

## Pliocene and Pleistocene Equids: palaeontology versus molecular biology

With 21 figs, 2 pls

Véra EISENMANN

### Abstract

Palaeontological data are compatible with the current biomolecular views about the emergence of *Equus* 2.3 Ma and of Hemiones around 1.1 Ma. There is, however, no evidence for an early separation of the Caballine branch. Recognizable Caballines appear at the beginning of the Middle Pleistocene, not between 2.2 and 1.6 Ma. At that period, two groups are documented: one with a Zebra-like skull and Zebra-Ass-like upper and lower dentitions, another with a very peculiar lower dentition. Probable descendants of the latter (unformally named “Sussemiones” because of some resemblances between Süssenborn and Hemione cheek teeth) are extremely widespread, from North America to Ethiopia, and include dry-adapted (*E. granatensis*-like) and humid-adapted (*E. coliemensis*-like) species. Their extinction seems contemporary with the appearance of Caballines and other species closely related to extant: *E. hydruntinus* related to Hemiones, *E. melkiensis* related to Asses, and *E. mauritanicus* and *E. capensis* related to Plains Zebras.

Key words: *Equus*, *Allohippus*, *Plesippus*, palaeontology, molecular biology

### Introduction

A horizontal plane on which modern species are placed according to their resemblances is a simple way to illustrate inferred relations between them. We could go down in time and look at older and older planes. Eventually, by piling up these sections in time we could reconstruct a whole “tree”. For the moment, the “trees” are represented only on a vertical plane, not in three dimensions: complex resemblances cannot be illustrated. Let us, however, bring both kinds of representations together.

Figure 1–1 is the representation of the affinities given by BOURDELLE (1944) of extant species and subspecies of *Equus*. It is based on all his observations and anatomical studies (BOURDELLE 1934, 1936, 1941) including for instance dissections of the digestive system. BOURDELLE plotted separately each species or subspecies according to their closeness to two opposed morphological poles: Caballines (Cheval sauvage vrai) and Asses (Ane sauvage vrai). *E. quagga* (Couaggas) and *E. burchelli* (z. de Burchell, z. de Chapman, z. de Bohm, z. de Grant) are also known as Plains zebras. *E. zebra* (z. de Hartmann, z. vrai) are also known as Mountain zebras. *E. kiang* is sometimes considered as distinct from *E. hemionus* (Hémippe, Hémione, Onagres).

Figure 1–2 is a schematic representation of the first factorial plane of a multifactorial analysis of correspondence of skulls (EISENMANN & TURLOT 1978). In that study the domestic *E. caballus* and the wild *E. przewalskii* plot together (C+P) as well as *E. hemionus* and *E. kiang* (H+K), the wild *E. africanus* and the domestic *E. asinus* (AF+AS), and *E. burchelli* and *E. quagga* (B+Q), though *E. quagga* is also closer to Caballines. The similarity of these representations is striking. Both are circular. In both, Hemiones – justifying their very name of “Half-Asses” – are placed between Caballines and Asses. In both, the order in which the three main groups of Zebras (Mountain zebras, Plains zebras, Grevy’s zebras) are placed between Asses and Caballines is the same.

To what extent the evident morphological relations reflect phylogeny is another matter. HENNIG’S (1966) approach is certainly useful at high systematic levels. But at low levels like species groups, polarities of characters and dichotomies are seldom evident. Even at a generic level, it is only recently that one single apomorphy could be documented for the modern *Equus* genus to distinguish it from the Pliocene *Plesippus* and *Allohippus* genera (EISENMANN & BAYLAC 2000). Many trees based on anatomical observations of extant and fossil equids have been proposed (for

