

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 *Hemionos* (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 occurrence 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-*

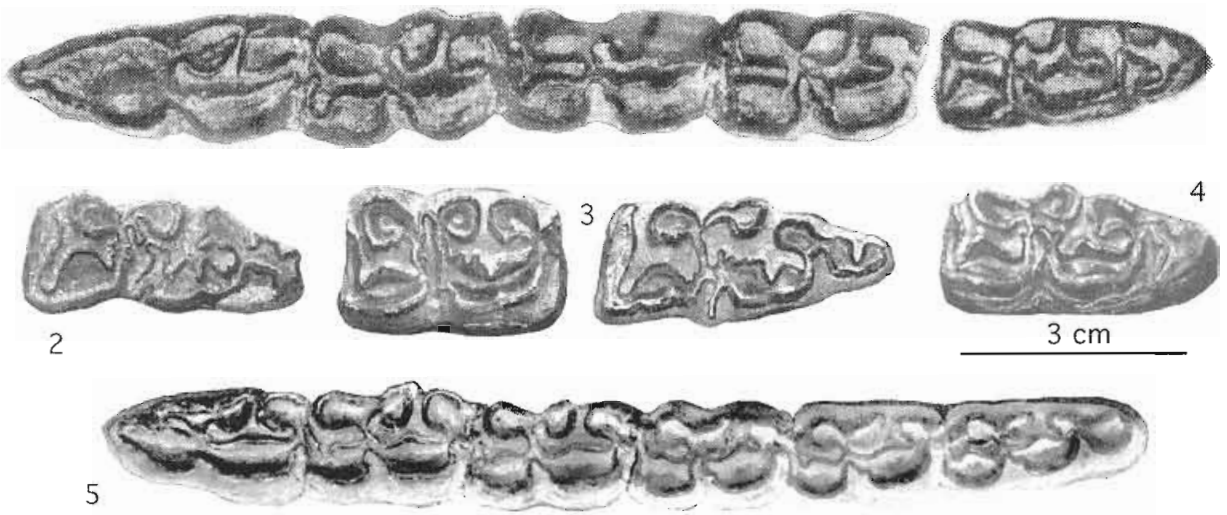


Fig. 17: Lower cheek teeth. 1. *E. coliemensis*, Chukochya, IA 1721, P/2-M/1 and M/3, after LAZAREV (1980). 2. *E. verae*, Chukochya, PIN 3341-689, M/3. 3. *E. verae*, Chukochya, associated M/1 and M/3, PIN 3100-333. 4. *E. verae*, Old Crow, Loc. 9, NMC 32165, M/3. 5. *Equus* sp., Dry Mountains loc., 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 FORSTEN (1986). They are large and could belong to *E. moshbachensis*. 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 several species. Beside the large and flat specimens (n=3 to 6) referable to *E.*

