THE HOMINIDS AND THEIR ENVIRONMENT DURING THE LOWER AND MIDDLE PLEISTOCENE OF EURASIA

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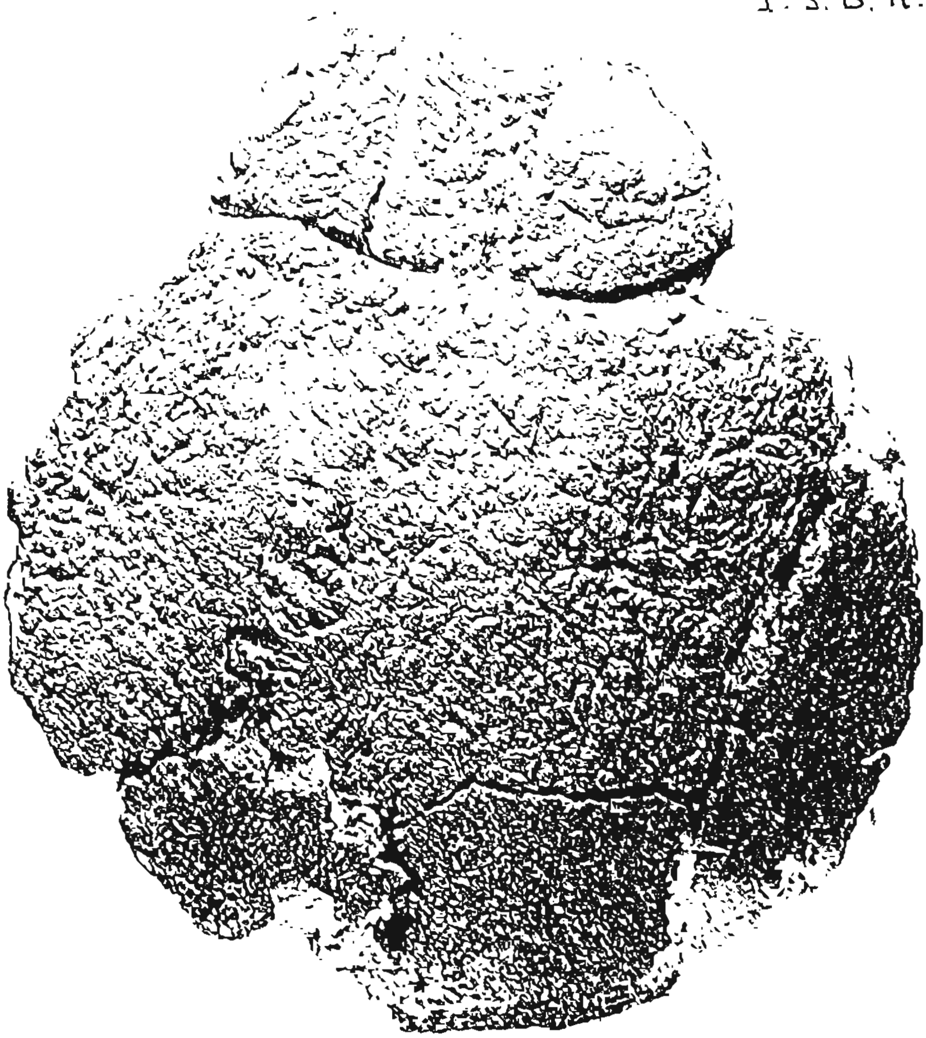

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Equus granatensis of Venta Micena and evidence for primitive non-stenonid horses in the Lower Pleistocene

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Abstract

Comparison of metapodial shape, limb segments proportions, upper and lower cheek teeth, shows that *Equus granatensis* differs as much from *E. stenonis*, as a modern hemione differs from a plains zebra. *E. granatensis* is specially well documented at Venta Micena, but can be traced back to Huelago where two larger but otherwise similar metapodials, clearly distinct from the *E. stenonis* of El Rincon, were found. If Huelago and El Rincon have the same age, two different species of *Equus* coexisted in Spain during the Villafranchian. Such evidences exist also for East and North Africa. The affinities of *E. granatensis* with other cursorial forms from Hagerman, Aïn Boucherit, Aïn Hanech, Pirro, Süssenborn, Akhalkalaki, Roterberg, and San Sidero, are documented and discussed.

Résumé

L'étude des proportions squeletuques d'*Equus granatensis*, représenté en abondance dans le gisement pléistocène inférieur de Venta Micena, montre qu'il diffère autant d'un *E. stenonis* qu'un Hémione actuel diffère d'un Zèbre de plaine. Une forme semblable à *Equus granatensis*, quoique plus grande, est attestée par deux métapodes dans le gisement de Huelago. Ce dernier est considéré comme contemporain de celui de Rincon (2,5 mA), où des restes d'un grand *E. stenonis* ont été trouvés. Deux lignées d'*Equus* semblent donc avoir coexisté en Espagne, de même qu'en Afrique. *Equus granatensis* est comparé à *E. numidicus* (Aïn Boucherit), *E. tabeti* (Aïn Hanech), *E. altidens* (Süssenborn), *E. cf. altidens* (Pirro), *E. hipparionoides* (Akhalkalaki) et *E. hydruntinus* ainsi qu'à *E. simplicidens* de Hagerman.

Introduction

The very rich and very well preserved *Equus* material of Venta Micena is stored at the Institut Paleontologic Dr M. Crusafont, in Sabadell (Barcelona), and at the Museo de Prehistoria J. Gibert, in Orce (Granada). There are no skulls but numerous teeth and limb bones. The whole material was studied in detail but only part of the data are published here to complement the precise description already given by Marin (1987).

The measurements (tables 1 to 6) were done according to the technics described in Eisenmann (1986). A look at the tables is enough to show the contrast between most of the mentioned equids, poorly or uncompletely documented, and a few forms for which we have satisfactory data, at least for the teeth and the limb bones (skulls are known only for *E. stenonis*): *E. granatensis* of Venta Micena is one of the latter. Obviously, the comparisons are limited to what material is available, and the reliability of the observations depends on the quality and quantity of the material.

Ratio diagrams (Simpson, 1941) evidence resemblances and differences. Some of them deal with one type of bone (fig. 1-3), others with limb segment proportions (fig. 4, 5). An attempt was also made to illustrate different typologies of non-caballines *Equus* species (fig. 6 to 9), using the most satisfactory samples and the best known anatomical parts: metapodials and cheek teeth. The reference line is the extant *E. hemionus onager*.

What species of Equus, when and where?

Some time around the Olduvai paleomagnetic event (Torre, 1987) one species of Equus, *Equus stenonis*, is fairly well documented in Europe (Azzaroli, 1990; Caloi, 1994). It was described in Italy (Azzaroli, 1965; De

Giuli, 1972; De Giuli 1987), but was found also in older localities in France (Viret, 1954; Prat, 1986; Prat, 1980). *Equus stenonis* is a large horse. The skull is characterized by a very deep narial notch (Olivola, Saint-Vallier). The lower cheek teeth have a primitive pattern of the double knot but the ectoflexid may be shallow on the molars (Olivola, Saint-Vallier); this is an evolved character for equids. The diaphyses and distal epiphyses of the third metapodials (Eisenmann, 1979) are wide and flat. The posterior first phalanges are nearly as long as the anterior (more than 96% at Saint-Vallier, Chilhac, and La Puebla de Valverde).

In Africa, some limb bones resemble *Equus stenonis* at Aïn Jourdel, Algeria, and in the member G of the Shungura Formation, Omo, Ethiopia (Eisenmann, 1992). The skull of *E. koobiforensis* (Eisenmann, 1983) has a very deep narial notch.