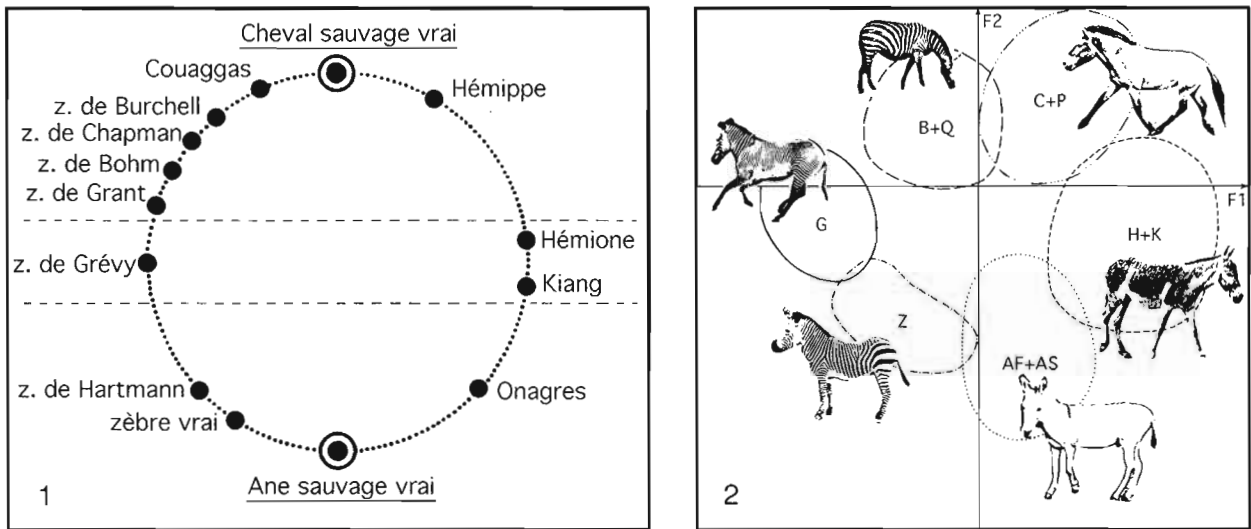


Fig. 1: Apparent resemblances of extant species of *Equus*. 1. According to BOURDELLE (1944). 2. According to EISENMANN & TURLLOT (1978).

instance AZZAROLI 1995, BENNETT 1980, EISENMANN 1979, KUZMINA 1997). Most imply an alleged descent of modern *Equus* from *Plesippus* – the latter considered only as a subgenus of *Equus*. The molecular approach brings new insights.

### Molecular biology

Figure 2 includes the current biomolecular ideas (OAKENFULL et al. 2000) about the time and order of differentiation of extant species. The molecular clock was set at 0.7 Ma – probable date (GERAADS et al. 1986) of emergence of the first fossil resembling Plains zebra (EISENMANN 1980) – the Algerian *E. mauritanicus* of Tighennif. Using this calibration point, the common ancestor of extant *Equus* appeared about 2.3 Ma ago, and the common ancestor of Hemiones, Asses and Zebras between 2.19 and 1.62 Ma ago. Later on emerged Hemiones, Asses, Grevy's zebras, Plain's zebras and Mountain zebras. It is remarkable that the proposed order is in accordance with the geography: NE to SW. OAKENFULL et al. (2000: 348) point, however, that the branching order of Hemiones, Asses and Zebras lacks in resolution. According to them, the single certain point is the early divergence of the Caballine group from the common ancestor of other *Equus*. This happened between 2.19 and 1.62 Ma.

### Molecular biology and Palaeontology of extant species

The implications of the biomolecular model for a palaeontological approach are that beginning at 2.19 Ma and at least at 1.6 Ma, we could be able to recognize Caballines and a number of "Other *Equus*" without distinction; at 1 Ma – Caballines, Hemiones, and "Other *Equus*". The

"Other *Equus*" may be ancestors of extant species or fossil species, which have not survived. We may now compare anatomical, palaeontological and molecular studies (fig. 2) and see how they fit together.

1. The first modern *Equus* is not 3.4 Ma or even earlier, as was supposed when *Plesippus* was included in *Equus*. This is in agreement with craniology (EISENMANN & BAYLAC 2000).

2. The first modern *Equus* is at the most 2.3 Ma. A skull (IVCM 2673) dated to about 2 Ma was found at Anza Borrego (California) and referred to *Plesippus* (DOWNS & MILLER 1994). Actually, its basicranial proportions show that it belongs to modern *Equus* (fig. 3). This is a second point of agreement.

3. Between 2.19 and 1.62 Ma there is a separation between the Caballine line and the common ancestor of other extant species. Judging from the Palatal index (EISENMANN 2006), the Anza Borrego skull is not clearly a Caballine (fig. 4). Moreover, the upper and lower cheek teeth are not caballine at all (Plate I–1, 6). The earliest caballine species is the North-American *E. scotti* (Rock Creek, Texas) and one of the earliest skulls is that from Ulakhan Sular, Adycha, North-Eastern Siberia (EISENMANN 2006). Both are probably about 0.7 Ma. A skull found on the Iana river, chosen as lectotype of *E. nordostensis* by LAZAREV (1980), actually belongs to the same species. In Europe the first evidence of a Caballine is at Mosbach, i.e. at 0.5 Ma (MAUL et al. 2000). In Israel, at Gesher Benot Ya'akov, Middle Pleistocene (GOREN-INBAR et al. 2004), a lower premolar looks caballine. So does a M/3 in the Middle Pleistocene of Ain Maarouf, Algeria (GERAADS & AMANI 1997). In the Late Pleistocene of Rabat, Morocco (VANDERMEERSCH 1994), a Caballine is most probably represented by two or three fragmentary skulls (MOC 151 and 152, Laboratoire de Paléontologie, Paris). ENNOUCHI (1951, 1953a) tentatively referred them (plus another specimen) to *E. mauritanicus* but the proportions of the



