiensis* (BAGTACHE et al. 1984). *E. melkiensis* is mainly known from its teeth and metapodials, and possibly a fragmentary skull. The teeth are similar to *E. africanus*, but the metacarpals are more robust and thicker.

E. tabeti (A?) from Aïn Hanech (Algeria, around 1.4 Ma?) has more primitive lower cheek teeth than the wild asses, but judging from the shape of its metacarpals could be the ancestor of *E. melkiensis*. *E. melkiensis* may be represented in younger deposits by a metacarpal from Salé and a fragmentary skull from Rabat (Morocco) whose

		1.5	1.4	1.3	1.2	1.1	1	J 0.9	0.8	BRUNHES 0.7	0.6	0.5	0.4	0.3	0.2	0.1
		Early IRVINGTONIAN			Late IRVINGTONIAN									RANCHOLABREAN		
					CHUKOCHYAN					AKANYAN						
Nebraska	Red Cloud			C ?												
Texas	Rock Creek									S,H						
	Channing												H			
Kansas	Gravel Pit									H						
Wyoming	Natural Trap															H
Oregon	Fossil Lake															HY
Yukon	Old Crow									S						
	Dawson, Gold Run															HY
Alaska	Lost Chicken															HY
North-Eastern Siberia										S-				S +		
N China	Dalian															HY
S USSR	Binagady															H
Iraq	Umdabayah															H
Israel	Oumm Qatafa														C,HY ?	
Syria	El Kowm 2															H
Greece	Pyrgos		C ?													
	Petralona													HY ?		
Italy	Selvella					C ?										
	Romanelli, etc.															HY
	San Teodoro															H
Spain	Huescar I, CB 1					C ?										
France	Arago												C			
	Lunel-Viel													HY		
	La Fage I, etc.													S +		
Germany	Sussenborn									A ?						
	Mosbach 2										C					
	Roterberg,etc															HY
North Sea																HY
England	Little Oakley									C ?						
	Hoxnian													S +		
N Africa	Allobroges, etc.															C

Table 3: Spatio-temporal distribution of true Horses, Hemiones, and *E. hydruntinus*. C = caballine Horses in general; S = *E. scotti* and morphologically close forms, possibly more evolved (S +) or more primitive (S-). H = Hemiones. HY = *E. hydruntinus*. A = *E. altridens*, possible ancestor of *E. hydruntinus*.

ages are uncertain: close to 400 000 years for Salé, certainly younger for Rabat (HUBLIN 1985). *E. tabeti* possibly derives from *E. numidicus* (A?, Ain Boucherit, Algeria).

In East Africa, asinine (A?) metacarpals are found in member G 5 of the Shungura formation (Ethiopia), in the FLK NI site of Olduvai Bed I (Tanzania), and below KF and Chari Tuffs in East Turkana (Kenya). The sub-Chari unit is older than 1.4 Ma and member G is dated between 2.33 and 1.9 Ma (BROWN et al. 1985).

A species very close to *E. tabeti* is also represented at 'Ubeidiya, Israel, (ST3?, or A?), probably around 1.5 Ma ago, and in Europe at Dmanissi, Pirro and Selvella (ST3).

In the Upper Pleistocene and Holocene, asses may also have existed outside Africa: in Arabia (UERPMANN 1991), Syria (Mureybit, DUCOS 1986), possibly Israel (Qafzeh). *E. graziosi* (AZZAROLI 1979) differs from all asinines I know, both in its teeth and in the shape of its muzzle.

Hemione-like *Equus*

These taxa are presently restricted to Asia. They are equids best adapted to dry conditions, abrasive food, open landscapes and (usually) hard ground. Appropriately, they have very hypsodont teeth with long protocones, slender limb bones, elongated distal segments and (usually) narrow hooves. The skull shape of hemiones is intermediate between that of horses and asses. Unfortunately, good data on the shape of the double knots are still lacking, but the vestibular grooves on the molars are usually shallow.

