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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

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Author's address: Dr. Véra Eisenmann, MNHN, Département Histoire de la Terre, CP 38, UMR 5143 du CNRS, Paléobiodiversité et Paléoenvironnements, 8 rue Buffon, 75005 Paris, <vera@mnhn.fr>

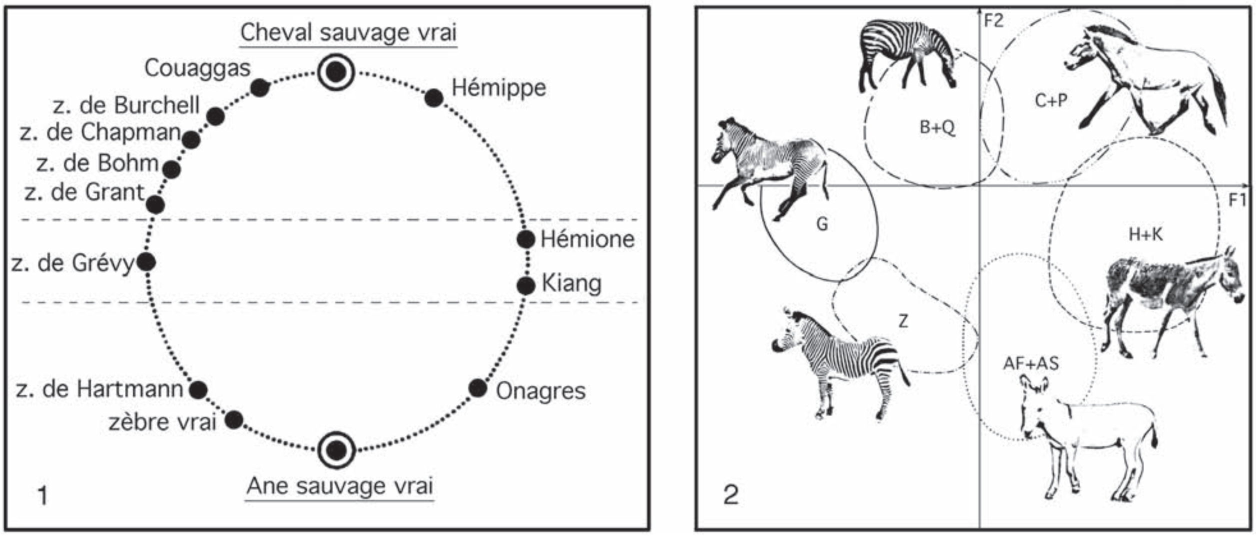

Fig. 1: Apparent resemblances of extant species of *Equus*. 1. According to Bourdelle (1944). 2. According to Eisenmann & Turlot (1978).

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, Midde Pleistocene (Goren-Inbar et al. 2004), a lower premolar looks caballine. So does a M/3 in the Middle Pleistocene of Aïn 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

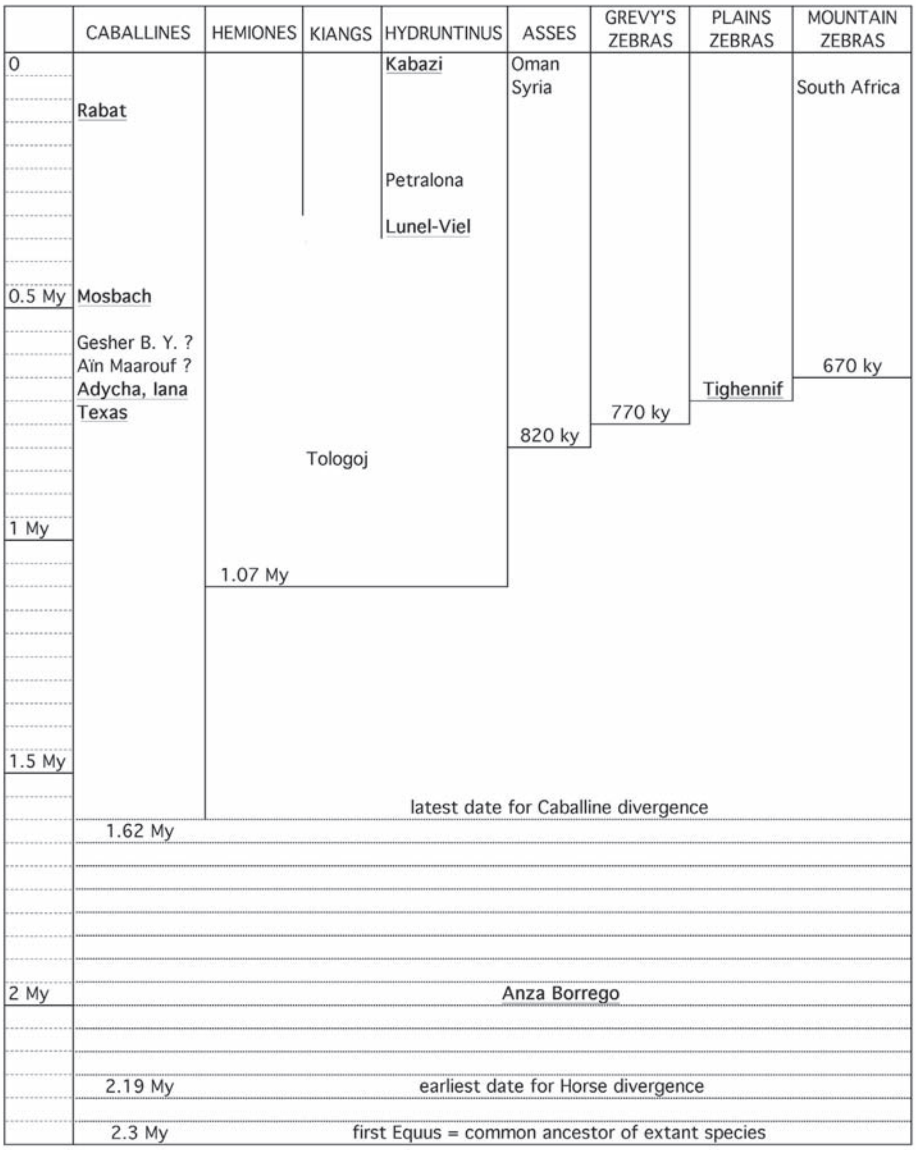

Fig. 2: Confrontation of biomolecular interpretations and palaeontological data. In bold and underlined, localities having yielded skulls.

crania preserved in Paris are rather Caballine than Plains Zebra-like (fig. 5). Thus, we face a notable discrepancy between the molecular and the palaeontological evidence for first Caballines: an over 1Ma gap lies in between.

4. At about 1 Ma, Hemiones have diverged from Asses and Zebras. At Tologoj, in the late Early Pleistocene (Vogt et al. 1995), there is probably a Hemione, judging by lower cheek tooth pattern and metapodial proportions. There is no skull.

We know now that *E. hydruntinus* belongs to the Hemione group (Burke et al. 2003). The earliest fossil was found at Lunel-Viel, at about 400 ka (Bonifay 1991). That is consistent with a possible separation of *E. kiang* and *E. hemionus* at 310 ka (Oakenfull et al. 2000). *E. petralonensis* (Tsoukala 1991) is closely related to *E. hydruntinus*.

5. Asses may have been the next to diverge. However, the first Asses really resembling the extant ones are poorly documented and of Holocene age: a metatarsal from Tell Muraibit, Syria (Ducos 1986) and another one from Maysar, Oman (Uerpmann 1991).