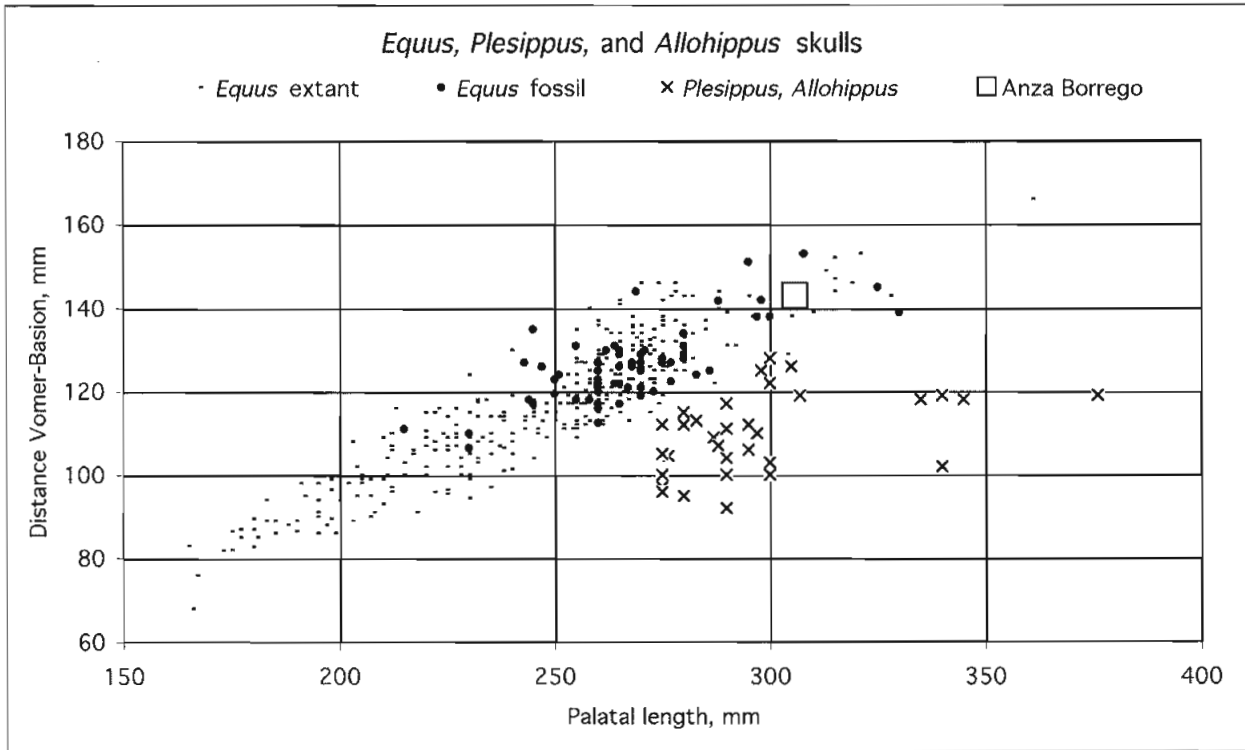


Fig. 3: Scatter diagram of two basicranial measurements. The palatal length includes the muzzle.