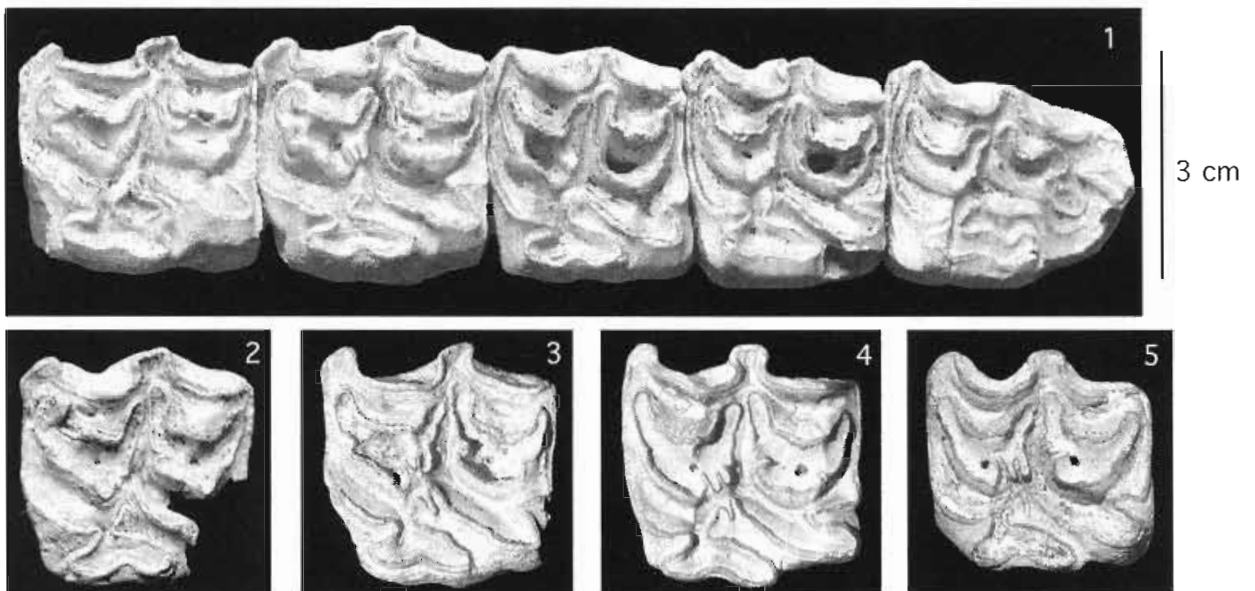


Fig. 18: *Equus* sp., Süßenborn, Upper cheek teeth. 1. S 9180, P3/-M3/. 2. S 9264, P3/ or P4/. 3. S 9276, P3/ or P4/. 4. S 9265, M1/ or M2/. 5. S 617, M1/ or M2/.

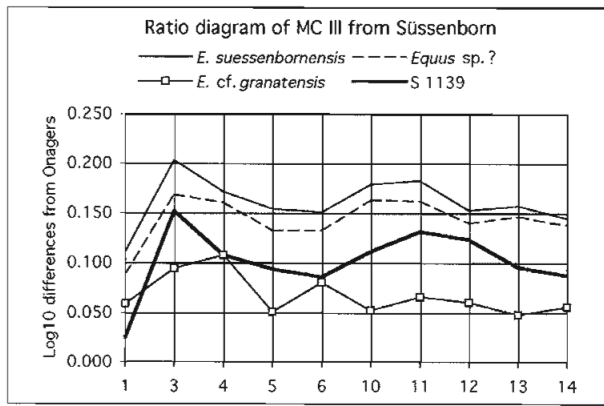


Fig. 19: Ratio diagram of third metacarpals. See fig. 6.

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.

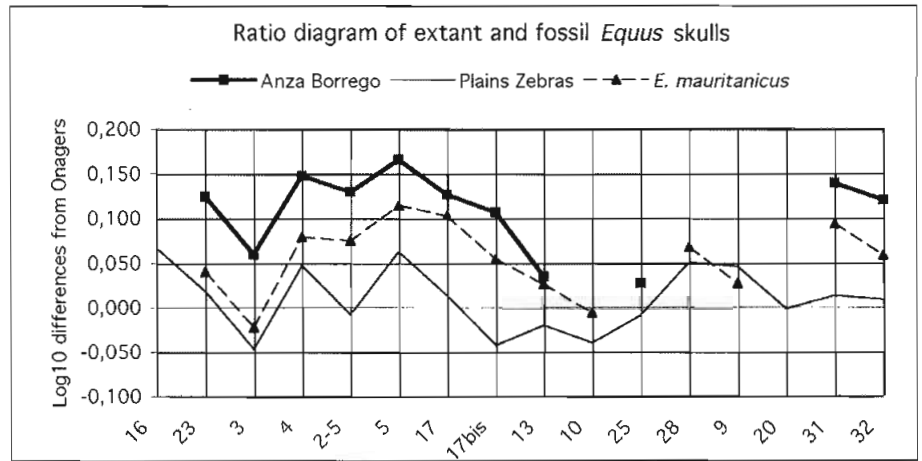


Fig. 20: Ratio diagram of skulls. See fig. 8.