A very well preserved and fossilized metacarpal was described by Astre (1948) as a new species of Ass, *E. lauracensis*. It is indeed most similar to the metacarpals I have collected in Cameroun - remains of Donkeys fed to Lions in a Zoological Park. It does not resemble *E. hydruntinus* (fig. 6).

6. The divergence of Grevy's zebra shortly after the Asses is not documented in the palaeontological record. To my knowledge, fossils recognizable beyond doubt as Grevy's Zebras have not been described at all.

7. Since the date of 700 ka for *E. mauritanicus* from Tighennif is the calibration point, the agreement between molecular and palaeontological evidence is implicit. In the Middle Pleistocene of South Africa there is a larger

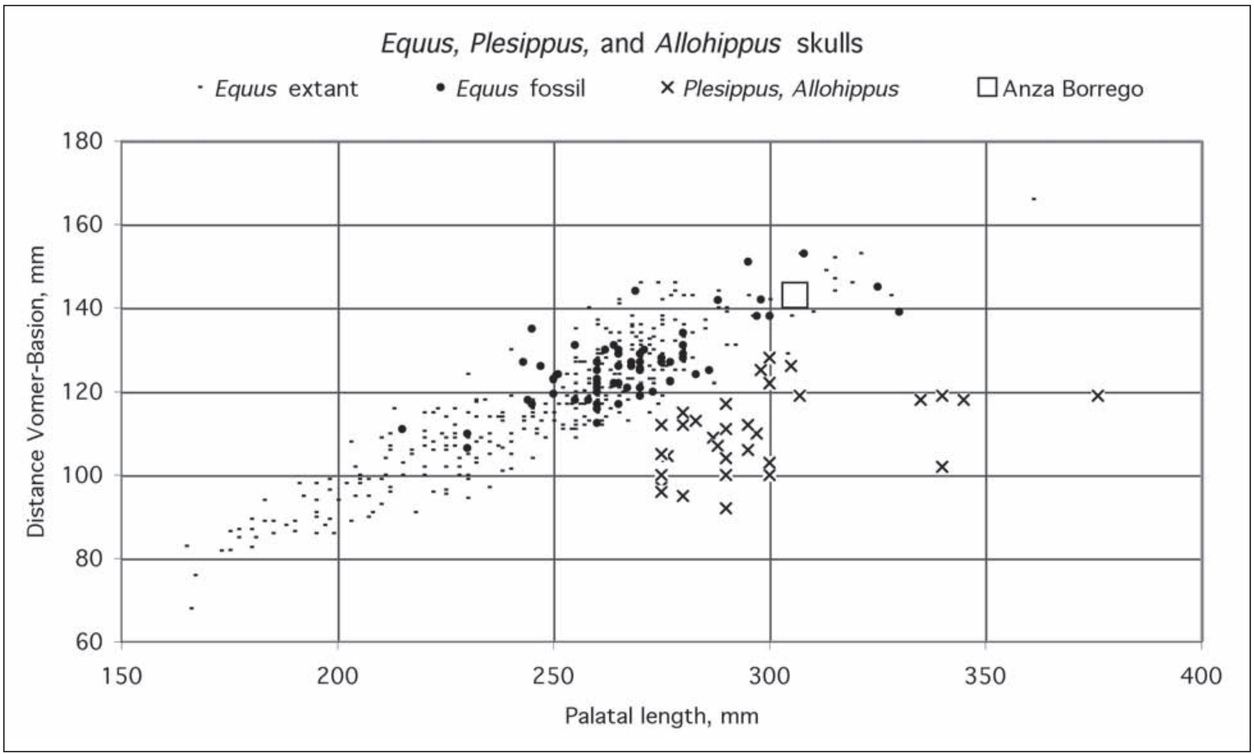

Fig. 3: Scatter diagram of two basicranial measurements. The palatal length includes the muzzle.

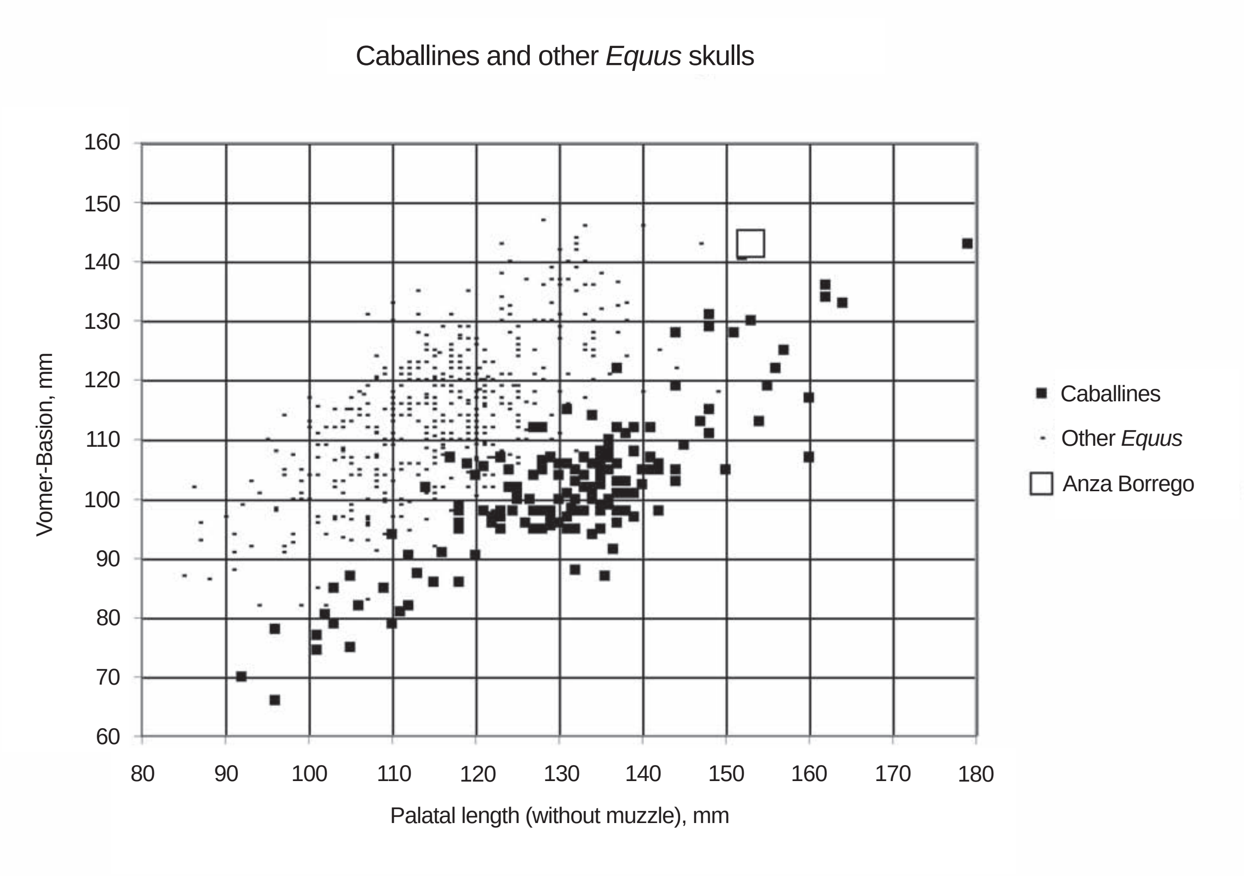

Fig. 4: Scatter diagram of two basicranial measurements.