A few hundred thousands years earlier, about 2.5 ma ago, very large forms were present at Montopoli in Italy (Caloi, 1994), and at El Rincon, in Spain (Alberdi et al., 1989). The Montopoli material is very poor, but at El Rincon, the metapodials are typically stenonine and the length ratio between posterior and anterior phalanges is the same as in *E. stenonis*. Neither skulls nor teeth are known for this form.

Equus stenonis was first considered to be closely related to *E. simplicidens* of North America. The latter, very well documented about 3.4 ma. ago at Hagerman, Idaho, (Repenning, 1987), is however very different. On the skull, the narial notch is much shorter; the choanae are very long and narrow, the distance between the palatal rear border and the vomer notch is very long (Forsten and Eisenmann, 1995). On the lower cheek teeth, the ectoflexid is always deep on the molars, and sometimes on the premolars also. The metapodials are slenderer and antero-posteriorly deeper than in *E. stenonis*, in particular at the distal ends (Eisenmann and Karchoud, 1982). Like in modern hemiones, the third phalanges are narrow. Like in modern hemiones also, the first posterior phalanges are much shorter than the anterior ones: their relative length is less than 92%. Let us remark immediately that such proportions are exceptional: only the hemiones among all the extant *Equus* have similar values; for the three species of zebras and the asses, the same index is between 94 and 95%. Thus, *E. simplicidens* and *E. stenonis* are certainly distinct; they are even at the extremes of the variation observed in *Equus* for the relative lengths of the first phalanges. *E. simplicidens* of Hagerman seems very well adapted to a dry climate (slender bones), hard ground (narrow third phalanges), and open landscape (cursorial proportions of the limb segments). These adaptations (Eisenmann, 1984) are less pronounced, if pronounced at all, in *E. stenonis*.

Later on, stenonine characters are found on some North-American skulls (Anza-Borrego, California: Downs and Miller, 1994) and metapodials (Broadwater, Quarry 4), while non-stenonine forms seem to persist. The latter may be represented at San Pedro, Arizona, and Santo Domingo, New Mexico (Azzaroli and Voorhies, 1993), by very long and very slender matapodials.

Equus simplicidens was never recognized in Europe, but metapodials close in shape to those of Hagerman are present in Spain (Huelago and Venta Micena), and possibly in Netherlands (Tegelen). These forms are here referred as "E. simplicidens-like", although, naturally, there is no ground to refer them to the actual north-american *E. simplicidens*.

Huelago is supposed to be as old as El Rincon (Alberdi et al., 1989) and the metapodials of the *Equus* from Huelago were referred to the same large form, "E. livenzovensis", which, according to Alberdi *et al.* (1998), is also present in Montopoli and Livenzovka. The material is very poor at Montopoli, very heterogeneous at Livenzovka (Baïgusheva, 1978; personal observations). I believe, however, that at least two *Equus* metacarpals from Huelago do not fall inside the variation of El Rincon (table 1, fig. 1) and that they do not belong to the *E. stenonis* morphotype (fig. 2; Eisenmann, 1979, tables 7-8). Indeed, they have the same shape as the metacarpals of Venta Micena but are larger (table 2, fig. 3).

In East Africa, slender and deep metapodials are found in member G of the Shungura Formation, in units KBS- and KF- of the Koobi Fora Formation and in Bed I of Olduvai (Eisenmann, 1992). In North Africa, *E. numidicus* of Aïn Boucherit probably belongs in the same group. It seems thus that, as well as in Europe, both stenonine and "E. simplicidens-like" forms coexisted in East Africa about 2 ma. years ago (member G of the Shungura Formation, Bed I of Olduvai), and possibly also in North Africa, if Aïn Boucherit and Aïn Jourdel are of similar age.

During the Pleistocene, "E. simplicidens-like" equids are still rare: *E. hipparionoides* of Akhalkalaki (Vekua, 1962) and possibly *E. altidens* of Süssenborn (Musil, 1969) belong in this group, as well as *E. hydruntinus*. In Africa, *E. tabeti* of Aïn Hanech may be similar. In most cases, however, the material is not very rich. The fossil rests of *Equus* found at Venta Micena are most interesting because they form the richest sample of this kind for the whole Pleistocene of Europe. I shall refer to this horse as *E. granatensis*.

DESCRIPTION OF EQUUS GRANATENSIS

Teeth

1. Permanent upper cheek teeth (Plate I, fig. 1-6)

The enamel is not very plicated, but the pli caballin is always present on the premolars, and may be observed in molars. The maximal crown heights for the P2, P3, P4, M1, M2 and M3 are respectivelly 63, 73, 78, 70, 78, and 72 mm. The hypsodonty indices (= 100 average tooth length/maximal height) for the P3, P4, M1 and M2 are respectively: 40,7; 36,7; 36,3; 33,1.

Other biometrical data are in table 3.

2. Permanent lower cheek teeth (Plate I)

On the P3 and P4, the shape of the double knot varies from typically stenonine (with a rounded metaconid and a rounded or slightly pointed metastylid, separated by a pointed and deep lingual groove: Plate I, fig. 9, 10) to a rather hemionine type (elongated and oblong metaconid, pointed metastylid, separated by a shallow lingual groove: Plate I, fig. 7). On the M1 and M2, the ectoflexid (vestibular groove) is always very deep. It may also be deep on some premolars.

Plis protostylid are frequent on P3 and P4, exceptional on P2.

Plis caballinid are usual. On one M3 (Plate I, fig. 8), there is an ectostylid, which may result from the isolation of a pli caballinid.

3. Permanent lower incisors

Cups are present on all not too worn I1 and I2: they may be present or underdeveloped on I3.

Limb bones

The relative lengths of the limb bones are of a cursorial type (Eisenmann, 1984). As already stated, the first posterior phalanges are relatively short. All limb bones and in particular the metapodials (fig. 3) are slender and antero-posteriorly deep. The third phalanges are narrow. Biometrical data are in the tables 2, 4, and 5.

COMPARISONS

Extant species

Equus granatensis of Venta Micena is larger than *E. grevyi*, which is the largest extant *Equus*. The relative lengths of the limb bones are more cursorial than in *E. grevyi*, close to what is observed in hemiones (table 5, fig.4).

On the lower P3 and P4, the double knot is sometimes very much like in hemiones. But unlike in hemiones, the vestibular groove is deep on the M1 and M2.

The upper cheek teeth have very short protocones, shorter than in hemiones and indeed than in any extant species of *Equus*.

Middle and Upper Pleistocene species

Equus granatensis of Venta Micena has several points in common with *Equus hydruntinus*: cursorial limb proportions, very short protocones on the upper chek teeth, long ectoflexids on the lower molars. *Equus hydruntinus*, however, was much smaller, more hypsodont (at Roterberg, the hypsodonty indices reach 36.5 for an upper premolar, and 31 for one molar), and had possibly a still more pronounced difference in length between the anterior and posterior first phalanges (fig. 4, table 5). *E. hydruntinus* is mostly an Upper Pleistocene species, but a smaller form has been found also in the Middle Pleistocene at Lunel-Viel, France (Bonifay, 1991). At Petralona, Greece, *E. petralonensis* (Tsoukala, 1991) is intermediate in size between *E. granatensis* and *E. hydruntinus*.

The material of the Upper Pleistocene of Florisbad and Vlakkraal, South Africa, referred to *Equus lylei*, was recently re-examined by Brink (1994a) who stressed its resemblances to asses rather than hemiones and remarked on its possible relation to *E. hydruntinus* (1994b). As much as I can tell from the casts kindly provided by J.S. Brink, *E. lylei* is indeed very close, if not conspecific, to *E. hydruntinus*: deep ectoflexids on lower molars (unlike asses and hemiones), antero-posteriorly deep metapodials, strong difference in length between anterior and posterior first phalanges (table 5, fig. 4).