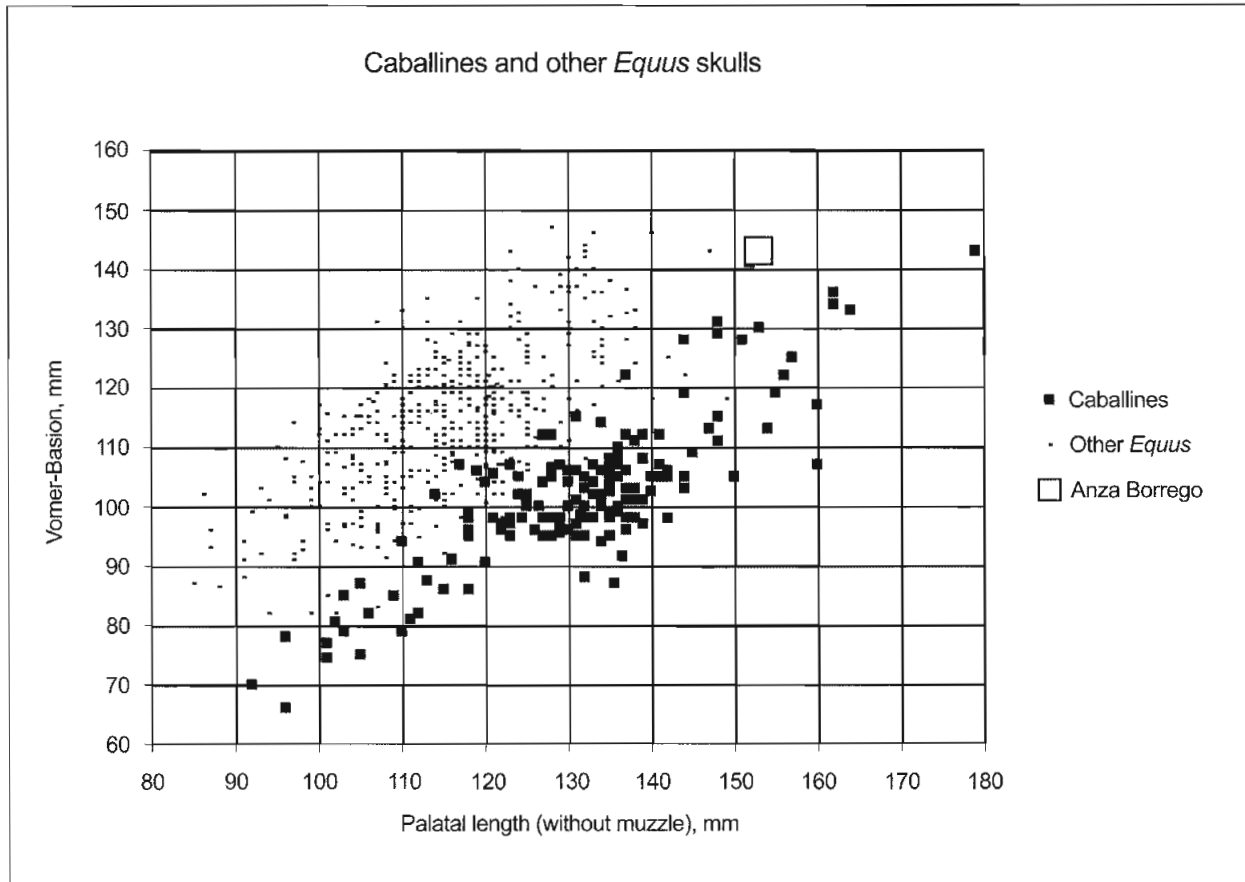


Fig. 4: Scatter diagram of two basicranial measurements.

Fig. 5: Ratio diagram of skull measurements. P2/orb = distance between anterior borders of orbit and P2/. 13 = frontal width. 14 = bizygomatic width. 15 = cranial width. 34 = width of post-orbital constriction. 21 = orbital antero-posterior diameter. 22 = orbital dorso-ventral diameter. 26 = facial height between P4 and M1. 27 = facial height behind M3.

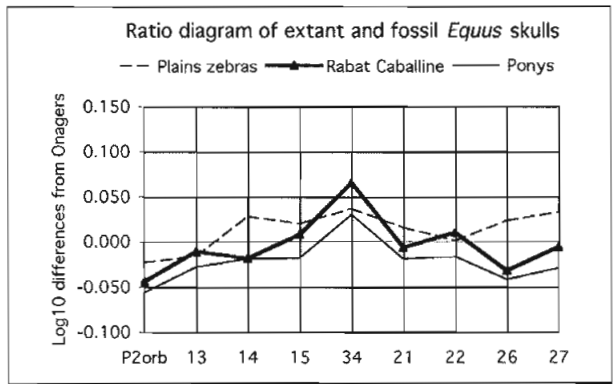
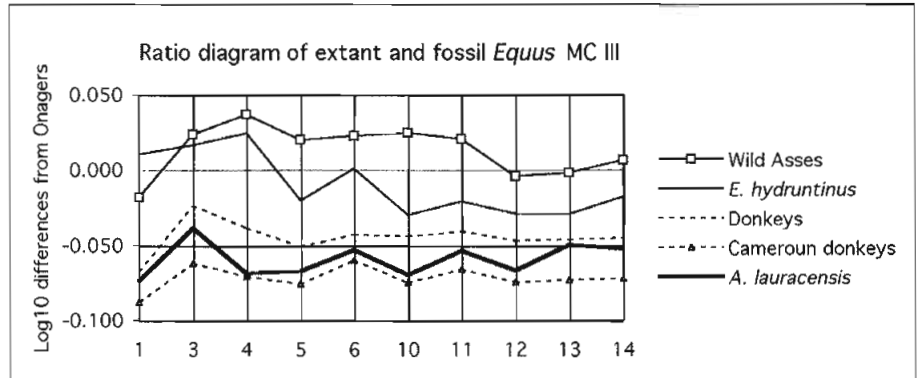


Fig. 6: Ratio diagram of third metacarpals (MC III). 1 = greatest length. 3 = mid-shaft width. 4 = midshaft depth. 5 = proximal articular width. 6 = proximal articular depth. 10 = distal supra-articular width. 11 = distal articular width. 12 = distal articular depth. 13 = distal minimal depth of medial condyle. 14 = distal maximal depth of medial condyle.



species, *E. capensis* (fig. 7), which certainly belongs to a kind of Plains Zebra (EISENMANN 2000, EISENMANN & KUZNETSOVA 2004).

8. Mountain Zebras would be the last to diverge, shortly after. There is scanty evidence (a few limb bones) in South Africa's Late Pleistocene (Black Earth Cave 3).

To summarize: according to palaeontological observations, the first fossil that can be attributed to one of the extant species is not a Caballine but a Hemione (Tologoj). At about the same time come Caballines and Plains Zebras. Recognizable Asses, Grevy's Zebras, and Mountain Zebras appear very late in the palaeontological record.

Nonetheless, during the Early and Middle Pleistocene, there were numerous fossil species which were certainly or presumably belonging to *Equus*. Some of them were related to extant forms, while some were not. We will begin with a brief review of the first.

### Middle and Late Pleistocene *Equus* possibly related to Asses (fig. 7)

#### 1. *Equus graziosii*

Described from the Late Pleistocene of Maspino, Italy, by AZZAROLI (1979), *E. graziosii* is represented by most of a skull, which the author referred to an Ass. The skull shows a mixture of *E. grevyi* and Ass characters (fig. 8).

The upper cheek teeth (fig. 9–1) resemble those of Asses (fig. 9–4).