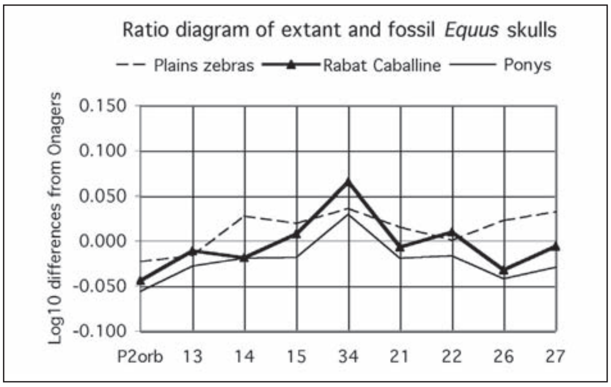

Fig. 5: Ratio diagram of skull measurements. P2/orb = distance between anterior borders of orbit and P2/. 13 = frontal width. 14 = bizygomatic width. 15 = cranial width. 34 = width of post-orbital constriction. 21 = orbital antero-posterior diameter. 22 = orbital dorso-ventral diameter. 26 = facial height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

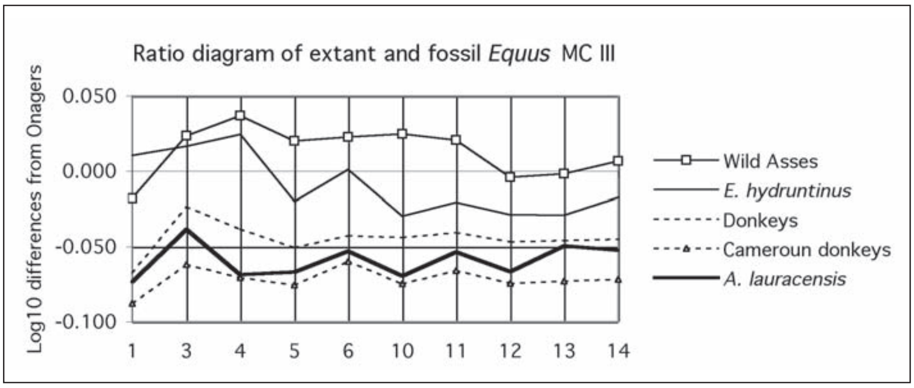

Fig. 6: Ratio diagram of third metacarpals (MC III). 1 = greatest length. 3 = mid-shaft width. 4 = midishaft depth. 5 = proximal articular width. 6 = proximal articular depth. 10 = distal supra-articular width. 11 = distal articular width. 12 = distal articular depth. 13 = distal minimal depth of medial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

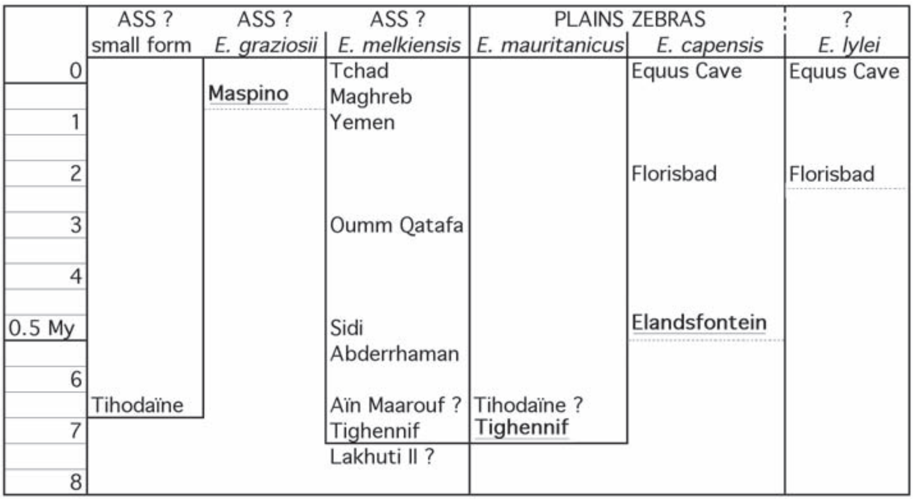

Fig. 7: Fossil species related to extant Plains Zebras and possibly related to extant Asses. In bold and underlined, localities having yielded skulls.

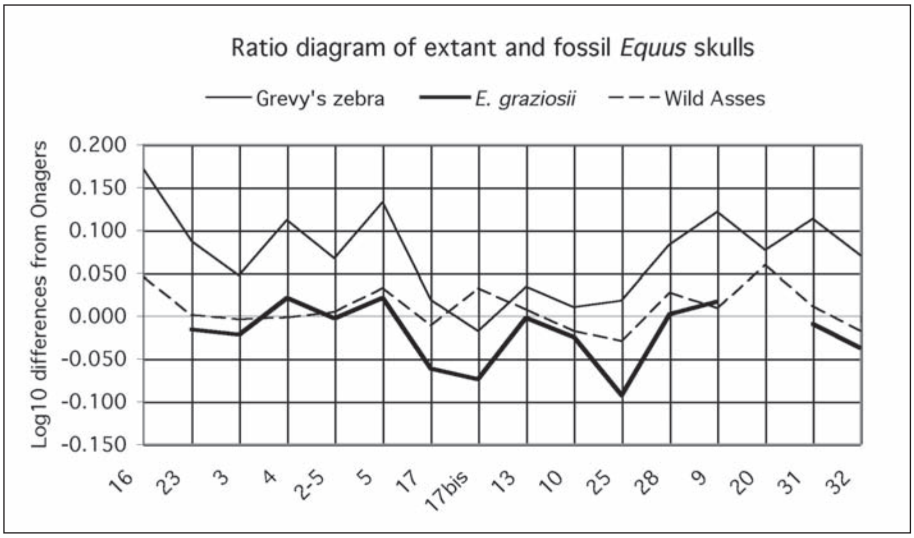

Fig. 8: Ratio diagram of skull measurements. 16 = Greatest width of the supra-occipital tuberosity. 23 = anterior ocular line. 3 = vomerine length. 4 = post-vomerine length. 2–5 = palatal length (without the muzzle). 5 = muzzle length. 17 = muzzle width behind the I3/. 17bis = minimal muzzle width (on 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 audirory meatus height. 31 = length of naso-incisival notch. 32 = cheek length.

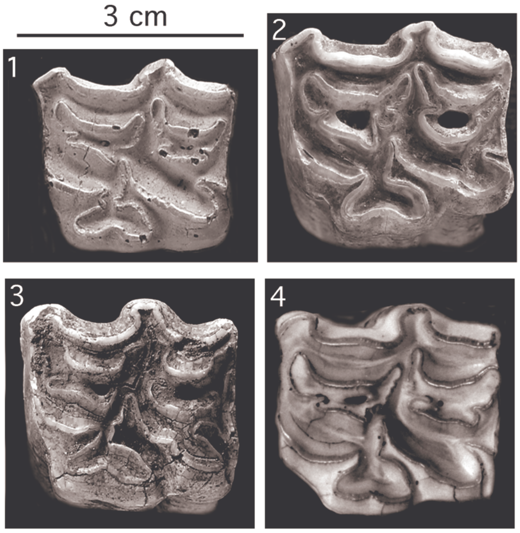

Fig. 9: Upper premolars. 1. *E. graziosii*, near Arezzo, IGF 192V, P4/. 2. *E. melkiensis*, Filfila, P3/ or P4/. 3. *E. melkiensis*, Sidi Bouknabel MOC 153, P3/ or P4/. 4. Poitou donkey (Ouragan 1), P3/.