Musil (1969) and Forsten (1986; 1990) already pointed the possible relations between *E. hydruntinus*, *E. altidens* and *E. hipparionoides*. The upper cheek teeth of Süssenborn, Germany, referred to *E. altidens* have relatively long protocones; hypsodonty indices reach 36,2% for one P4, 32% for two M2. There are few limb bones (tables 5 and 6). The material of *E. hipparionoides* of Akhalakalaki, Georgia (Vekua, 1969) is very poor for the teeth, a little better for the limb bones (tables 5 and 6). It seems, however, that the distal limb segments have proportions similar to those of *E. lylei* and *E. hydruntinus* (fig. 4).

It is interesting to note that during the Middle and the Upper Pleistocene, all these relatively small and slender species are associated with much bigger Equids: *E. suessenbornensis* and *E.* cf *suessenbornensis* at Süssenborn and Akahalkalaki, *E. capensis* in South Africa, large *E. caballus* in Lunel-Viel and in Upper Pleistocene sites.

Lower Pleistocene and Pliocene

Although *E. granatensis* was considered (Alberdi and Ruiz Bustos, 1985; 1989) as a subspecies of *E. stenonis*, it is in my opinion very different. Even the slender forms of *E. stenonis*, like those of Dmanissi (Georgia) or El Rincon and La Puebla de Valverde (Spain) have relatively long posterior phalanges (fig. 5; table 5). Although the samples are poor, the same seems true for the younger forms of Sainzelles (France) and Selvella (Italy) which are at times referred to *E. altidens* (Forsten, 1990; Caloi, 1994). Surprisingly enough, the same is observed also in *E. tabeti* of Aïn Hanech (Algeria), and *E. cf. tabeti* of Ubeidiyeh (Israel).

Among all the Lower Pleistocene-Pliocene forms, *Equus* cf. *altidens* of Pirro is the only one to resemble *E. granatensis*: slender and deep metapodials, cursorial proportions, short protocones. One should note, however, that the few first anterior and posterior phalanges do not look as dimorphic as in *E. granatensis*. More data than I presently have on Pirro are needed to ascertain the relations between the two equids.

SCHEMATIC TYPOLOGIES OF NON CABALLINE SPECIES OF EQUUS

The next diagrams attempt to summarize the best known characters of the different non-caballine *Equus*. They are established on the most satisfactory samples: Hagerman for *E. simplicidens*, Saint-Vallier and La Puebla de Valverde for *E. stenonis*, Pirro, Süssenborn and Akhalkalaki for *E.* cf *altidens*, *E. altidens* and *E. hipparionoides*, Aïn Hanech for *E. tabeti*, Roterberg for *E. hydruntinus*, and naturally Venta Micena for *E. granatensis*. These diagrams combine data on the metapodials (length, distal articular width, depth at mid-diaphysis) and on the upper cheek teeth (average of length and width of P3-P4 and M1-M2, average protocone lengths for the same teeth). The data are in table 6.

Compared to *E. hemionus onager* (fig. 6), *E. stenonis* has more robust (relation between length and distal width) and more antero-posteriorly deep (relation between length and depth at mid-diaphysis) metapodials, larger teeth and smaller protocones. The form of La Puebla de Valverde is slenderer, has larger teeth, and smaller protocones than *E. stenonis vireti* of Saint-Vallier. Both sampls of *E. stenonis* are rich and therefore reliable.

E. granatensis (fig. 7, 8, 9), for which the sample is also very good, is nearly as slender as *E. hemionus onager* but has deeper metapodials. The teeth are a little smaller and have much shorter protocones. On fig. 6, *E. granatensis* is drawn as if it had the same length of the metapodials as *E. stenonis* of La Puebla de Valverde. Naturally, it is not true -as can be seen from tables 2 and 5, *E. granatensis* has much longer metapodials- but this representation endeavours to facilitate comparisons. Compared to *E. stenonis*, *E. granatensis* has much slenderer and a little flatter diaphyses, much smaller teeth and shorter protocones.

Relatively to *E. hemionus onager* (fig. 7), the very well documented *E. simplicidens* of Hagerman shows the differences already mentioned for *E. granatensis*, but the teeth are larger and the protocones longer, especially on M1 and M2. The same figure shows the resemblances between *E. simplicidens* and *E. numidicus* of Aïn Boucherit. For the latter species, however, the sample is relatively poor.

For *E. altidens* of Süssenborn, we have relatively good data on teeth, few data on metapodials; data are a little better for the metapodials of *E. hipparionoides* of Akhalkalaki, but there is only one worn upper cheek row. *E. cf. altidens* of Pirro is moderately well documented, Figure 8 shows a strong difference between the teeth of *E. altidens* and *E. granatensis*: the former has much longer protocones while the rest of the parameters are very close. Other affinities and differences evidenced on fig. 8 should be checked on better samples. If the sample of upper cheek teeth from Pirro is representative, *E.* cf. *altidens* is possibly closer to *E. granatensis* than to *E. altidens*.

The last diagram (fig. 9) compares the good samples of *E. granatensis* and *E. tabeti* of Aïn Hanech, and the poorer sample of *E. hydruntinus* from Roterberg, Germany. *E. tabeti* looks closer to *E. hydruntinus* than to *E. granatensis*. *E. granatensis* has the shortest protocones on the molars, and the relatively shortest protocones on the premolars.

CONCLUSIONS

It seems thus that there are two main groups of non-caballine primitive *Equus*: the stenonine type and the simplicidens-like type.

The stenonine group has distally flat metapodials (fig. 2), not very cursorial proportions and long posterior first phalanges (fig. 5). In this group belong certainly the fossils of El Rincon, Chilhac, Olivola, Matassino, Valdarno sensu lato, and Dmanissi. In the same group belong probably the less documented *Equus* of Selvella, Casa Frata, and Sainzelles. In the best known samples (Saint-Vallier and La Puebla de Valverde) the teeth are large, the protocones are short (fig. 6).

The simplicidens-like group is characterised by distally deep metacarpals (fig. 3), cursorial proportions of the limb segments and relatively short first posterior phalanges (fig. 4). I refer to this group *E. numidicus* of Aïn Boucherit, one metacarpal of Tegelen, part of the fossil material of Huelago, *E. granatensis* of Venta Micena, *E. cf. altidens* of Pirro, *E. altidens* of Süssenborn, *E. hipparionoides* of Akhalakalaki. Teeth are relatively large in *E. simplicidens* and *E. numidicus*, relatively small in *E. granatensis*, *E. altidens*, and *E.* cf. *altidens*. Protocones are long in *E. altidens*, very short in *E. granatensis*. May be also related to this group *E. tabeti* of Aïn Hanech and *E. hydruntinus*.

What kind of significance, ecological, systematical, and chronological can be attached to these groups ? Obviously, the limb proportions of the simplicidens-like equids indicate a better cursorial adaptation than in *E. stenonis* (Caloi, 1994). By modern standards, i.e. judging by what may be observed in extant species of *Equus*, *E. stenonis* was like a large plains zebra, *E. granatensis*, like a large hemione. The scope of differences between these two fossil *Equus* is much larger than what can be expected for a modern intraspecific variation. The hypsodonty indices (relative crown heights of the teeth) are certainly related to the feeding: small indices (relatively high crowns) evidencing an adaptation to abrasive food. Unfortunately I have no good data on their ranges of variation, intraspecific or interspecific, not even for extant species of *Equus*. Judging from the few values I have, hypsodonty indices are similar on the upper P3 and P4 of *E. granatensis*, *E. altidens*, and *E. hydruntinus*; the upper M1 and M2 may be less hypsodont in *E. granatensis* than in the other two species. Other characters considered as "evolved" and "adaptative" in equids are long protocones on upper cheek teeth and shallow ectoflexids on lower molars. For these characters *E. granatensis* and *E. hydruntinus* are very "primitive", very poorly adapted. The protocones are much more "advanced" in *E. altidens*, but its lower molars are as primitive as in the others. Since obviously the three species are very close in their general habit, it may be after all that protocone length and ectoflexid depth are not as "adaptative" as is believed. Whatever the case, the protocone length suffers strange avatars inside the simplidens-like group: short in *E. simplicidens*, long in *E. altidens*, very short in *E. granatensis*, *E. tabeti*, and *E. hydruntinus*. It does not look like a character easy to use for biostratigraphy.