#### 2. *Equus melkiensis* and *E. cf. melkiensis*

Described from the Aterian (Late Pleistocene) of Allobroges, Algeria (BAGTACHE et al. 1984), *E. melkiensis* is represented by a few teeth and metapodials. More or less similar metapodials (fig. 10–12) and/or teeth were found in the Late Pleistocene of Maghreb: in Algeria at Filfila (fig. 9–2) by GINSBURG et al. (1968) and Guyotville (SOUVILLE 1958), in Morocco at Bou-Knabel (fig. 9–3) by ENNOUCHI (1953b) and Mugharet el Alya, and in Tanger.

The earliest possible ancestors of *E. melkiensis* (*E. cf. melkiensis*) in Africa are found at Tighennif (a few metapodials somewhat longer and deeper than those of *E. mauritanicus*), perhaps at Aïn Maarouf (GERAADS & AMANI 1997), Algeria, and at Sidi Abderrhaman, Morocco.

Figures 11 and 12 show that the metapodials of *E. melkiensis* do not resemble those of extant Wild Asses: they are much more robust and have deeper proximal epiphyses. At Tighennif, a third metacarpal (Ter 404) has the proportions of *E. melkiensis* (fig. 11) while another third metatarsal resembles more those of Wild Asses (fig. 12). At Aïn Maarouf, a metatarsal seems to have a deep proximal epiphysis like *E. melkiensis*, but the upper cheek teeth are not typical.

Upper cheek teeth resembling *E. melkiensis* were found at Lakhuti II, Tadjikistan (fig. 13–1), at Oumm Qatafa,

	ASS ? small form	ASS ? <i>E. graziosii</i>	ASS ? <i>E. melkiensis</i>	PLAINS <i>E. mauritanicus</i>	ZEBRAS <i>E. capensis</i>	? <i>E. lylei</i>
0		<b>Maspino</b>	Tchad Maghreb Yemen		Equus Cave	Equus Cave
1						
2					Florisbad	Florisbad
3			Oumm Qatafa			
4						
0.5 My			Sidi Abderrhaman		<b>Elandsfontein</b>	
6	Tihodaïne					
7			Aïn Maarouf ? Tighennif Lakhuti II ?	Tihodaïne ? Tighennif		
8						

Fig. 7: Fossil species related to extant Plains Zebras and possibly related to extant Asses. In bold and underlined, localities having yielded skulls.

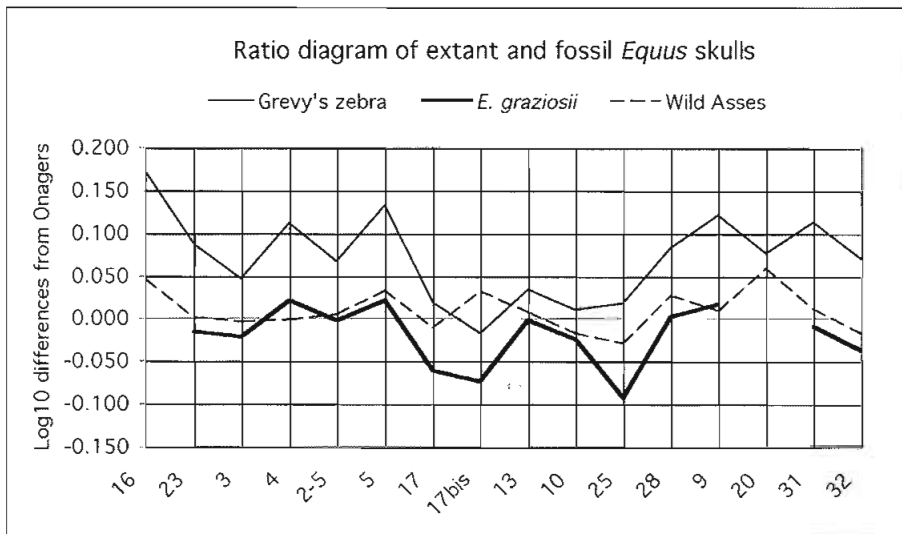


Fig. 8: Ratio diagram of skull measurements. 16 = Greatest width of the supra-occipital tuberosity. 23 = anterior ocular line. 3 = vomerine length. 4 = post-vomerine length. 2-5 = palatal length (without the muzzle). 5 = muzzle length. 17 = muzzle width behind the I3/. 17bis = minimal muzzle width (on the premaxillary ridges). 13 = frontal width. 10 = choanal width. 25 = facial height in front of P2/. 28 = cranial height behind the orbit. 9 = choanal length. 20 = external auditory meatus height. 31 = length of naso-incisival notch. 32 = check length.