The oldest hemione-like metapodials were described under the name of *E. calobatus*. They come from the Horse Quarry of Rock Creek (Texas) and from the Gravel Pit near Arkalon (Kansas). They are much larger than modern metapodials, but have the same proportions. According to KURTÉN & ANDERSON (1980:288), Arkalon is Irvingtonian. The age of Rock Creek will be discussed later. Both sites are tentatively placed around 0.7 Ma in Table 3.

Similar, though smaller, metapodials come from the Late Irvingtonian of Channing (Texas). In Table 3, Channing is very tentatively placed around 0.4 Ma. Hemione like metapodials are also present at Natural Trap (Wyoming), which is of Late Pleistocene age (GILBERT & MARTIN 1984:138).

While hemiones are found at Rock Creek (same quarry?) together with the caballine *E. scotti*, no hemione coexists with *E. scotti* in the Olyorian fauna. In the Old World, the earliest possible evidence for a small hemione is in the 'sub-Chari unit' of East Turkana (metacarpal KNM ER 2067, from loc. 103). If this specimen indeed comes from this level, it would be older than 1.4 Ma (BROWN et al. 1985). This seems doubtful, however, since hemiones do not seem to be found anywhere else before the Late Pleistocene or Holocene: Staroselie, Binagady (USSR), Umdabayah (Iraq), San Teodoro (Italy). VANGENGEIM & ZHEGALLO (1982:323) mention the possible occurrence of hemiones in arid zones of the USSR during the Middle Pleistocene, but no more is said about the question.

Why did hemiones of the New World, morphologically close to extant hemiones, not migrate to Eurasia at the same time as *E. scotti*? Or did they, and why are they in that case not found in the Olyorian of Siberia?

E. hydruntinus

Until recently no skull of *E. hydruntinus* was known and the species was defined by its microdont, primitive cheek teeth and slender limb bones. Since the discovery of the material from Lunel-Viel (BONIFAY 1991), our knowledge of this equid has much improved, although the skull is fragmentary and the limb bones smaller and more robust than in the usual (later) forms. Lunel-Viel is said to belong in the Mindel-Riss (it is placed around 0.3 Ma in Table 3), while typical *E. hydruntinus* comes from the Late Pleistocene.

The skull shape of the small equid from Lunel-Viel is closer to hemiones than to any other equid species. In its small size, it fits well with the hemippes of Syria (especially the specimen from the Museum of Comparative Zoology, Yale University). At Lunel-Viel and at other later sites, metapodials are often more robust than in hemiones (and especially more than in hemippes) but other proportions are close to those of hemiones.

Surprisingly enough, metacarpals from the Late Pleistocene of Dalian in China (ZHOU et al. 1990), referred to *E. hemionus*, resemble those of *E. hydruntinus*. Quite similar metapodials were also found at Dawson, Gold Run and Lost Chicken Creeks (Yukon and Alaska) and at Fossil Lake (Oregon).

No good fossils of *E. hydruntinus* earlier than Lunel-Viel are known. *E. petraloniensis* from Greece is larger than *E. hydruntinus* from Lunel-Viel, although the ages are supposed to be the same (TSOUKALA 1991); there is no skull, but the metapodials are rather similar.

Some older and larger metapodials may possibly belong to an ancestral form. A gigantic MC III, kindly shown to me by E. VANGENGEIM, comes from the Itantsian complex of Transbaïkal, which belongs in the Eopleistocene (between the Olduvai event and the Brunhes) according to VANGENGEIM & ZAZHIGIN (1982). Several MC III from Dmanissi in Georgia look very much like *E. altidens* of Süssenborn.