Ecologically adapted characters (mostly apparent on limb bones) are often considered as less reliable for phylogenies and systematics than neutral characters (mostly apparent on skulls), the former being more plastic and more easily subject to parallel evolutions. One could argue therefore, that *E. stenonis* of El Rincon (skull unknown) evolved into "E. stenonis granatensis" of Venta Micena (skull unknow) by reducing its size and acquiring a more cursorial habit. In that case, however, the material of Huelago should be heterogeneous in age, part of it belonging to a pliocene *E. stenonis*, while the two slender and deep metacarpals could be referred to a younger *E. granatensis*. But if the *Equus* material of Huelago is homogeneous in age and if it has the same age as the *Equus stenonis* of El Rincon (Alberdi et al., 1989), we have a good evidence of the coexistence of two very different *Equus* in the European Pliocene: a well represented "stenonine" form, and a poorly represented "E. simplicidens-like" form. Another point is the protocone length: why would it shorten during the evolution from *E. stenonis* to *E. granatensis*? Could not a short protocone be a neutral character with a phylogenetic significance? In that case, *E. granatensis* and *E. hydruntinus* could be related to each other, but not to *E. stenonis* or *E. altidens*.

I have no answers to these questions. I believe, however, that the ancient biostratigraphies (Marin, 1986; Alberdi & Ruiz-Bustos, 1989; Alberdi et al., 1991) based on the mere succession in time of "subspecies" of *E.*

stenonis -from the big *E. stenonis livenzovensis* (still to be defined among a mixture of different equids) to the slender *E. stenonis granatensis*- should be reconsidered. Presently, equids are good chronological landmarks only on a broad scale, and in particular when they immigrate: we may speak of an "*Hipparion* datum" or an "*Equus* datum", or an "*Equus caballus* datum" inside the Old World; they are much less clear in America where these forms evolved before migrating. To use equids in a precise biochronological way, a much better understanding of their evolutive mechanisms is clearly needed.

A recent paper by Alberdi *et al.* (1998) deals with European stenonid horses en general, and with *E. granatensis* in particular. The latter is now considered as a subspecies of *E. altidens*, not of *E. stenonis*. On the whole, I welcome this change of interpretation, although *E. granatensis* may well deserve a specific status beacause of its very short protocones (table 6). My main disagreement, however, concerns the phylogenetical interpretations of Alberdi *et al.* (1998). I Believe that species of *Equus* morphologically close to *E. granatensis* may be found much earlier (Hagerman, Huelago, Aïn Boucherit), and that they coexisted in time with species close to *E. stenonis*. Moreover, the horses from Livenzovka, are neither well dated enough, nor well understood enough to provide a phylogenetical "root" (Forsten, 1998).

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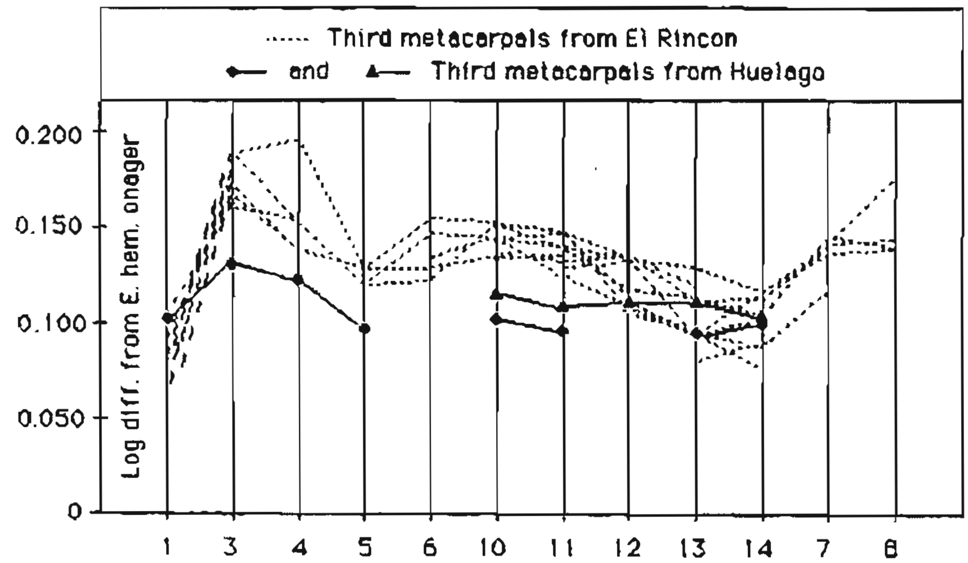

Fig. 1. Ratio diagrams of individual metacarpals from El Rincon and Huelago (Spain). The corresponding measure-ments are in table 1. The metacarpals of El Rincon are relatively wider at mid-diaphysis (measurement 3) and relatively shallower at the distal end (12, 13, 14).

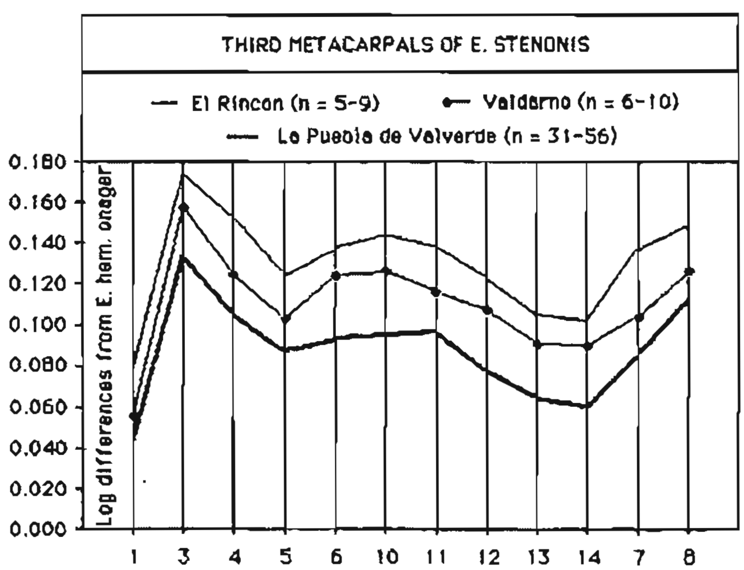

Fig. 2. Ratio diagrams of average metacarpal measure-ments in *E. stenonis* of old colecctions of Valdarno (Italy), El Rincon, and La Puebla de Valverde (Spain).

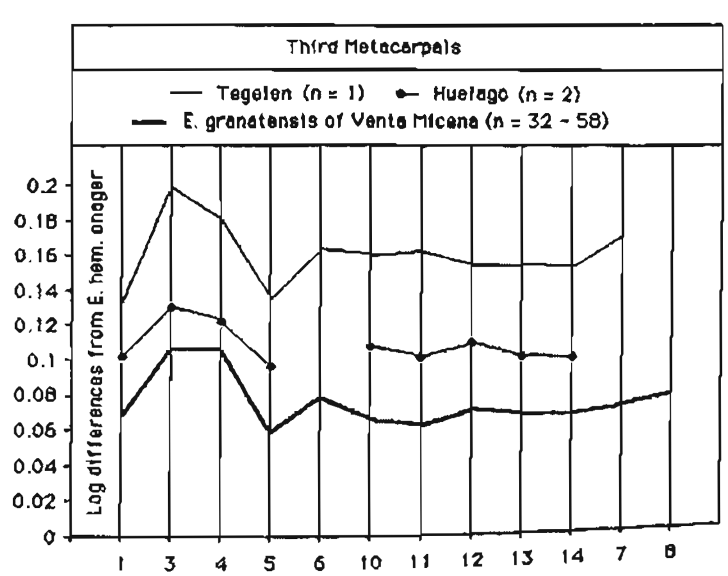

Fig. 3. Ratio diagrams of metacarpal measurements of *E. granatensis* from Venta Micena, *E.* cf. *granatensis* of Huelago, and of one metacarpal from Tegelen (Netherlands).