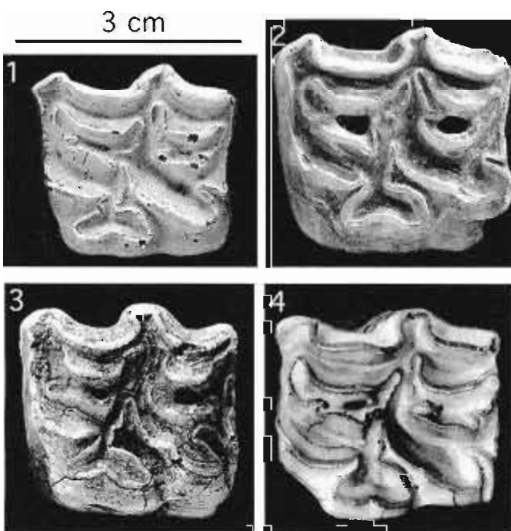


Fig. 9: Upper premolars. 1. *E. graziosii*, near Arezzo, IGF 192V, P4/. 2. *E. melkiensis*, Filfila, P3/ or P4/. 3. *E. melkiensis*, Sidi Bouknabel MOC 153, P3/ or P4/. 4. Poitou donkey (Ouragan 1), P3/.

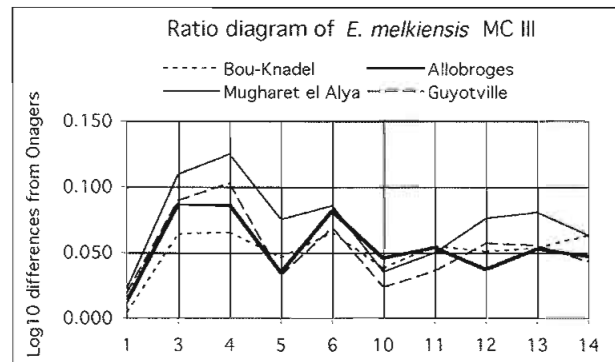


Fig. 10: Ratio diagram of third metacarpals. See fig. 6.

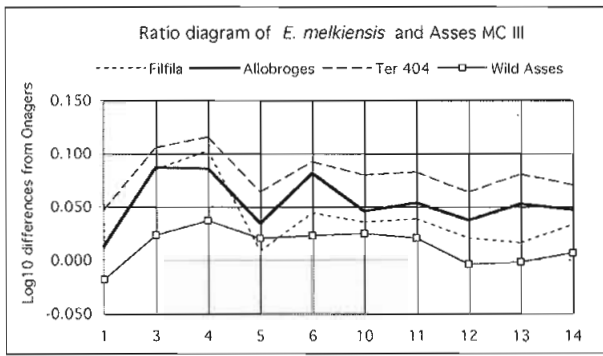


Fig. 11: Ratio diagram of third metacarpals. See fig. 6.

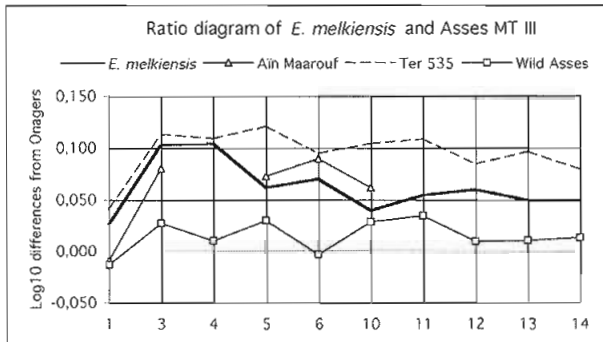


Fig. 12: Ratio diagram of third metatarsals (MT III). See fig. 6, but the proximal depth is intermediate between the articular and the maximal.

Israel (fig. 13–2) and in Yemen (a well fossilized upper premolar but of unknown age) (fig. 13–3). Lakhuti II is believed to be just below the Brunhes-Matuyama boundary (SOTNIKOVA 1989), Oumm Qatafa is referred to Isotope Stage 8 (TCHERNOV 1998).

### 3. Other *Equus*

At Gesher Benot Ya`akov (Jordan Bank and Area C), a well preserved first phalanx resembles those of *E. africanus*, and some fragments of a MT III also remind those of extant Wild Asses. The cheek teeth are compatible with a primitive Ass.

A few bones of a small and very slender *Equus* were found in the Middle Pleistocene of Tihodaïne, Algeria (THOMAS 1978). In the same collection, there seems to be a large *Equus*, which may or may not be *E. mauritanicus*.

Other enigmatic specimens are represented in the Middle Pleistocene of South Africa (*E. lylei* discussed by BRINK 1994), as well as in the Late Pleistocene of Ain Metterchem (Tunisia) and Salé (Morocco).

## Early and Middle Pleistocene species with characteristic teeth: “Sussemiones”

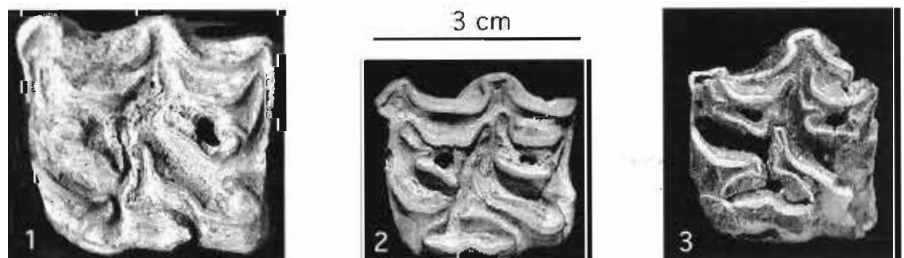
The first question is whether these species belong to *Equus* or to *Allohippus*. Until two skulls from Ceysaguet, which is dated to 1.2 Ma (AOUADI 1999), were described, both *Allohippus* and *Plesippus* could be considered already extinct at that time. The complete and well preserved specimen n°6238, however, is attributable to *Allohippus*, although being a less than 1 year old individual. If the specimen is properly dated, *Equus* and *Allohippus* coexisted for almost 1 Ma (fig. 14). Since the two taxa can be distinguished only from their skulls, most of the species older or about the age of Ceysaguet may belong to either genera. We have thus to rely only on tooth and limb bone resemblances to tell them apart.