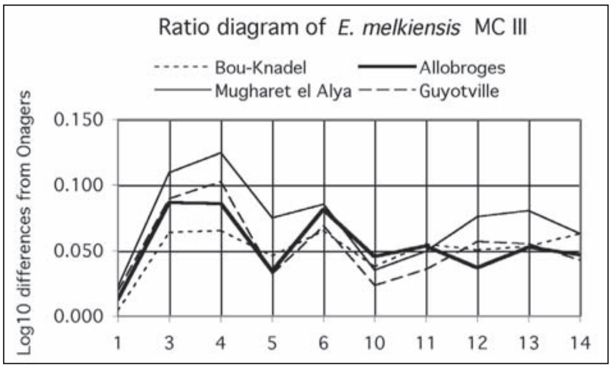

Fig. 10: Ratio diagram of third metacarpals. See fig. 6.

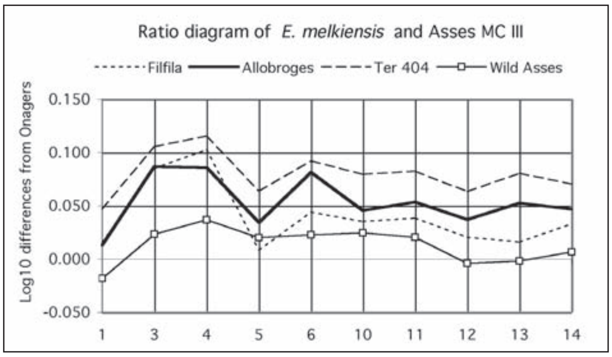

Fig. 11: Ratio diagram of third metacarpals. See fig. 6.

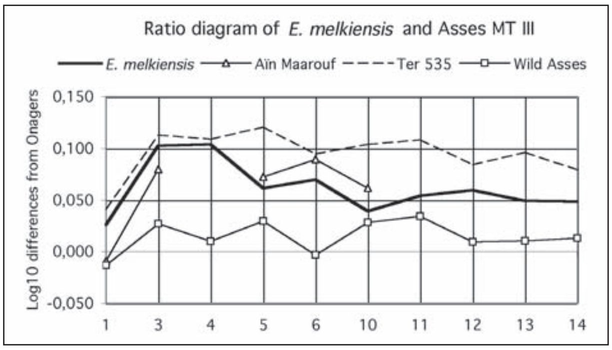

Fig. 12: Ratio diagram of third metatarsals (MT III). See fig. 6, but the proximal depth is intermediate between the articular and the maximal.

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 Aïn 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 Ceyssaguet, 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 Ceyssaguet 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 (Harington 1989), hypostylids may be extremely developed (fig. 15–4, fig. 17–1, 2, 4) or even isolated on M/3 (fig. 15-3).

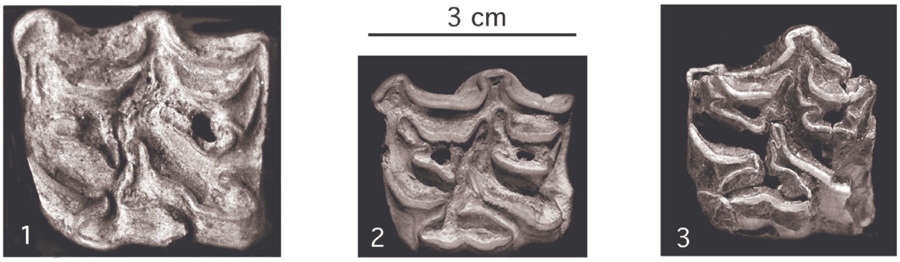

Fig. 13: Upper premolars of *E.* cf. *melkiensis*. 1. Lakhuti II (Loc. 67) PIN 3848–281, P4/. 2. Oumm Qatafa, OK 5, P3/ or P4/. 3. Yemen, P3/ or P4/.

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

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 Hemiones (*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 Hemiones, 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-

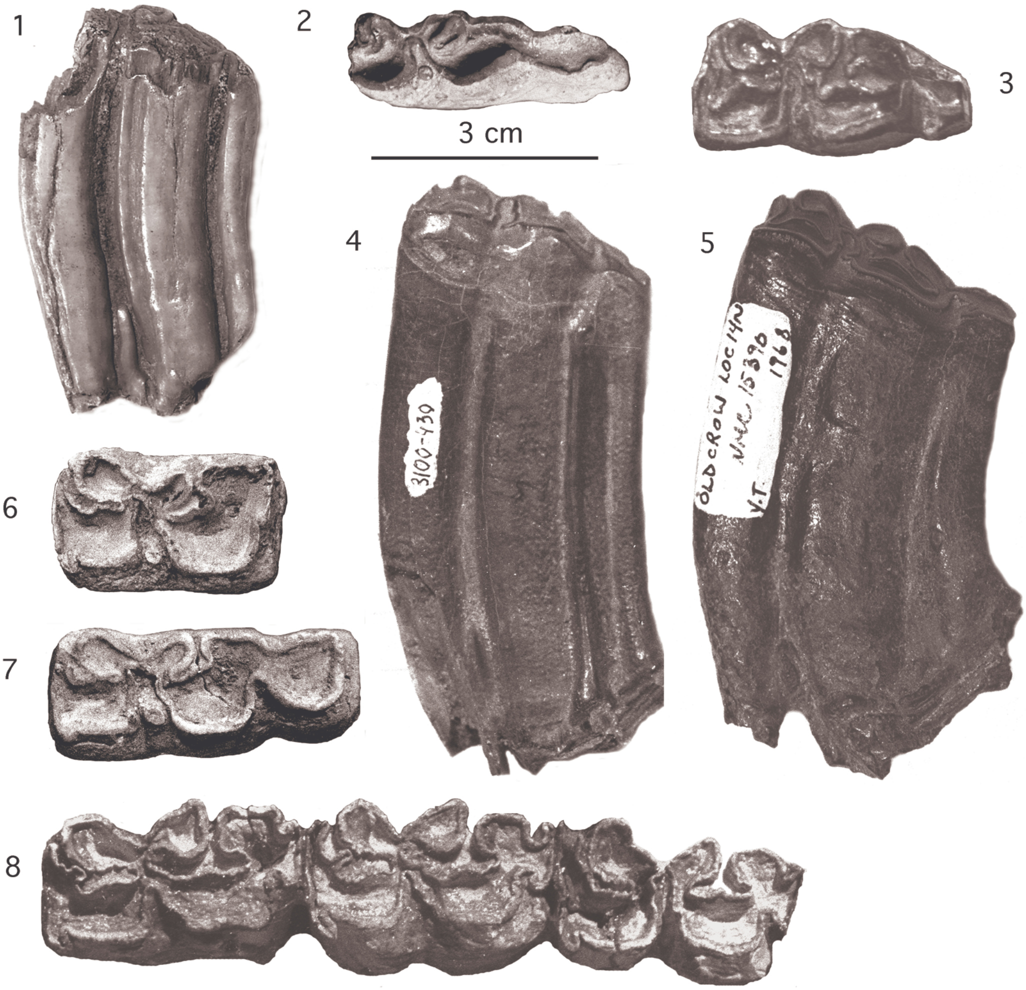

Fig. 15: Lower cheek teeth with stylids. 1. *E. suessenbornensis*, Süssenborn E 23, M/3. 2. *E. granatensis*, Venta Micena 84 C3 J9 16, M/3. 3. *E. verae* type, Loc. 21 835–123, M/3. 4. *E. verae*, Loc 22 3341–30, M/3. 5. *E. verae*, Old Crow Loc 14N NMC 15390, M/3. 6–7. *E.* cf. *suessenbornensis*,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