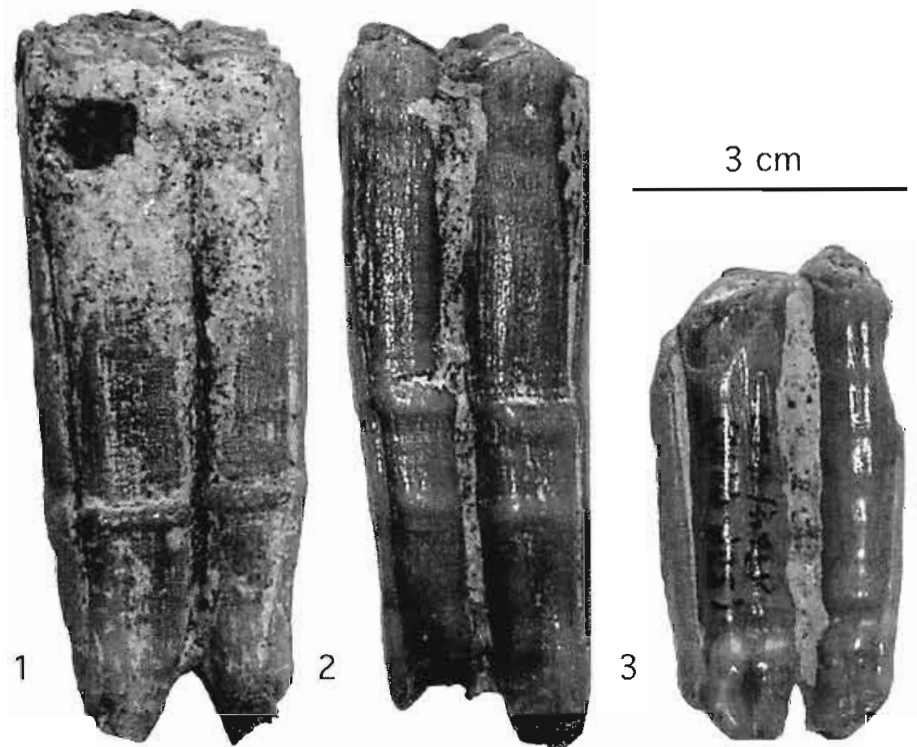


Fig. 21: Hypoplasia on lower cheek teeth, Süssenborn. 1. *E. suessenbornensis*, S 5203, P/3 or P/4. 2. *E. marxi*, S 482, P/3 or P/4. 3. *E. marxi*, S 9176, M/1 or M/2.

Acknowledgements

My first thanks go to all curators of all collections I visited during more than thirty years. Unfortunately, it is impossible to name them all here. Since the present work is largely based on Akhalkalaki, Beringida, Süssenborn, and Venta Micena materials, I am happy to be able to thank at least Dr. A. K. VEKUA, Dr. A. V. SHER, Dr. P. A. LAZAREV, Dr. C. R. HARRINGTON, Prof. H. D. KAHLKE, Dr. R.-D. KAHLKE, Dr. L. C. MAUL, and Dr. J. GIBERT. Much help was provided for the illustrations by D. GEFFARD, H. LAVINA, Ph. LOUBRY, Dr. L. C. MAUL, and D. SERRETTE. Many thanks are also due for exciting discussions on evolution and its representations to Dr. M. GODINOT and

D. GEFFARD as well as to Drs. A. ATHANASSIOU and J. L. FRANZEN for their thorough work as reviewers and for their very valuable suggestions.

References

AOUADI, N. (1999): Etude préliminaire des restes crâniens de chevaux villafranchiens (Ceysaguet, Haute-Loire). — Bulletin du Musée d'Anthropologie préhistorique de Monaco, **40**: 23–42; Monaco.

ASTRE, G. (1948): Petit Asinien Pléistocène du Lauraguais. — Bulletin de la Société d'histoire naturelle de Toulouse, **83** (1^{er} et 2^{ème} trimestre): 118–128; Toulouse.