Early and Early-Middle Pleistocene equids have been often likened to Zebras, to Asses, or to Hemiones. Many of them, however, exhibit some very special features. For convenience, I’ll call these equids «Sussemiones» because of some resemblances between Süssenborn and Hemiones cheek teeth.

### 1. Lower cheek teeth

On the lower cheek teeth the occurrence of stylids, sometimes isolated, is remarkable. Isolated ectostylids are characteristic of late African hipparions but I have never seen them in extant *Equus*. They do exist, however, at Süssenborn (fig. 15–1), Venta Micena (fig. 15–2), and Akhalkalaki (fig. 15–6, 7) and possibly in Chukochya and Old Crow, Yukon (fig. 15–4, 5). Plis protostylids on P/2 are characteristic of extant Grevy’s zebras (EISENMANN 1976). They are present at Akhalkalaki and frequent at Venta Micena (Plate I–2). Plis protostylids on P/3-M/2 may also be observed in extant species but they are seldom as developed as at Akhalkalaki (fig. 15–8) where they suggested the name “*E. hipparionoides*” (VEKUA 1962, 1986). In Chukochya and Yukon (HARRINGTON 1989), hypostylids may be extremely developed (fig. 15–4, fig. 17–1, 2, 4) or even isolated on M/3 (fig. 15-3).

Fig. 13: Upper premolars of *E. cf. melkiensis*. 1. Lakhuti II (Loc. 67) PIN 3848–281, P4/. 2. Oumm Qatafa, OK 5, P3/ or P4/. 3. Yemen, P3/ or P4/.



	<i>EQUUS</i>				<i>ALLOHIPPIUS</i>	<i>PLESIPPUS</i>
	"SUSSEMIONES"		"ZEBRASSES"			
	<i>cf. E. coliemensis</i>	<i>cf. E. granatensis</i>				
0.5 My						
	Süssenborn	Cullar de Baza Süssenborn Trimingham		Süssenborn ?		
		Huescar	Gesher Benot Y.			
	Cueva Victoria Akhalkalaki Gomboré II	Cueva Victoria Akhalkalaki	<u>Apollonia</u>			
1 My	<u>Chukochoya</u>		Nalaikha <i>E. sp. B</i>	<u>Nalaikha</u>		
					<u>Ceyssaguet</u>	
					Pirro	
					Sainzelles	
					Saint Prest	
					Selvella	
	Garba IV					
1.5 My		Venta Micena				
					Loc D	
					<u>Koobi Fora</u>	
2 My	Alaska	Arizona	<u>Anza Borrego</u>		<u>Senèze</u>	
					<u>Saint-Vallier</u>	
						<u>Bajiazui</u>
					Huelago	Huelago ?
2.5 My					El Rincon	Loc 32
						<u>Longdan</u>

Fig. 14: Fossils of *Equus*, *Allohippus* and *Plesippus*. In bold and underlined, localities having yielded skulls.

The shape of the double knot in many lower premolars resembles the extreme pattern (fig. 16-1) exhibited by a few extant Eastern Hemionines (*E. hemionus* and *E. kiang*): the metaconid is elongated (fig. 16-3), sometimes bilobated (fig. 16-2, 4, 6), the lingual valley is shallow, at times nearly absent (fig. 16-5, plate I-3, 5).

Unlike Hemionines, another particularity is the frequency of very deep vestibular valleys, on molars (fig. 16-5, 8,

9; MUSIL 1969: plate 37-2) and even on some premolars (fig. 16-7, plate I-4). The depth of the vestibular valley, however, is very variable: associated teeth may have very deep and very shallow valleys (fig. 17-3). Both features are uncommon in extant species.

All these patterns are radically different from *Allohippus*. The lower cheek tooth morphology of *Allohippus* is very stable: metaconid and metastylid are equally devel-