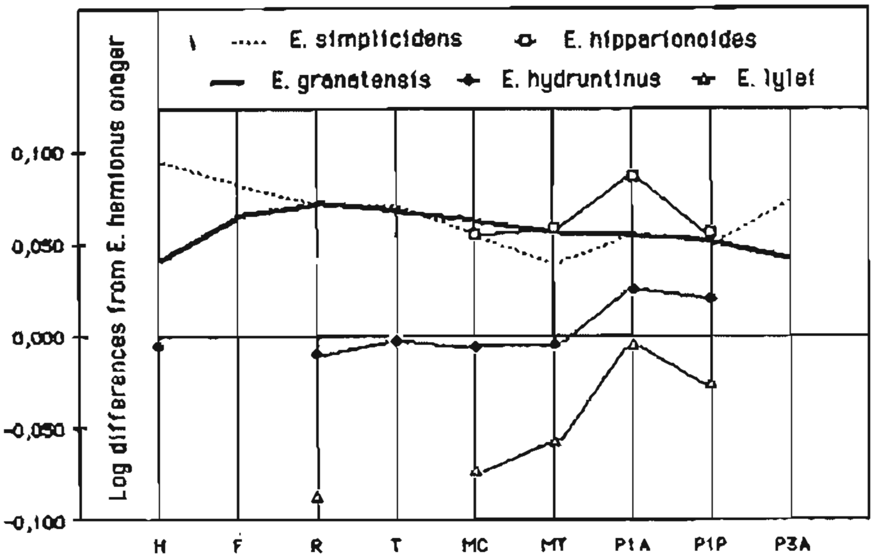

Fig. 4. Ratio diagrams of lengths of humerus (H), femur (F), radius (R), tibia (T), third metacarpal (MC), third metatarsal (MT), first anterior phalanx (P1A), first posterior phalanx (P1)P), and breadth of the third anterior phalanx (P3A). The corres-ponding data are in table 5. *E. granatensis* is larger but has the same proportions as *E. hemionus onager*. In all the represented species, the first posterior phalanges are short relatively to the anterior ones.

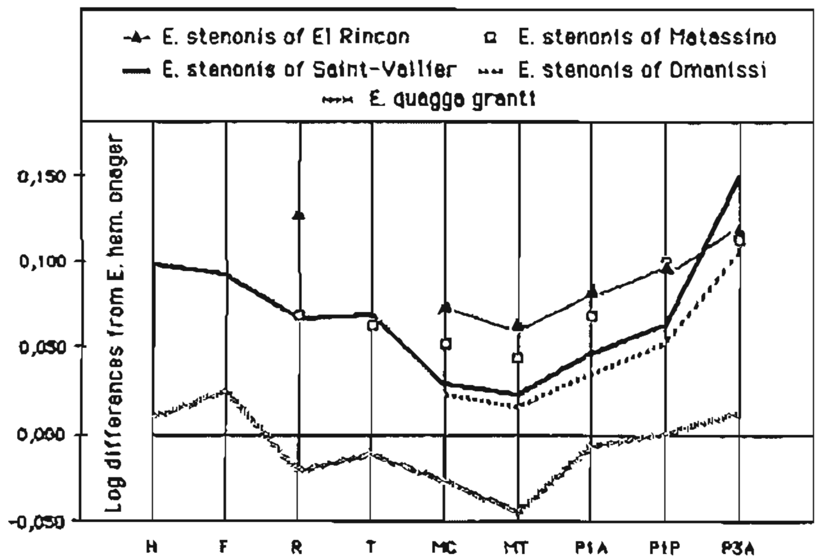

Fig. 5. Ratio diagrams of limb bone lengths and first anterior phalanx /breadth in *E stenonis* and in the extant plains zebra. Measurements are in table 5. Like *E. quagga granti*, *E. stenonis* have long proximal bones relatively to metapodials, and relativel/y, long first posterior phalanges.

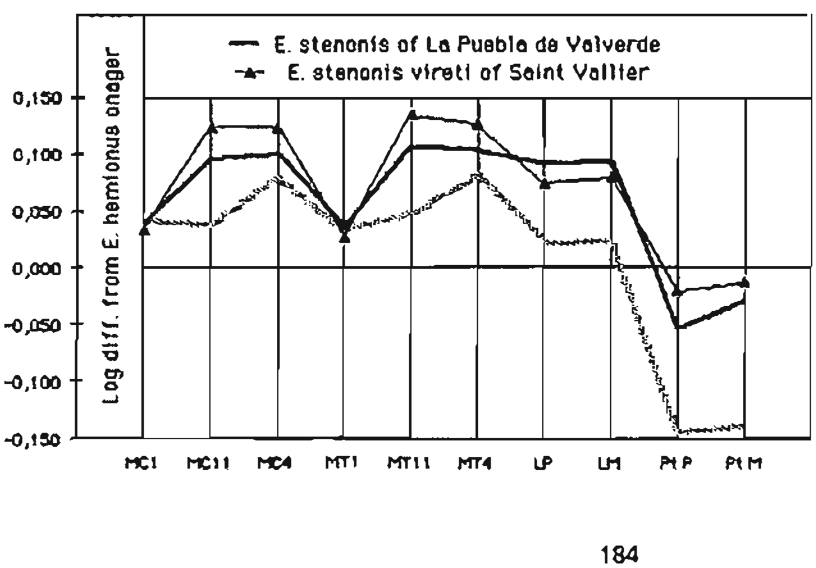

Fig 6. Ratio diagrams of metapodial and upper cheek teeth measurements. MC1: length oof third metacarpal; MC11: distal articular width of the same; MC4: depth at mid-diaphysis of the same; MT1: length of third metatarsal; MT11: distal articular width; MT4: depth at mid-diaphyses; LP: average of length and width of P3 an P4; LM: average of length and width of M1 and M2; PtP: length of protocone on P3 and P4; PtM: length of protocone on M1 and M2. The corresponding data are in table 6. *E. granatensis* is drawn as if it had the same metacarpal length as *E. stenonis* of La Puebla de Valverde in order to show that it has relatively less wide distal articulations (MC11 and MT11), relatively smaller teeth (LP and LM), and relatively shorter protocones (PtP and PtM) than *E. stenonis*.

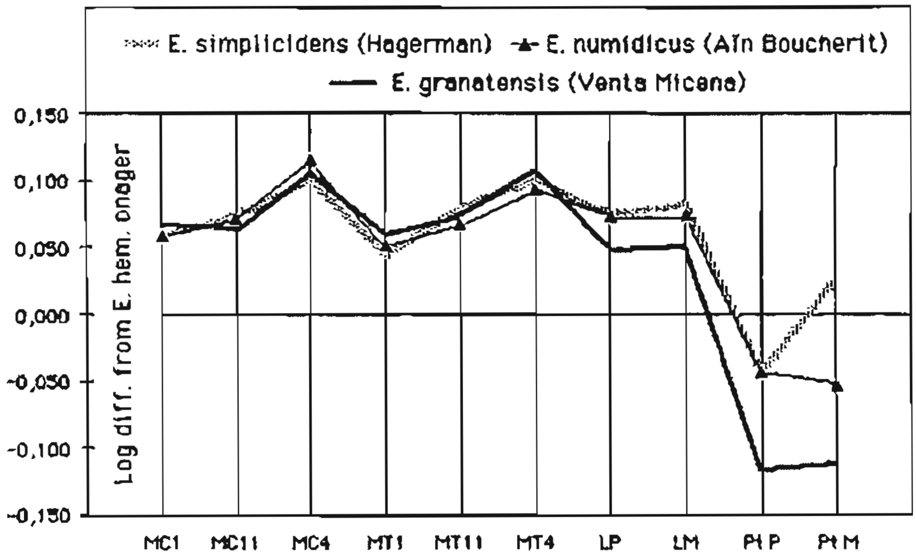

Fig. 7. Ratio diagrams of metapodial and upper cheek teeth measurements for *E. simplicidens*-like *Equus*. Same abbreviations as in figure 6. *E. granatensis* has relatively smaller teeth and relatively shorter protocones than *E. simplicidens* and *E. numidicus*.