AZZAROLI, A. (1979): On a Late Pleistocene Ass from Tuscany; with

- notes on the History of Asses. — *Palaeontographia Italica*, **71**, n. s. **41**: 27–47; Pisa.
- AZZAROLI, A. (1995): A synopsis of the Quaternary species of *Equus* in North America. — *Bolletino della Società Paleontologica Italiana*, **34** (2): 205–221; Modena.
- AZZAROLI, A., & VOORHIES, M. (1993): The Genus *Equus* in North America. The Blancan species. — *Palaeontographia Italica*, **80**: 175–198; Pisa.
- BAGTACHE, B., HADJOUIS, D., & EISENMANN, V. (1984): Présence d'un *Equus* caballin (*E. algericus* n. sp.) et d'une autre espèce nouvelle d' *Equus* (*E. melkiensis* n. sp.) dans l'Atérien des Allobroges, Algérie. — *Comptes Rendus de l'Académie des Sciences*, II, **298** (14): 609–612; Paris.
- BENNETT, D. K. (1980): Stripes do not a zebra make. — *Systematic Zoology*, **29** (3): 272–287; Washington.
- BONIFAY, M.-F. (1991): *Equus hydruntinus* REGALIA *minor* n. ssp. from the caves of Lunel-Viel (Hérault, France). — In: MEADOW, R. H., & UERPMANN, H.-P. (Eds.): Equids in the ancient world, vol. II. — Beihefte zum Tübinger Atlas des Vorderen Orients, Reihe A (Naturwissenschaften), **19** (2): 178–216; Wiesbaden (Dr. Ludwig Reichert Verlag).
- BOURDELLE, E. (1934): Notes anatomiques et considérations zoologiques sur les Zèbres. — Congrès des Sociétés savantes, **67**: 99–112; Paris (Imprimerie nationale).
- BOURDELLE, E. (1936): Quelques caractères anatomiques du Zèbre de Hartmann (*E. zebra hartmannae* Matschic). — *Bulletin du Muséum national d'Histoire Naturelle de Paris*, 2ème série, **8** (6): 473–477; Paris.
- BOURDELLE, E. (1941): Zèbres et Couaggas. — *Bulletin de la Société nationale d'Acclimatation de France*, **88** (4): 169–177; Paris.
- BOURDELLE, E. (1944): Chevaux, Anes et Zèbres. — *Bulletin de la Société nationale d'Acclimatation de France*, **91** (1): 49–71; Paris.
- BRINK, J. S. (1994): An ass, *Equus (Asinus)* sp., from the late Quaternary mammalian assemblages of Florisbad and Vlakkrak, central southern Africa. — *Suid-Afrikaanse Tydskrif vir Wetenskap*, **90**: 497–500; Pretoria.
- BURKE, A., EISENMANN, V., & AMBLER, G. (2003): The systematic position of *Equus hydruntinus*, an extinct species of Pleistocene equid. — *Quaternary Research*, **59**: 459–469; Washington.
- DE GIULI, C., MASINI, F., & TORRE, D. (1987): The latest villafranchian faunas in Italy: the Pirro Nord fauna (Apricena, Gargano). — *Palaeontographia Italica*, **74**: 51–62; Pisa.
- DOWNES, T., & MILLER, G. J. (1994): Late Cenozoic Equids from Anza-Borrego Desert of California. — *Contributions in science of the Natural History Museum of Los Angeles County*, **440**: 1–90; Los Angeles.
- DUCOS, P. (1986): The Equid from Tell Muraibit, Syria. — In: MEADOW, R. H., & UERPMANN, H.-P. (Eds.): Equids in the ancient world. — Beihefte zum Tübinger Atlas des Vorderen Orients, Reihe A (Naturwissenschaften), **19** (1): 237–245; Wiesbaden (Dr. Ludwig Reichert Verlag).
- EISENMANN, V. (1976): Le protostylide: valeur systématique et signification phylétique chez les espèces actuelles et fossiles du genre *Equus* (Perissodactyla, Mammalia). — *Zeitschrift für Säugetierkunde*, **41** (6): 349–365; Hamburg, Berlin.
- EISENMANN, V. (1979): Caractères évolutifs et phylogénie du genre *Equus* (Mammalia, Perissodactyla). — *Comptes Rendus de l'Académie des Sciences*, Série D, **288**: 497–500; Paris.
- EISENMANN, V. (1980): Les Chevaux (*Equus* sensu lato) fossiles et actuels: crânes et dents jugales supérieures. — *Cahiers de Paléontologie*: 1–186; Paris.
- EISENMANN, V. (1999): *Equus granatensis* of Venta Micena and evidence for primitive non-stenonid horses in the Lower Pleistocene. — In: GIBERT, J., SANCHEZ, F., GIBERT, L., & RIBOT, F. (Eds.): The hominids and their environment during the Lower and Middle Pleistocene of Eurasia. Proceedings of the International Conference of Human Palaeontology Orce 1995: 175–189; Baza (Imprenta Cervantes).