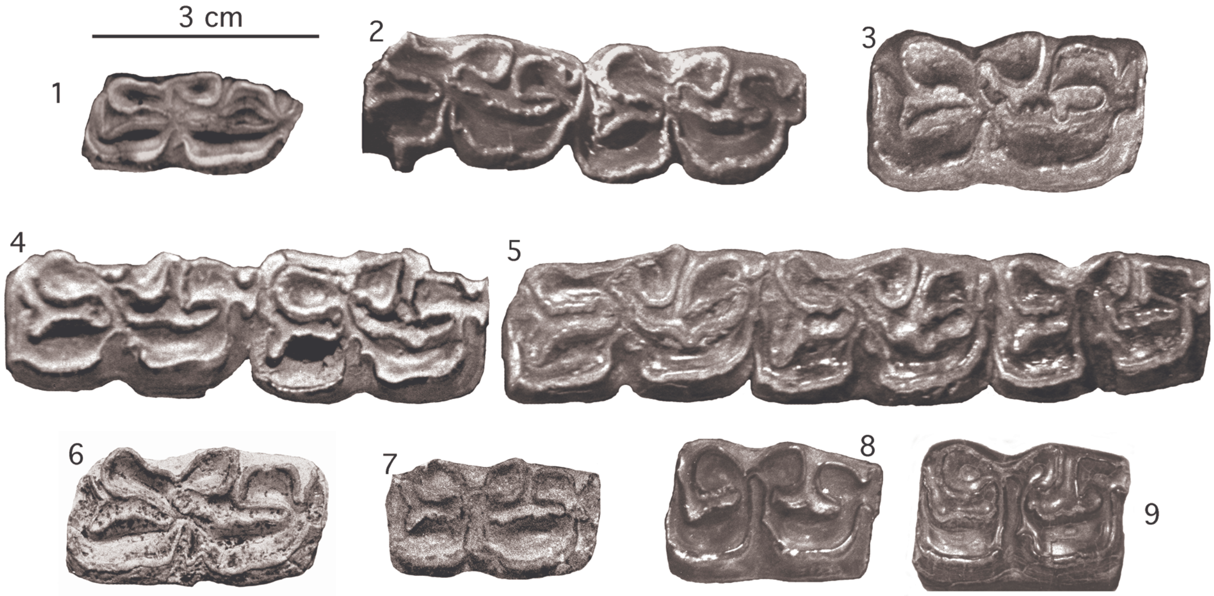

Fig. 16: Lower cheek teeth. 1. *E. kiang*, ZIN 5227, P/3. 2. *E.* cf. *marxi*, Cullar de Baza 15730, P/3–P/4. 3. *Equus* ?, Livenzovka RGU 570, P/3. 4. *E.* cf *verae*, Chukochya 3341–606, P/3-P/4. 5. *Equus sp.*, Krestovka 851–74/8, P/3–M/1. 6. *E. marxi* paratype, Süssenborn 1368, P/4. 7. *E. granatensis*, Venta Micena 3564, P/4. 8. *Equus* ?, Livenzovka RGU 92, M/1. 9. *E. verae*, Old Crow Loc 11A, NMC 17949, M/1.

tocene. Although not perfectly preserved, it most probably belongs to *Equus*. The skull is as large as that of a Grevy's Zebra but its proportions recall those of Hemiones (Eisenmann & Kuznetsova 2004). The upper cheek teeth are plicated and have wide-based plis caballins (plate II–7). There are no associated lower cheek teeth but some were referred to *E. coliemensis* by Lazarev (fig. 17–1). In the lower cheek teeth, the enamel is plicated and the hypostylid very developed on M/3. We may tentatively refer to this group many teeth from Alaska, Yukon, and Chukochya (including *E. verae* Sher 1971, 1987), *E. suessenbornensis* (including Akhalkalaki, Cueva Victoria) and a few teeth from Ethiopia (plate II–9–10). The resemblance with some teeth from Khapry and Livenzovka is striking (plate II–8, 14, 16; fig. 16–8). The metapodials are large and robust.

– *Equus granatensis* group

E. granatensis was described at Venta Micena as a subspecies of *E. stenonis* (Marin 1987). Because no skull has been found, this equid could be possibly attributed to *Allohippus*, for instance to the variety present at Pirro (De Giuli et al. 1987). The upper cheek teeth of the Venta Micena representative have in fact plications and small protocones (plate II–3–5) very similar to those shown by the Pirro specimens. Several characters, however, distinguish it from *Allohippus stenonis* (Eisenmann 1999). In particular, the occurence of stylids and of hemione-like patterns in the lower cheek teeth strongly suggests that *E. granatensis* is indeed an *Equus*. The metapodials are very slender.

To the same group belong *E. hipparionoides* of Akhalkalaki, the very poorly defined *E. altidens*, and the just better defined *E. marxi* of Süssenborn. Teeth and/or metapodials of this group are found in the Forest Beds (Trimingham), and in Spain (Cueva Victoria, Cullar de Baza, Huescar).

Other Early and Middle Pleistocene species: "Zebrasses"

- unformal grouping of fossils sharing Zebra and Ass characters.

1. *E. nalaikhaensis*

Undoubtedly belonging to *Equus*, this Mongolian species exhibits a mosaic of Hemione, Ass, and Grevy's zebra characters (Eisenmann & Kuznetsova 2004).

2. *E. apolloniensis*

Described by Koufos et al. (1997) from Apollonia, Greece, Latest Villafranchian, it is represented by a skull incontestably of *Equus*. The skull is slightly larger than that of *E. nalaikhaensis*, with wider frontals and a shorter snout. The upper and lower cheek teeth could be referred to an Ass. The metapodials, however, are rather robust and resemble *E.* sp. B of Nalaikha.

3. *Equus* sp. of Süssenborn

About 20 upper cheek teeth were found at Süssenborn. They are somewhat smaller than those of *E. suessen-*

Fig. 17: Lower cheek teeth. 1. *E. coliemensis*, Chukochya, IA 1721, P/2–M/1 and M/3, after Lazarev (1980). 2. *E. verae*, Chukochya, PIN 3341–689, M/3. 3. *E. verae*, Chukochya, associated M/1 and M/3, PIN 3100–333. 4. *E. verae*, Old Crow, Loc. 9, NMC 32165, M/3. 5. *Equus sp.*, Dry Mountains loc., Arizona, AMNH 116502, P/2–M/3, after Azzaroli & Voorhies (1993).

bornensis, and morphologically different from both *E. suessenbornensis* and *E. marxi* (fig. 18). Unlike both the latter, the Süssenborn teeth are not very hypsodont. They are not as plicated as the teeth of *E. suessenbornensis*, and their postprotoconal valley is not as deep as in the teeth of *E. marxi*. They often bear two plis on the posterior border of the prefossette, constantly in the same place. The protocone is bilobated. They are rather Zebra-like.