E. altidens (A?) from Süssenborn (tentatively placed at around 0.7 Ma in Table 3) may have evolved from some European late *E. stenonis* (ST3) and be ancestral to *E. hydruntinus* (FORSTEN 1986). In that case, *E. hydruntinus* would be the result of a local European evolution. However, the hemione affinities of *E. hydruntinus*, the occurrence of *E. hydruntinus* - like metapodials in the Late Pleistocene of China and Yukon, and the presence of typical hemiones since the Irvingtonian in North America, raise the question of possible migration(s) of *E. hydruntinus* and/or *E. altidens* from the New World.

Caballine *Equus*

Modern horses have very characteristic 'caballine' double knots on the lower cheek teeth, which in most cases enable us to discriminate them from all other species, modern or fossil. The upper cheek teeth have long protocones, but this character may also be found in association with 'non-caballine' double knots. Skull proportions are intermediate between those of plains zebras and hemiones. Individual metapodials may be difficult to discriminate from *E. stenonis*, but a good sample is determinable.

True horses are supposed to have appeared in North America and migrated into Eurasia. According to AZZAROLI (1990) the oldest record is probably a still unpublished mandible from the early Irvingtonian Red Cloud Formation of Nebraska. The Early Irvingtonian is presently considered to range from 1.9 to 1.3 Ma (LUNDELIUS et al. 1987; REPENNING 1987). In Table 3 it is very tentatively placed at 1.3 Ma. The most complete evidence for a true horse in North America at this time is found at Rock Creek (Texas): skull, teeth and metapodials are all 'caballine'. The main fauna (with *Soergelia*) was supposed to be of an early Irvingtonian age, but the horse *E. scotti* comes from another quarry (KURTEN & ANDERSON 1980:35). WINANS (1985:150) considers it to be about 0.9 Ma years old and does not discuss the matter of the quarry. According to LUNDELIUS et al. (1987), the local fauna of Rock Creek should, however, be younger: it is situated 30m above the Cerro Toledo X Ash dated at 1.2 to 1.3 Ma but only 4.5m below the Lava Creek B Ash dated at 0.61 Ma. REPENNING (1987, fig. 8.1) also places the Rock Creek fauna in the Irvingtonian II, not in the Early Irvingtonian. Accordingly, it is here placed around 0.7 Ma (Table 3). Judging from metacarpals and metatarsals, *E. scotti* is also present at Old Crow (Yukon). Its age is uncertain but I assume for it the same age as for Rock Creek.

A skull similar to that of *E. scotti* (S) from Rock Creek is the specimen Bet 55, found in redeposited sediments of Adytcha, at Ulakhan-Sular, Siberia. The age is probably Akanian (= upper Olyorian) (SHER pers. comm.). According to SHER (1986, 1987) the Olyorian Mammal Age terminates in the early part of the Brunhes, and this specimen is from a level within the Brunhes, as is the MC/3723.95, which is also *E. scotti* - like but possibly less / Ⅱ evolved (S-). In Table 3, the Siberian *E.* cf. *scotti* is placed close to 0.7 Ma, in agreement with its resemblance to the Rock Creek species. Other metacarpals and metatarsals (collections of the Paleontological Institute, and of the Severtsov Institute of Evolutionary Animal Morphology and Ecology, Moscow) of uncertain age but morphologically very close to those of Rock Creek and Old Crow were also found in the area. The MC III 3100.488 is shorter, more robust and more 'evolved' in its distal proportions (S+) and looks like the metacarpals of La Fage I, Lower Achenheim Loess, and of the Hoxnian (SUTCLIFFE 1986: Swanscombe, Grays, Clacton) of England (S+), in agreement with its supposed Middle/Late Pleistocene age (SHER pers. comm.). Horses from La Fage I, LAI of Achenheim, and the Hoxnian sites of England are tentatively dated between 0.3 and 0.4 Ma, and are referred to *E. achenheimensis*. All three horses (*E. scotti* from North America and Siberia, and the European *E. achenheimensis*) seem adapted to a cool, though not very cold, environment (EISENMANN 1991).