- EISENMANN, V. (2000): *Equus capensis* (Mammalia, Perissodactyla) from Elandsfontein. — *Palaeontologia Africana*, **36**: 91–96; Johannesburg.
- EISENMANN, V. (2003): Gigantic Horses. — In: PETCULESCU, A., & STIUCA, E. (Eds.): A tribute to C. RADULESCU and P. M. SAMSON, Advances in Vertebrate Paleontology 'Hen to Panta'. — 31–40; Bucharest.
- EISENMANN, V. (2006): Discriminating *Equus* skulls: The Franck's Index and the new Palatal Index. — In: MASIHKOUR, M. (Ed.): Equids in Time and Space, 9th ICAZ Conference, Durham 2002. — 172–182; Oxford (Oxbow Books).
- EISENMANN, V., & BAYLAC, M. (2000): Extant and fossil *Equus* (Mammalia, Perissodactyla) skulls: a morphometric definition of the subgenus *Equus*. — *Zoologica Scripta*, **29** (2): 89–100; Oxford.
- EISENMANN, V., & KUZNETSOVA, T. (2004): Early Pleistocene equids (Mammalia, Perissodactyla) of Nalaikha (Mongolia) and the emergence of modern *Equus*. — *Geodiversitas*, **26** (3): 535–561; Paris.
- EISENMANN, V., & TURLOT, J. C. (1978): Sur la taxinomie du genre *Equus* (Equidés). — *Cahiers de l'Analyse des Données*, **III** (2): 179–201; Montreuil.
- ENNOUCHI, E. (1951): Nouveaux documents fossiles du Quaternaire de Rabat. — *Comptes Rendus des Sciences naturelles du Maroc*, **7**: 88–89; Rabat.
- ENNOUCHI, E. (1953a): Ossements fossiles découverts dans les fondations d'une maison à Rabat. — *Comptes Rendus des Sciences naturelles du Maroc*, **1**: 14–16; Rabat.
- ENNOUCHI, E. (1953b): La faune des limons rouges de Bou-Knabel (Maroc). — Actes du IV^{ème} Congrès International du Quaternaire, Rome-Pise, Août – Septembre 1953: 3–4; Rome.
- FORSTÉN, A. (1986): A review of the Süssenborn horses and the origin of *Equus hydruntinus* REGALIA. — *Quartärpaläontologie*, **6**: 43–52; Berlin.
- GERAADS, D., & AMANI, F. (1997): La faune du gisement à *Homo erectus* de l'Aïn Maarouf, près de El Hajeb (Maroc). — *L'Anthropologie* (Paris), **101** (3): 522–530; Paris.
- GERAADS, D., HUBLIN, J.-J., JAEGER, J.-J., TONG, H., SEN, S., & TOUREAU, P. (1986): The Pleistocene hominid site of Ternifine, Algeria: new results on the environment, age, and human industries. — *Quaternary Research*, **25**: 380–386; Washington.
- GINSBURG, L., HILLY, J., & TAQUET, P. (1968): Une faune würmienne dans un remplissage de fente du massif du Filfila (littoral nord-constantinois, Algérie). — *Compte rendu sommaire des séances de la Société géologique de France*, **5**: 157–158; Paris.
- GOREN-INBAR, N., ALPERSON, N., KISLEV, M. E., SIMCHONI, O., MELAMED, Y., BEN-NUN, A., & WERKER, E. (2004): Evidence of Hominin control of fire at Geshar Benot Ya'akov, Israel. — *Science*, **304**: 725–727; Washington.
- GROMOVA, V. I. (1952): Gippariony (rod Hipparion) po materialam Taraklii, Pavlodara i drugim. — *Trudy Paleontologicheskogo Instituta Akademii Nauk SSSR*, **36**: 1–475; Moscow. [in Russian]
- HARINGTON, C. R. (1989): Pleistocene vertebrate localities in the Yukon. — In: CARTER, L. D., HAMILTON, T. D., & GALLOWAY, J. P. (Eds.): Late Cenozoic History of the Interior Basins of Alaska and the Yukon. — U.S. Geological Survey Circular **1026**: 93–98; Denver.
- HENNIG, W. (1966): Phylogenetic Systematics. — IV + I–263; Urbana (University of Illinois Press).
- KOUFOUS, G. D., KOSTOPOULOS, D. S., & SYLVESTROU, I. A. (1997): *Equus apolloniensis* n. sp. (Mammalia, Equidae) from the latest Villafranchian locality of Apollonia, Macedonia, Greece. — *Palaeontologia i Evolució*, **30–31**: 49–76; Sabadell.
- KUZMINA, I. E. (1997): Loshadi Severnogo Evrazii ot Pliotsena do Sovremennosti. — *Rossijskaja Akademiya Nauk, Zoologicheskij Institut, Trudy*, **273**: 1–221; St. Petersburg. [in Russian]
- LAZAREV, P. A. (1980): Antropogonovye loshadi Iakutii. — 1–190; Moskva (Nauka). [in Russian]
- MARIN, M. (1987): *Equus stenonis granatensis* en el Pleistoceno inferior de Venta Micena (Granada, España). — *Paleontologia i Evolució, Memoria Especial I*: 255–282; Sabadell.
- MAUL, L. C., REKOVETS, L., HEINRICH, W.-D., KELLER, T., & STORCH, G. (2000): *Arvicola mosbachensis* (SCHMIDTGEN 1911) of Mosbach