The Süssenborn deposits are about 23 m deep and may cover as much as 100 ka (R.-D. Kahlke and L. Maul, pers. comm.). Climatic changes certainly occurred over this period of time, and the conditions may have changed from humid to dry. The very plicated teeth of *E. suessenbornensis* may be related to a moister period than the poorly plicated ones of *Equus* sp. and of the Hemione-like *E. marxi*. *Equus* sp. might have evolved from *E. suessenbornensis*.

Some lower caballoid cheek teeth have already been illustrated and discussed by Forstén (1986). They are large and could belong to *E. mosbachensis*. There are a few other smaller teeth with the stenonine pattern shared by some Zebras and Asses. Unlike *E. marxi*, the double knot of the premolars is symmetric, rounded, and with a pointed and well marked lingual valley. They may belong to *Equus* sp.

The polymorphy in the small sample of MC III (fig. 19) also indicates the presence of general species. Beside the large and flat specimens (n=3 to 6) referable to *E.*

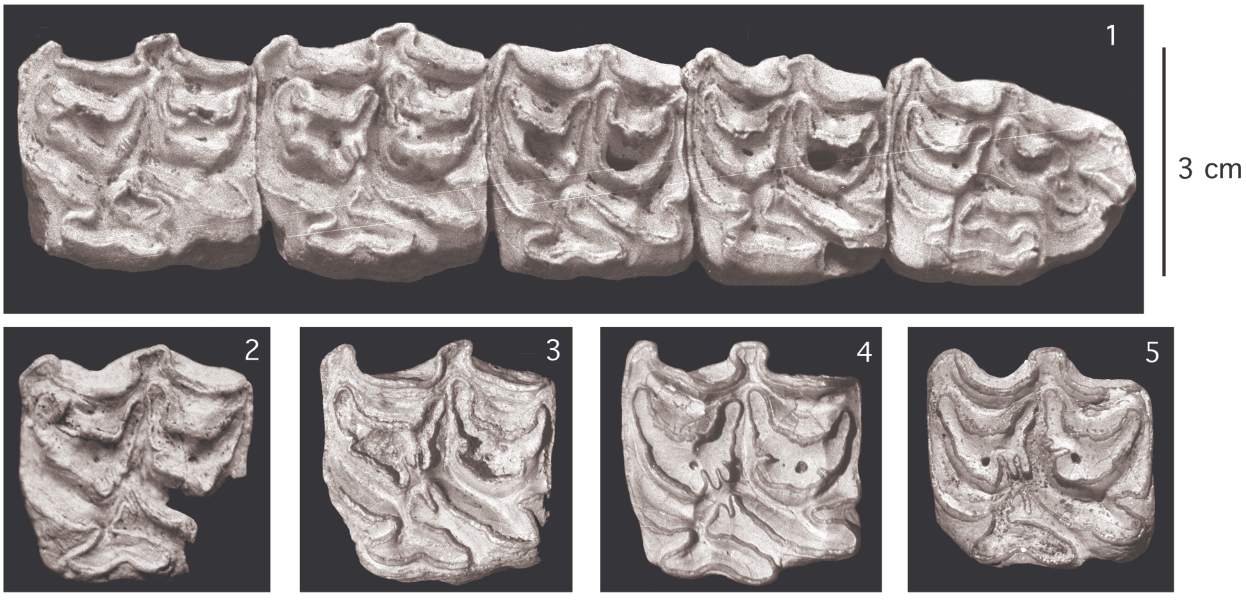

Fig. 18: *Equus sp.*, Süssenborn, Upper cheek teeth. 1. S 9180, P3/–M3/. 2. S 9264, P3/ or P4/. 3. S 9276, P3/ or P4/. 4. S 9265, M1/ or M2/. 5. S 617, M1/ or M2/.

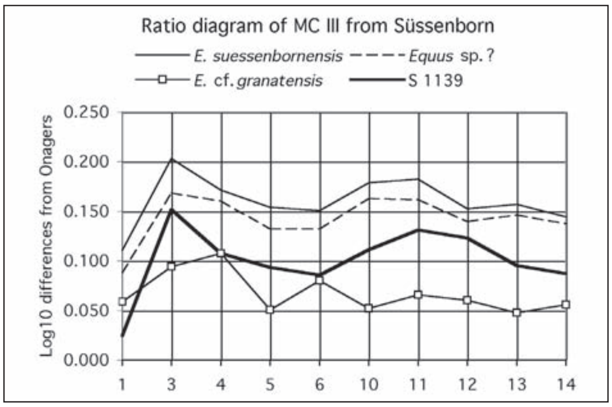

Fig. 19: Ratio diagram of third metacarpals. See fig. 6.

suessenbornensis and the much smaller, slender specimens referable to *E.* cf. *granatensis* (two well preserved), there are two other morphs. The first (n=2 to 4) is intermediate in length between the morphs of *E. suessenbornensis* and *E.* cf. *granatensis*, more slender than that of *E. suessenbornensis*, and deeper in the diaphysis. The second (S 1139) is shorter than any other, robust, and could belong to a small Caballine, or possibly to a Zebra.

Discussion and Conclusions

Palaeontological data indicate that *Equus* existed in California, at Anza Borrego, about 2 Ma ago. Although larger, the Californian skull resembles extant Plains Zebras as well as their Middle Pleistocene relative, *E. mauritanicus* (fig. 20). According to the illustrations (plate I–1 and 6) adapted from DOWNS & MILLER (1994), the upper and lower cheek teeth resemble those of *Plesippus* and *Allohippus*, and of extant non-caballine species. They have no Hemione-like character. In the late Blancan of Arizona, there is a much smaller species (AZZAROLI & VOORHIES 1993) with lower cheek teeth which remind our "Sussemiones" (fig. 17–5). Another, much larger species, with marked Sussemiones characters (plate I–5) was found in Alaska, probably in Pliocene deposits (over 2 Ma, A. SHER, pers. comm.). Two groups therefore coexist since the first appearance of *Equus*: a Zebrass-like and a Sussemione-like. They are contemporary with *Allohippus* (fig. 14). There is no evidence for any Caballine-like species, or at least caballine characteristic lower cheek teeth.

The success of the "Zebrasses" is difficult to evaluate because they are mostly defined by the lack of original characters. The "Sussemiones" seem to have been very successful, judging by the vast geographical distribution from Arizona to Ethiopia, and by the chronological span from about 2 Ma to about 0.5 Ma. *Allohippus* had a similar distribution and a somewhat longer chronological span (fig. 14). Sussemiones seem to have become extinct, at least in Europe, at the time when Caballines appeared.

Judging by the tooth and limb bone morphology, the *E. granatensis* group lived and/or fed under drier conditions than the *E. coliemensis* group. Did both groups really coexist ? There is no evidence of "*E. coliemensis*" in the very rich sample of Venta Micena, nor of "*E. granatensis*" in Chukochya. The time encompassed by the Süssenborn deposits is very ample. Cueva Victoria may have been equally heterogeneous. Akhalkalaki seems the only place where both have coexisted, at least in the broad palaeontological sense.