The most complete evidence for a true horse in Europe is from Graues Mosbach (or Mosbach 2): skulls and lower teeth are perfectly caballine, but protocones are relatively short and metapodials more 'primitive' than usual in horses. According to BRÜNING (1978) *E. mosbachensis* comes from above the Brunhes-Matuyama magnetic inversion. It is unclear how much above. Mosbach 2 is tentatively placed at around 0.6 Ma in Table 3.

The skulls of *E. scotti* and *E. mosbachensis* are not very different in size and proportions, but the metapodials are smaller and usually more 'evolved' in *E. scotti* from Rock Creek and Old Crow than in *E. mosbachensis*. So, if we stick to the best and/or richest fossils (Rock Creek, Siberia, and Mosbach) and their rather imprecise ages, there is no evidence that caballine horses migrated from east to west rather than from west to east, nor is there any way of saying at exactly what date they 'appeared,' nor where.

If we consider 'second best data,' the problem still remains. AZZAROLI mentions an 'Early' Irvingtonian age (older than 1.2 Ma?) for the unpublished mandible from Nebraska, but there are also rather old, possibly caballine lower cheek teeth in Europe (Selvella, Cullar de Baza 1), as well as metapodials (Huescar 1, Pyrgos). While Selvella, Cullar de Baza I, and Huescar 1 may be considered of broadly the same age around the Farneta unit, Pyrgos is correlated with Tasso. The Farneta unit is about 1 Ma old, the Tasso unit could be as old as 1.3 Ma (TORRE 1987). Is the Red Cloud Formation of Nebraska older or younger than the Tasso unit, and are the Nebraska mandible and the Pyrgos metapodial sufficiently diagnostic?

Discussion

In order to establish the migration of a taxon, there are two prerequisites: the recognition of the same taxon in different geographical areas and the knowledge of the relative and/or absolute age of its occurrences. Obviously, the difficulty of the task will depend on the desired degree of precision (for example: subspecific or generic level; differences in age of a few years or of hundreds of thousands of years).

For a paleontologist, the recognition depends on the existence of valid, taxonomically discriminating osteological characters, implying a good knowledge of individual variation. Moreover, there is an underlying assumption that the characters are in some way linked: a zebra skull should not be associated with horse teeth, nor with hemione metapodials. This is not true, however, even for modern forms: *E. grevyi* combines a very

characteristic skull with rather ass-like metacarpals and rather hemione-like metatarsals. Fossils may also evidence anatomical contradictions, so that safe determination is only possible when the material is varied (because of the problem of character association) and rich (because of the problem of individual variation). These three questions (are the characters really discriminating; are they necessarily linked; are the ages of the fossils well known) are always limiting factors.

In a recent paper FORSTEN (1991) considers the implications of mitochondrial-DNA studies (GEORGE & RYDER 1986) on the time of differentiation of species of *Equus*, and hence on the number of migrations to be expected between the New World and the Old World. In many cases the ages of fossils are not precise enough to confirm or refute the mitochondrial dates. Usually, however, the paleontological data point to a younger age for the 'branchings off' than those proposed by GEORGE & RYDER (1986). One interesting exception concerns the bifurcation time of *E. grevyi* from *E. burchelli*. According to GEORGE & RYDER (1986) these species diverged about 1.6 Ma ago, but more or less recognizable fossils of both species seem to occur earlier.

The precise number and nature of migrations is presently impossible to ascertain, because even when a new species like *E. hydruntinus* 'appears,' local evolution can never be excluded. At least two primitive *Equus* may have migrated from America to Eurasia: an *E. simplicidens* - like form, SI, giving rise to African zebras (cf. SI), and 'asses' (ST3, A? and A), and a more evolved typical stenonine form which did not survive. The typical *E. stenonis* may or may not be at the origin of ST1 and ST2. Hemiones have migrated from America to Eurasia at least once, possibly twice (*E. hydruntinus*). The migrations of caballine horses are very hypothetical as to their number, time, and direction.

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