- 2: a basic sample for the early evolution of the genus and a reference for further biostratigraphical studies. — *Senckenbergiana lethaea*, **80** (1): 129–147; Frankfurt am Main.
- MUSIL, R. (1969): Die Equidenreste aus dem Pleistozän von Süßenborn bei Weimar. — *Paläontologische Abhandlungen A*, **III** (3–4): 317–364; Berlin.
- OAKENFULL, E. A., LIM, H. N., & RYDER, O. A. (2000): A survey of equid mitochondrial DNA: Implications for the evolution, genetic diversity and conservation of *Equus*. — *Conservation Genetics*, **1**: 341–355; Durham.
- ORLANDO, L., EISENMANN, V., REYNIER, F., SONDAAR, P., & HÄNNI, C. (2003): Morphological convergence in *Hippidion* and *Equus* (*Amerhippus*), Southern-American Equids elucidated by ancient DNA analysis. — *Journal of Molecular Evolution*, **57** (suppl. 1): 29–40; Berlin.
- SHER, A. V. (1971): Mlekopitajushchie i stratigrafia Pleistotsena krainego severo-vostoka SSSR i severnoi Ameriki. — 1–310; Moskva (Nauka). [in Russian]
- SHER, A. V. (1987): Olyorian land mammal age of Northeastern Siberia. — *Palaeontographia Italica*, **74**: 97–112; Pisa.
- SOTNIKOVA, M. V. (1989): Khishchnye Mlekopitayushchie Pliotsena — Rannego Pleistotsena. — *Akademia Nauk SSSR, Ordena trudovogo krasnogo znameni Geologicheskij Institut, Trudy* **440**: 1–121; Moscow. [in Russian]
- SOUVILLE, G. (1958): Atlas préhistorique de l'Algérie, feuille n°5 P-Alger. — 215–259; Alger (Imprimerie Officielle).
- TCHERNOV, E. (1998): An attempt to synchronize the faunal changes with the radiometric dates and the cultural chronology in Southwest Asia. — *Archaeozoology of the Near East III*, ARC Publicaties **18**: 7–44; Groningen.
- THOMAS, H. (1978): Géologie et paléontologie du gisement acheuléen de l'Erg Tihodaïne. — *Mémoires du Centre de Recherches Anthropologiques, Préhistoriques et Ethnographiques d'Alger*, **27**: 1–122; Alger.
- TSOUKALA, E. (1991): Contribution to the study of the Pleistocene fauna of large mammals (Carnivora, Prissodactyla, Artiodactyla) from Petralona Cave (Chalkidiki, N. Greece. Preliminary report. — *Comptes Rendus de l'Académie des Sciences*, (II) **312**: 331–336; Paris.
- UERPMMANN, H.-P. (1991): *Equus africanus* in Arabia. — In: MEADOW, R. H., & UERPMMANN, H.-P. (Eds.): *Equids in the ancient world*, vol. **II**. — Beihefte zum Tübinger Atlas des Vorderen Orients, Reihe A (Naturwissenschaften), **19** (2): 12–33; Wiesbaden (Dr. Ludwig Reichert Verlag).
- VANDERMEERSCH, B. (1994): Rabat. — In: LEROI-GOURHAN, A.: *Dictionnaire de la Préhistoire*, 2ème édition augmentée et mise à jour. — 1–1263; Paris (Presses Universitaires de France).
- VEKUA, A. K. (1962): Akhalkalakskaia nijnepleistotsenovaja fauna mlekopitayuschikh. — 1–207; Tbilisi (Isdatelstvo Akademii Nauk Gruzinskoj SSR). [in Russian]
- VEKUA, A. K. (1986): The Lower Pleistocene Mammalian Fauna of Akhalkalaki (Southern Georgia, USSR). — *Palaeontographia Italica*, **74**: 63–96; Pisa.
- VOGT, T., ERBAJEVA, M., & VOGT, H. (1995): Premières preuves de conditions périglaciaires au Pléistocène inférieur en Transbaïkalie (Sibérie, Russie). — *Comptes Rendus de l'Académie des Sciences*, **IIa**, **320**: 861–866; Paris.
- WEINSTOCK, J., WILLERSLEV, E., SHER, A., TONG, W., HO, S. Y.O., RUBENSTEIN, D., STORER, J., BURNS, J., MARTIN, L., BRAVI, C., PRIETO, A., FROESE, D., SCOTT, E., XULONG, L., & COOPER, A. (2005): Evolution, Systematics, and Phylogeography of Pleistocene Horses in the New World: A Molecular Perspective. — *PLoS Biology*, (3) **8**: e241; Lawrence.