Compared with all other monodactyl equids, the *E. coliemensis* group seems affected by a whole range of excesses: largest teeth and metapodials (EISENMANN 2003), most complicated tooth patterns, deepest vestibular valleys, shallowest lingual valleys, most developed stylids. The teeth morphology suggests an "excess" of enamel connected with an unstable pattern: the vestibular valleys can be either very deep or very shallow (fig. 17–3). GROMOVA (1952: 92) interpreted the evolution from deep to shallow vestibular valleys as a strengthening of the tooth: a vestibulo-lingual ridge composed of two layers of enamel would be more resistant filled with dentin than filled with cement. Whatever the case, vestibulo-lingual ridges are often well marked on both lower (plate I–4) and upper (plate II–17) cheek teeth. They contrast with the flat, grinding, occlusal surface usually observed in *Equus*. Again, the pattern is not stable. On the whole, it seems that there were various attempts to react to a new or more pronounced stress. Hypoplasia rings on some tooth crowns, at least at Süssenborn (fig. 21), indicate that the individuals suffered stresses during their lifetime.

One may expect that the *Equus* species that precede the differentiation of extant ones are "cocktail species" in which modern characters are variously mixed. This actually occurs in the Sussemiones and Zebrasses (the only modern character that does not appear is the typical caballine double knot). Even admitting the very early separation of the Caballine branch proposed by molecular biology (fig. 2), there is no palaeontological gap between this point and the branching off of the rest of the extant species: the "gap" may be easily filled by Sussemiones (Venta Micena, Garba IV) and Zebrasses (Nalaikha, Lakhuti II). Since Sussemiones left no survivors, they cannot be taken into account by molecular biology.

Palaeontological data suggest a nearly simultaneous appearance of all extant species, at the earliest at the beginning of the Middle Pleistocene, excepted Hemiones which may have differentiated a little earlier (Tologoj). The late appearance of Caballines is in contradiction with biomolecular interpretations. Perhaps, the impossibility till recently to use an adequate outgroup was misleading. It would be very interesting, now that some molecular data exist on South American equids (ORLANDO et al. 2003), to use them as the outgroup. Whether these data concern *Amerhippus*, as indicated by ORLANDO et al. (2003), or *Hippidion*, to which the fossil morphology seems to point (WEINSTOCK et al. 2005), they would belong to a much closer relative than Rhinoceroses.

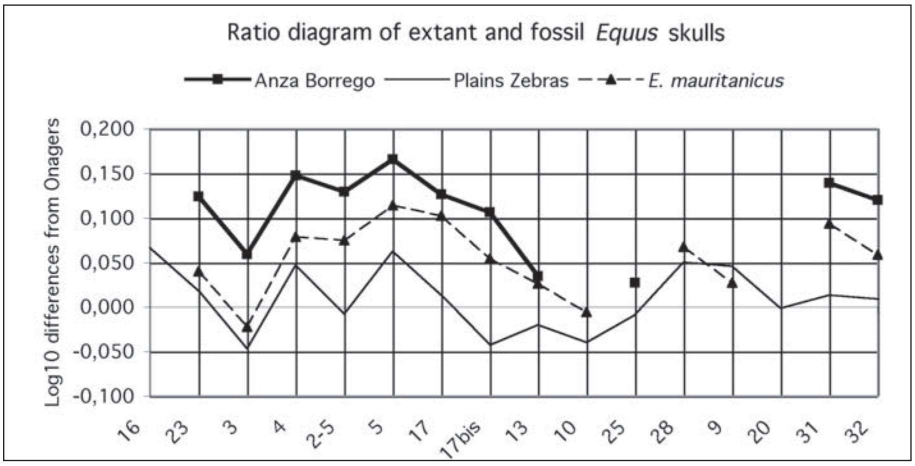

Fig. 20: Ratio diagram of skulls. See fig. 8.

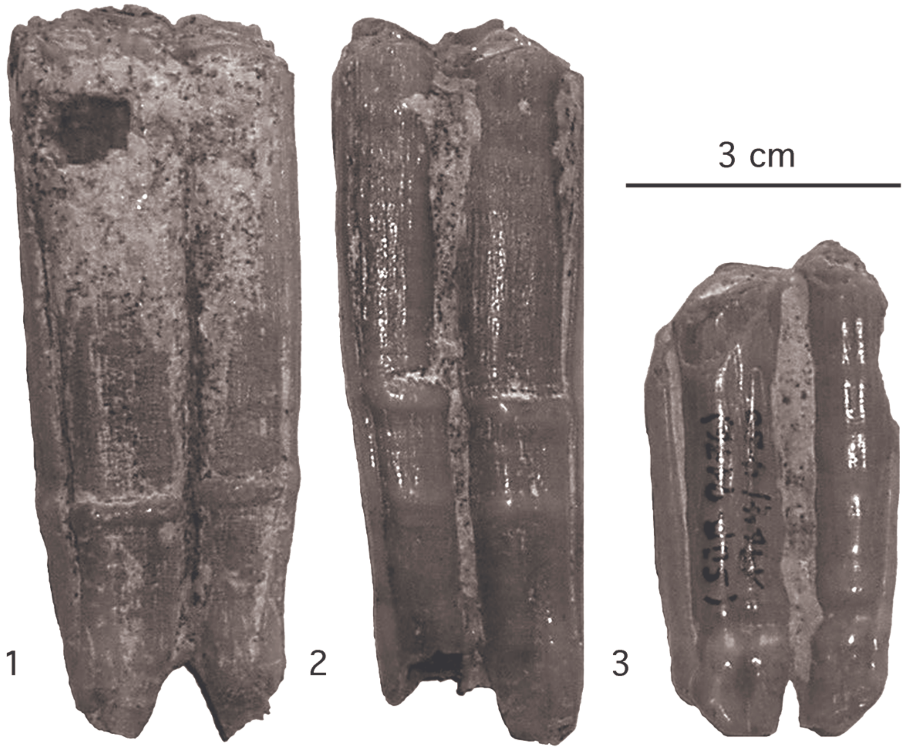

Fig. 21: Hypoplasia on lower cheek teeth, Süssenborn. 1. *E. suessenbornensis*, S 5203, P/3 or P/4. 2. *E. marxi*, S 482, P/3 or P/4. 3. *E. marxi*, S 9176, M/1 or M/2.

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Plate I

Upper and lower cheek teeth.

1: *Equus* sp., upper cheek series IVCM 2673, Anza Borrego, Loc. IVCM 790, after Downs & Miller (1994).

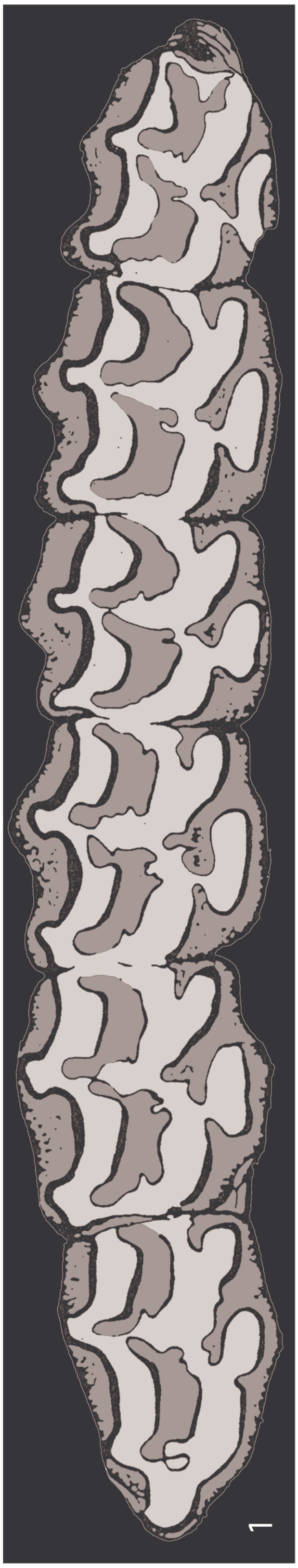
2: *E. granatensis*, lower P/2 VM 3572, Venta Micena.