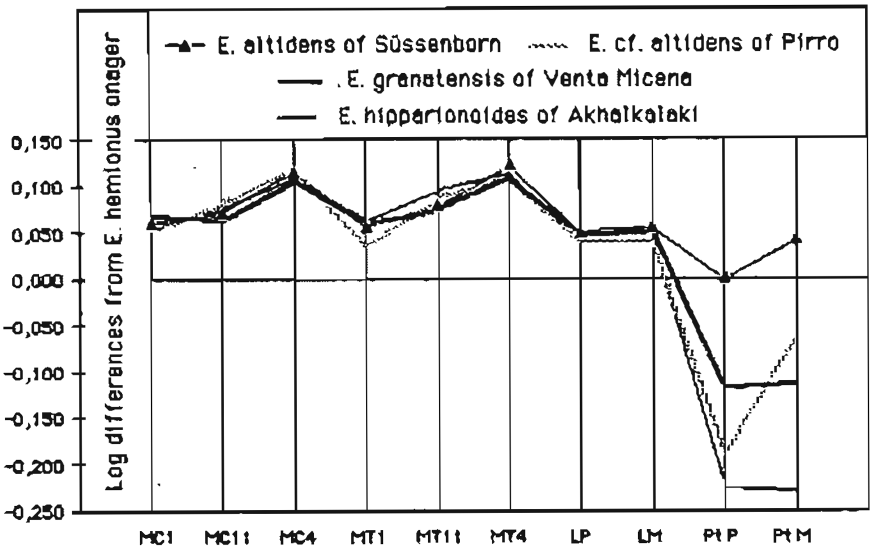

Fig. 8. Ratio diagrams of metapodial and upper cheek teeth measurements for *E. simplicidens*-like *Equus*. *E. altidens* has relatively longer protocones than the three other species.

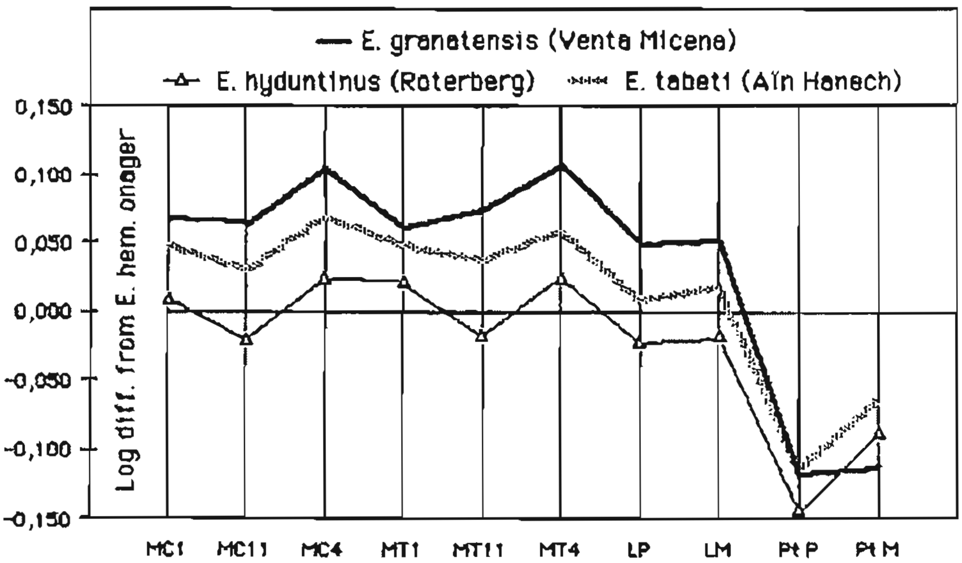

Fig. 9. Ratio diagrams of metapodial and upper cheek teeth measurements for *E. simplicidens*-like *Equus*.

	El Rincon	El Rincon	El Rincon	El Rincon	El Rincon	El Rincon
MC III	12439	12440	12441	12442	12443	12444
1: Maximal length	262.0	256,0	238,0	248,0	252,0	256.0
3: Minimal breadth	38,0	40,0	38,0	38,5		39.0
4: Depth at level of 3	29.0	(33)	29.0	29.0		
5: Proximal articular breadth	58,0	58,0				
6: Prox. art. depth	36.5	38.7			37,0	
10: Distal max. supra-art. breadth	52,8	55.0	53,5	54,0	54,0	53,0
11: Dist. max. art. breadth	52.2	54,0		53,0	51,2	52.0
12: Dist. max. depth of keel	40,2	37,5		40,0	37,8	40,0
13: Dist. min. depth of medial condyle	31,2	30,0	29,0	30,0	30,0	32,0
14: Dist. max. depth of med. condyle	33.7	34,0	32.0	31,0	31,8	33,0
7 : Max. diameter facet 3rd carpal	47.5	47.5			45,0	
8 : Diam. anterior facet 2nd carpal	17,2	18,5				17.5
	El Rincon	El Rincon	El Rincon	Huelago	Huelago	Tegelen
MC III	12445	12446	12451	79	88	
1: Maximal length	252,0	269,0		268,0		286,5
3: Minimal breadth	40,0	37,5		35,0		41,0
4: Depth at level of 3	30,0	30,0		28,0		32.0
5: Proximal articular breadth	57,0	57.0		54,0		59.0
6: Prox. art. depth	38.0	36,0				39.5
10: Distal max. supra-art. breadth	54,0	55,0	55,0	49,0	50,5	56,0
11: Dist. max. art. breadth	54,0	53,0	54,0	48,0	49,5	56,0
12: Dist. max. depth of keel	40,0	38,5	38,0		38,0	42,0
13: Dist. min. depth of medial condyle	32,5	31,3	30,0	30,0	31,2	34,5
14: Dist. max. depth of med. condyle	34,0	33,0	32,9	32,7	33,0	37,0
7 : Max. diameter facet 3rd carpal	47,0	48,0				51,0
8 : Diam. anterior facet 2nd carpal	17,0	17,0				

Table 1: Third metacarpals of El Rincon, Huelago and Tegelen: measuements in millimeters. Prox.: proximal; art.: articular; max.: maximal; Dist.: distal; min.: minimal; Diam.: diameter