Manuscript submitted 2005-10-04
Revised manuscript accepted 2006-07-14

Plate I

Upper and lower cheek teeth.

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

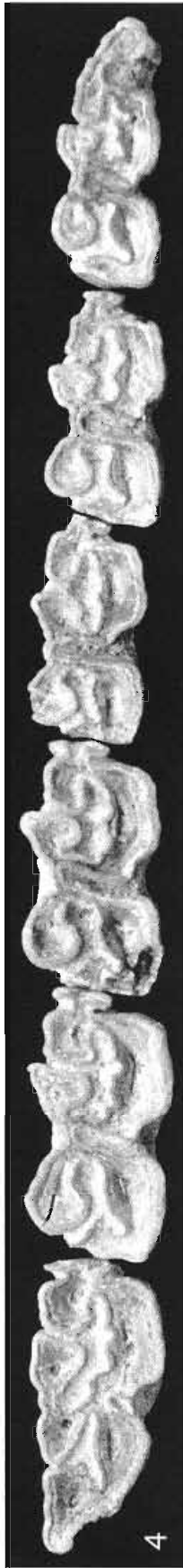
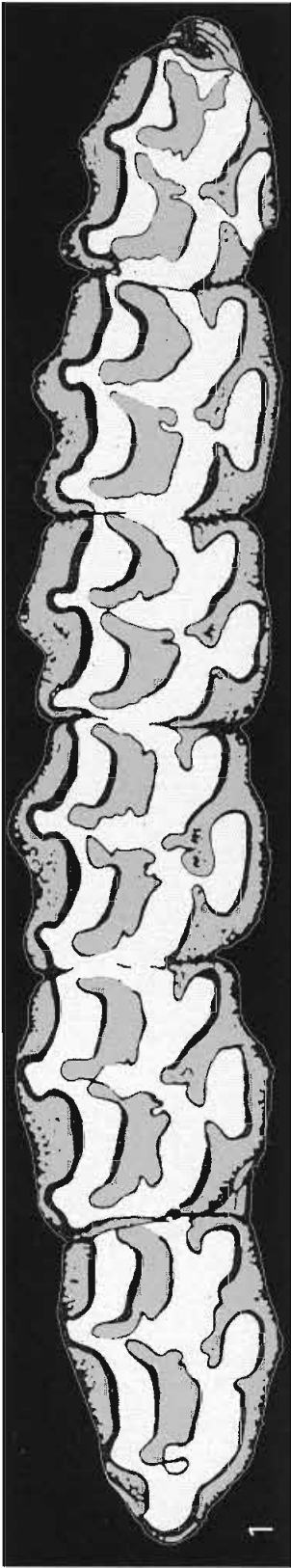
2: *E. granatensis*, lower P/2 VM 3572, Venta Micena.