3: *E. granatensis*, lower cheek series VM 84 C3 B9 12, Venta Micena.

4: *E. suessenbornensis*, lower cheek series S 9280, Süssenborn.

5: *Equus* sp., lower cheek series, Lost Chicken.

6: *Equus* sp., lower cheek series IVCM 2673, Anza Borrego, Loc. IVCM 790, after Downs & Miller (1994).


1


3


2


4


5


6

3 cm

Plate II

Upper cheek teeth.

1: *E. livenzovensis* Type L4, Livenzovka, M1/.

2: *E.* cf. *granatensis*, Süssenborn, S 4609, M1/.

3: *E. granatensis*, Fuensanta, 13540, M1/.

4–5: *E. granatensis*, Venta Micena, VM 82 1068 and VM K 11, M/ and P/.

6: *E. hipparionoides* Type, Akhalkalaki 100, P4/.

7: *E. coliemensis* Type IA 1741, Chukochya, upper series.

8: *Equus* ?, Khapry RGU 391, P3/ or P4/.

9: *Equus* sp., Melka Kunturé, Garba IV, MK 74-7150, P3/ or P4/.

10: *Equus sp.*, Melka Kunturé, Gomboré II MK 73–1978, P3/.

11: *E.* cf. *granatensis*, Süssenborn, Halle “P”, P3/ or P4/.

12: *Equus* ?, Livenzovka, L 1533, M1/ or M2/.

13: *Equus suessenbornensis*, Süssenborn, Halle “B”, M1/ or M2/.

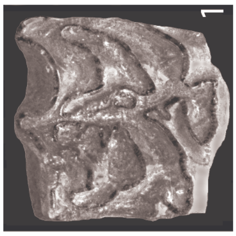
14: *Equus* ?, Livenzovka, L 131, P/ or M/.

15: *E.* cf. *verae*, Chukochya Loc 26, PIN 2998-243, P/ or M/.

16: *Equus* ?, Livenzovka, RGU 149, M?/.

17: *E. suessenbornensis*, Süssenborn, S 5226, P3/ or P4/.

18: *E. suessenbornensis*, Süssenborn, S 4219, P4/.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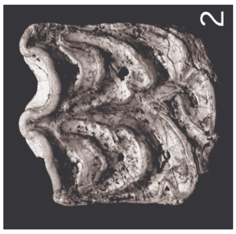
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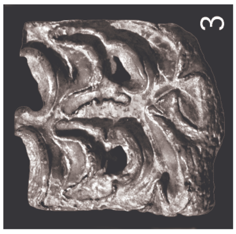
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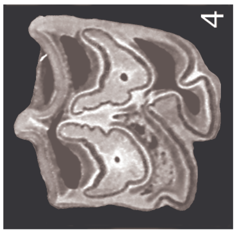
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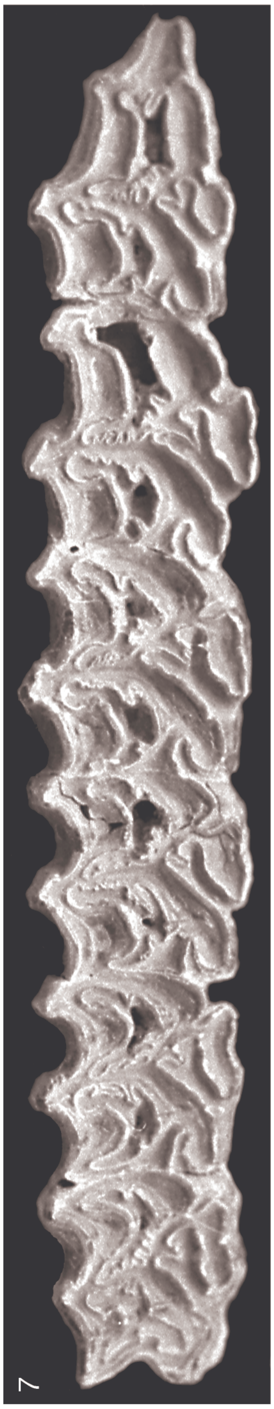
5


6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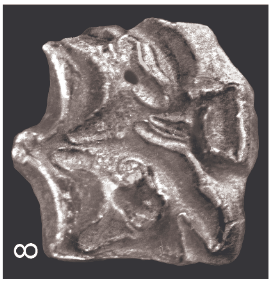
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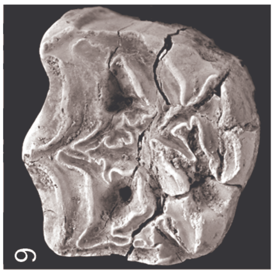
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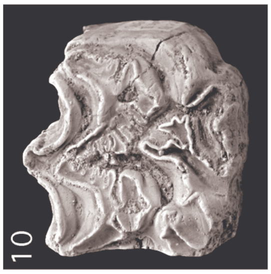
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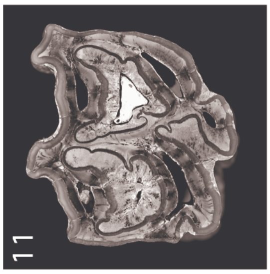
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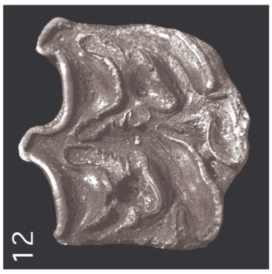
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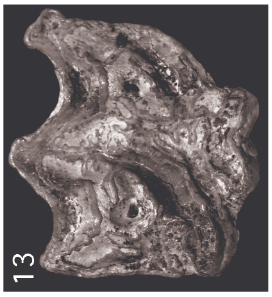
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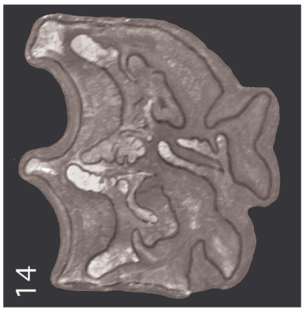
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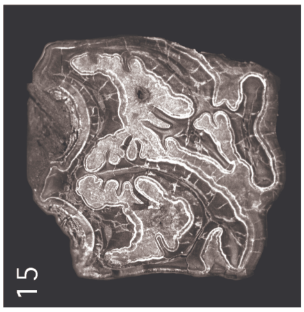
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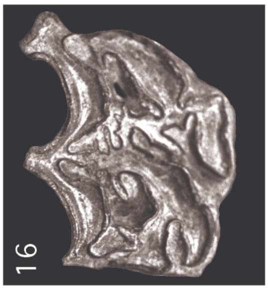
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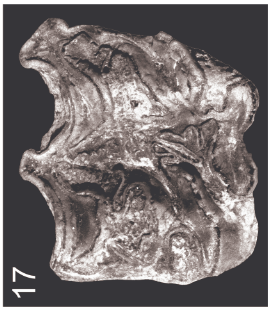
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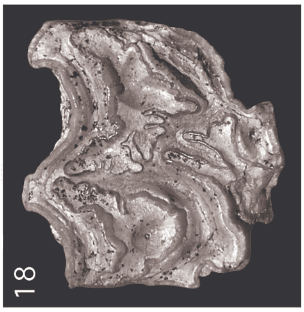
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3 cm