MC III	n	x	min	max	s	v
1: Maximal length	32	247,1	228,0	267,0	7,17	2,90
3: Minimal breadth	58	33,0	30,0	36,2	1,49	4,51
4: Depth at level of 3	56	26,9	25,0	29,0	1,03	3,81
5: Proximal articular breadth	56	49,3	45,0	55.0	2,19	4,43
6: Prox. art. depth	52	32,5	30,0	35,0	1,38	4,26
10: Distal max. supra-art. breadth	57	45,2	39,0	48,0	2,07	4,59
11: Dist. max. art. breadth	51	44,5	39,0	47,2	1,92	4,31
12: Dist. max. depth of keel	43	34,7	32,0	37,5	1,26	3,62
13: Dist. min. depth of medial condyle	54	28,3	25,5	30,7	1,13	4,01
14: Dist. max. depth of med. condyle	44	30,4	28,0	33,0	1,20	3,95
7 : Max. diameter facet 3rd carpal	51	40,6	36,0	45,0	2,05	5,04
8 : Diam. anterior facet 2nd carpal	56	14,8	12,0	18,0	1,13	7,65
MT III	n	x	min	max	s	v
1: Maximal length	32	284,6	270,0	302,0	8,76	3,08
3: Minimal breadth	73	32,9	29,0	36,5	1,57	4,78
4: Depth at level of 3	63	32,4	29,0	35,0	1,40	4,31
5: Proximal articular breadth	58	48,4	44,5	52,5	2,01	4,16
6: Proximal depth	50	39,6	36,0	42,5	1,67	4,21
10: Distal max. supra-art. breadth	82	45,9	42,0	49,5	1,90	4,13
11: Dist. max. art. breadth	77	44,4	40,0	49,0	1,56	3,52
12: Dist. max. depth of keel	77	35,6	33,5	38,0	0,99	2,77
13: Dist. min. depth of medial condyle	82	27,9	26,0	30,3	0,94	3,39
14: Dist. max. depth of med. condyle	76	30,6	28,0	33,0	1,03	3,37
7 : Max. diameter facet 3rd tarsal	43	44,2	40,0	48,5	1,96	4,43
8 : Diam. facet 2nd tarsal	38	11,2	9,0	14,0	1,30	11,55

Table 2: Third metacarpals (MCIII) and metatarsals (MT III) of Venta Micena. Measurements in millimetres. Some abreviations as in table 1. n: number of specimens; x: mean; min: minimal obsserved value; max: maximal observed value; s: standard deviation; v: coefficient of variation (v= 100 s / x).

		n	x	min	max	s	v
	L	31	38,7	35,0	42,0	1,97	5,09
P2	LP	33	7,0	5,5	9,0	0.92	13,14
	l	32	25,6	23,8	28,0	0,94	3,67
	IP	30	18.0	13,4	23,1	2,40	13,33
	L	25	29,7	27,0	32,0	1,24	4,18
P3	LP	24	8,4	6,8	11,5	1,34	15,95
	l	22	27,7	25,0	30,0	1,33	4,80
	IP	24	28,4	22,6	39,7	4,36	15,35
	L	27	28,6	26,0	31,5	1,34	4,69
P4	LP	27	8,9	7,0	11,1	1,36	15,28
	l	27	28,1	25,0	30,0	1,20	4,27
	IP	27	31,2	24,1	39,3	4,20	13.46
	L	52	29,2	26,0	32,0	1,39	4,76
P3 P4	LP	51	8,7	6,8	11,5	1,37	15,75
	l	49	27,9	25,0	30,0	1,26	4,52
	IP	51	29,9	22,6	39,7	4,47	14,95
	L	25	25,4	22,0	28,0	1,45	5,71
M1	LP	24	7,9	6,7	9,5	0,82	10,38
	l	23	26,4	25,0	28,5	0,99	3,75
	IP	24	31,2	26,7	37,5	2,85	9,13
	L	20	25,8	22,0	28,0	1,44	5,58
M2	LP	19	9,3	7,0	11,0	1,11	11,94
	l	17	25,7	24,0	27,0	0,82	3,19
	IP	19	36,0	30,4	41,5	3,53	9,81
	L	45	25,6	22,0	28,0	1,45	5.66
M1 M2	LP	43	8,5	6,7	11,0	1,18	13,88
	l	40	26,1	24,0	28,5	0,96	3,68
	IP	43	33,3	26,7	41,5	3,97	11,92
	L	41	27,8	25,0	32,0	1,44	5,18
M3	LP	40	9,5	8,0	12,2	1,21	12,74
	l	41	23,4	22,0	24,5	0,66	2,82
	IP	39	34,2	27,6	45,2	4,84	14,15

Table 3 Upper cheek teeth of Venta Micena. Measurements in millimeters. Same abreviations as in table 2. L: length; LP: length of protocone; 1: width; IP: protocone index (IP = 100 LP / l)

ANTERIOR I PHALANGES	n	x	min	max	s	v
1: Maximal length	16	86,5	82,0	91,0	2,73	3,16
3: Minimal breadth	17	31,0	29,0	33,0	1,15	3,71
4: Proximal breadth	13	49,3	47,0	53,0	1,65	3,35
5: Proximal depth	12	35,5	33,3	37,0	1,41	3,97
6: Dist. breadth at tuberosities	16	41,8	38,0	44,5	1,79	4,28
7: Max. length of trigonum phal.	16	53,4	47,0	62,0	3,69	6,91
10: Med. supratuberosital length	15	64,0	61,0	68,0	2,42	3,78
12: Med. infratuberosital length	16	13,7	12,0	16,0	1,30	9,49
14: Dist. articular breadth	16	40,5	39,0	42,5	1,10	2,72
POSTERIOR I PHALANGES	n	x	min	max	s	v
1: Maximal length	17	80,1	76,0	84,0	2,60	3,25
3: Minimal breadth	18	30,0	27,0	31,0	1,09	3,63
4: Proximal breadth	17	49,2	46,0	53,0	2,16	4,39
5: Proximal depth	16	36,4	34,0	39,0	1,17	3,21
6: Dist. breadth at tuberosities	15	40,1	36,5	42,0	1,47	3,67
7: Max. length of trigonum phal.	16	47,5	42,0	50,0	2,39	5,03
10: Med. supratuberosital length	15	55,7	52,0	60,0	2,34	4,20
12: Med. infratuberosital length	15	16,8	14,0	19,0	1,53	9,11
14: Dist. articular breadth	15	37,4	34,5	39,0	1,49	3,98

Table 4. First phanges of Venta Micena. Measurements in millimeters. Same abreviations as in tables 1 and. 2.

	H	n	F	n	R	n	T	n	MC	n	MT	n	P1A	n	P1P	n	P3A	n
E. simplicidens, Hagerman	300,4	10	398,1	11	345,4	8	368,3	13	242,9	48	274,1	48	86,9	19	79,8	15	64,1	12
E. stenonis, El Rincon					395,0	1			254,1	8	290,0	3	92,4	7	88,9	5	71,0	1
E. stenonis; La Puebla de Valverde	285,0	1	380,0	2	339,0	8	347,0	1	233,0	46	269,0	55	82,7	33	80,0	25	67,1	8
E. granatensis, Venta Micena	265,0	1	382,5	2	346,7	6	365,1	7	247,1	32	284,6	32	86,5	16	80,1	17	59,5	12
E. stenonis, Matassino					344,5	2	362,5	2	241,6	7	277,5	2	89,5	2	89,5	2	70,0	1
E. stenonis, Selvella					340,5	2			244,7	11	282,3	6	85,3	2	85,1	2	68,0	2
E. cf. altidens, Pirro	277,8	1	359,9	2	309,1	1			238,9	17	268,5	17	83,2	5	78,8	2	61,0	2
E. hydruntinus, San Sidero	240,0	1			287,0	2	310,5	2	211,3	3	247,8	1	80,8	2	74,5	1		
E. stenonis, Saint-Vallier	302,7	3	407,1	3	342,7	19	367,2	5	229,1	38	264,4	65	85,2	36	82,4	35	76,4	12
E. stenonis, Sainzelles					340,0	1			246,9	4	275,4	7	80,0	1	78,0	4		
E. altidens, Süssenborn									242,5	2	282,0	1			88,0	1		
E. stenonis, Dmanissi					328,0	2			225,8	8	260,3	8	82,9	4	80,3	9	69,0	2
E. hipparionoides, Akhalkalaki									243,0	2	286,4	7	93,0	1	81,0	1		
E. lylei, Florisbad					240,0	1			181,0	2	220,0	1	75,5	1	67,0	3		
E. tabeti, Aïn Hanech	250,0	1	340,0	1	313,0	3	335,0	1	236,1	22	276,8	38	83,6	10	79,3	14	61,0	1
E. cf. tabeti, Ubeidiyeh									237,8	3	270,7	3	78,3	4	78,8	2	70,0	1
E. grevyi	282,0	19	385,5	19	329,0	20	342,9	20	232,0	21	266,5	21	86,4	21	81,5	20	65,3	18
E. quagga granti	247,0	25	349,2	25	280,0	25	305,3	25	201,7	25	226,4	25	75,3	21	71,3	21	55,6	17
E. hemionus onager	241,3	10	329,7	9	293,5	10	313,0	10	214,1	10	250,8	9	76,3	10	71,2	10	54,0	8

Table 5. Lengths of humerus (H), femur (F), radius (R), Tibia (T) third metacarpal (MC), third metatarsal (MT), first anterior palanx (P1A), first posterior phalanx (P1P) and breadth of the third anterior phalanx (P3A). Measurements in millimeters. n: number of specimens.