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).



3 cm

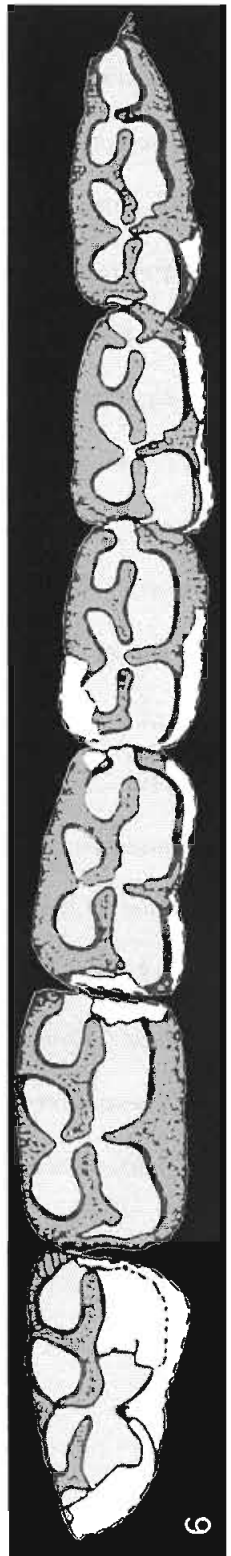
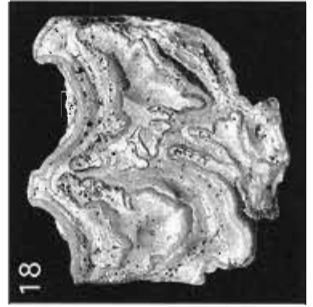
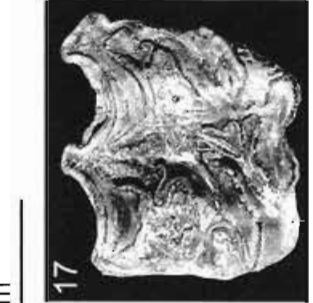
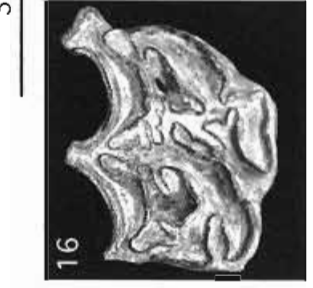
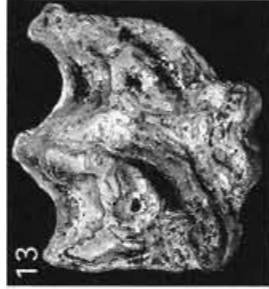
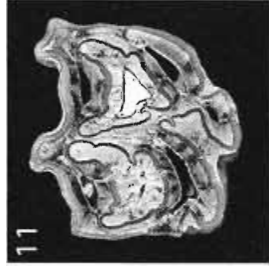
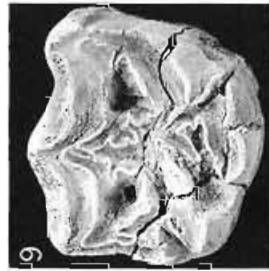
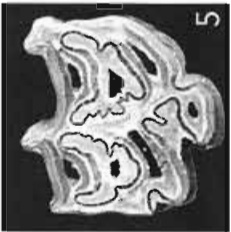
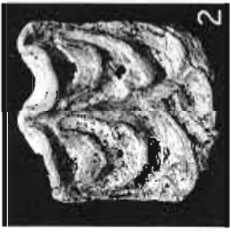


Plate II

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/.



3 cm