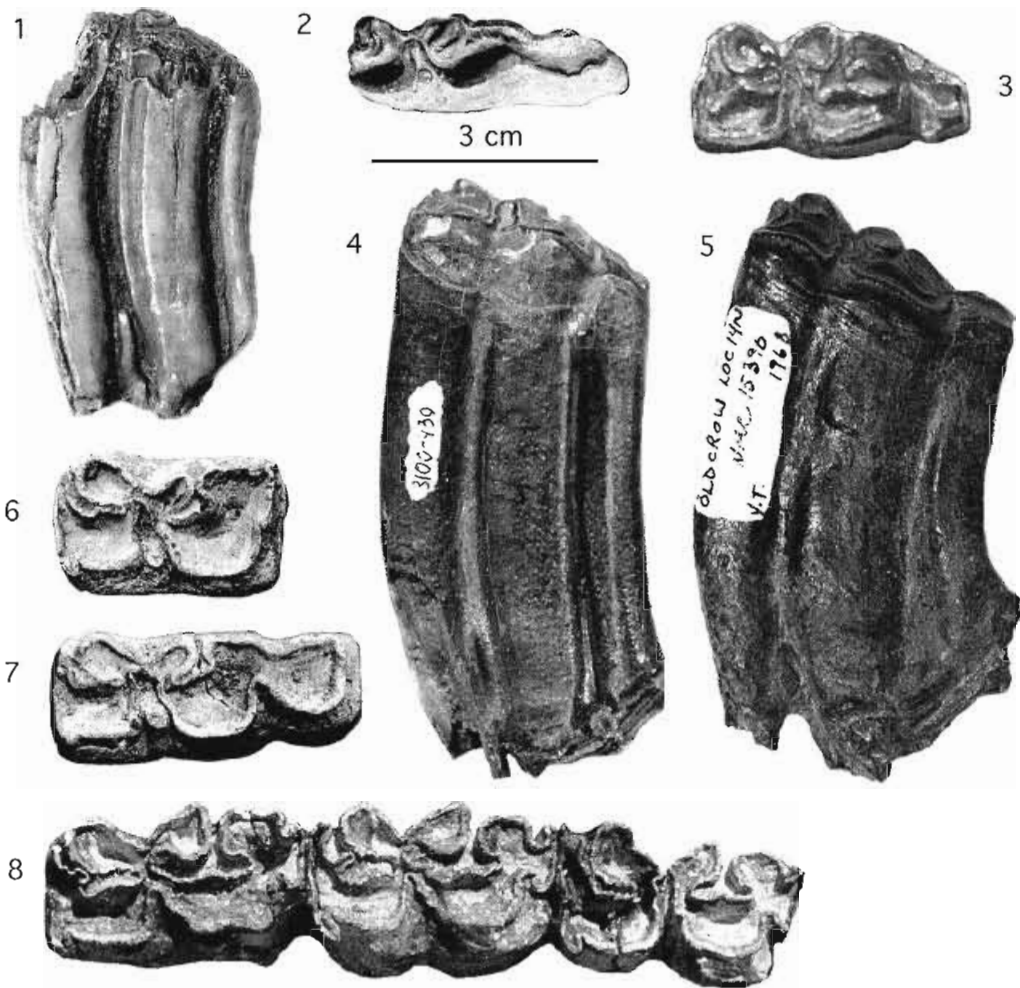


Fig. 15: Lower cheek teeth with stylids. 1. *E. suessenbornensis*, Süssenborn E 23, M/3. 2. *E. granatensis*, Venta Micena 84 C3 J9 16, M/3. 3. *E. verae* type, Loc. 21 835–123, M/3. 4. *E. verae*, Loc 22 3341–30, M/3. 5. *E. verae*, Old Crow Loc 14N NMC 15390, M/3. 6–7. *E. cf. suessenbornensis*, Akhalkalaki 4, associated P/4 and M/3. 8. *E. cf. suessenbornensis*, Akhalkalaki 99, P/3–M/1.

oped, both rounded and separated by a well marked and pointed lingual groove. The shape is the same from old representatives (Saint-Vallier) up to more recent ones (Pirro, Ceysaguet). There are no “Hemione-like” double knots, nor are there stylids.

## 2. Upper cheek teeth

In the upper cheek teeth, the plis caballins are very unusual. They may be multiple (plate II–13, 17), with a very large base (plate II–7, 9, 10, 15, 16, 18), club-shaped (plate II–6). Such morphologies are unknown in extant species as well as in *Allohippus*. They are frequent in Alaska, Chukochya, and at Süssenborn, but they occur even in Ethiopia, at Melka Kunturé (plate II–9, 10). The enamel is often very plicated and the postprotoconal valley may be very deep (plate II–15, 17, 18). However, plicated enamel and/or long thin plis caballins and deep postprotoconal valleys are known also at Chagny, Senèze, Khapry, and Livenzovka (plate II–8, 12, 14) so that the distinction between *Allohippus* and *Equus* is not as clear as in the lower cheek teeth.

Another peculiarity, also shared with some *Allohippus*, is the occurrence of extremely short protocones. They may be seen at Süssenborn (plate II–2, 11, 18), at Akhalkalaki in *E. hipparionoides* (plate II–6), at Venta Micena (plate II–4, 5), Fuensanta (plate II–3), but also at Livenzovka (plate II–1, 12). The shortness is independent of wear. In recent species, only *E. hydruntinus* has such small protocones.

## 3. Characterization and distribution (fig. 14)

The hemione pattern and the stylids shared by *E. coliemensis* and *E. granatensis* suggest a common origin of “Sussemiones” inside an *Equus* branch which did not yield extant survivors. The differences in size and morphology in the upper and lower cheek teeth clearly indicate that they belong to at least two species groups.

### – *Equus coliemensis* group

The skull, type of *E. coliemensis* (LAZAREV 1980) was found in Kolyma and is believed to be late Early Pleis-