	MC 1	n	MC 11	n	MC 4	n	MT 1	n	MT 11	n	MT 4	n	PL+1/2	n	ML+1/2	n	P prot	n	M prot	n
E. simplicidens, Hagerman	243,0	48	45,7	48	26,6	48	274,1	48	45,1	47	31,9	48	30,5	61	27,9	60	10,3	61	11,7	60
E. stenonis, Saint Vallier	229,1	38	51,0	38	28,0	50	264,4	65	51,1	68	33,8	79	30,4	28	27,7	31	10,9	28	10,7	31
E. stenonis, La Puebla de Valverde	233,0	46	48,0	37	26,6	57	269,3	55	47,7	59	32,1	80	31,6	22	28,6	20	10,1	22	10,3	19
E. granatensis, Venta Micena	247,1	32	44,5	51	26,9	56	284,6	32	44,4	77	32,4	63	28,6	52	25,9	45	8,7	51	8,5	43
E. cf. altidens, Pirro	238,9	17	46,5	17	27,6	17	268,5	17	45,6	17	32,4	17	28,0	5	25,2	8	7,4	5	9,5	8
E. altidens, Süssenborn	242,5	2	45,5	3	27,5	4	282,0	1	44,8	5	33,5	4	29,1	25	26,3	19	11,7	24	12,1	19
E. hipparionoides, Akhalkalaki	243,0	2	45,7	4	27,0	4	286,4	7	46,6	8	32,9	8	28,1	1	25,1	2	6,8	1	6,5	2
E. numidicus, Aïn Boucherit	242,0	5	45,4	5	27,5	5	278,8	3	43,7	4	31,4	4	30,3	9	27,3	10	10,3	9	9,7	10
E. tabeti, Aïn Hanech	236,1	22	41,2	25	24,7	34	276,8	38	40,7	30	28,9	47	26,1	83	24,0	100	8,8	89	9,5	110
E. hydruntinus, Roterberg	216,9	6	36,7	7	22,3	4	259,8	6	36,0	6	26,8	2	24,3	18	22,1	27	8,2	18	9,0	28
E. hemionus onager	212,0	16	38,5	16	21,1	16	247,5	16	37,4	16	25,3	16	25,6	47	23,0	48	11,4	47	11,0	48

Table 6. Metapodial and upper cheek teeth measurements in millimeters. MC1 . length of third metacarpal; MC11: distal articular width of the same; MC4: depth at mid-diaphysis of the same; MT1: length of third metataral; MT1 1: distal articular width; MT4: depth at mid-diaphysis; PL+1/2: average of length and width of P3 and P4; ML+1/2 average of length and width of M1 and M2; P prot: length of protocone on P3 and P4; M prot: length of protocone on M1 and M2; n: number of specimens

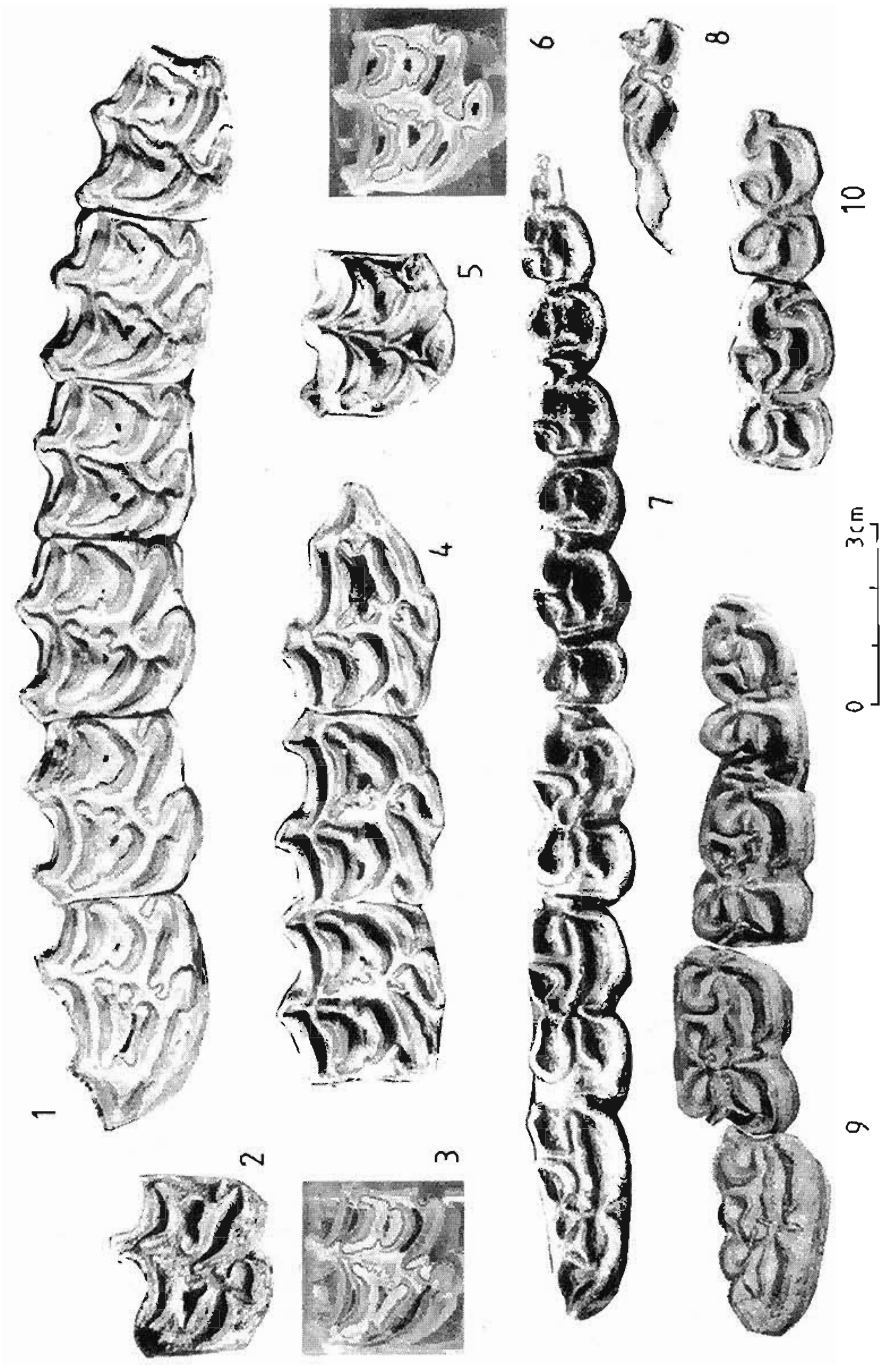

Plate I. 1 VM 84-C3-E9-52: Left upper cheek teeth row. 2 and 3. VM 83-C3-B5-1: Left. upper P3 or P4. Oclusal view. 3. Section at mid-crown. 4. VMD 69, 68, 67: Right upper P2 P3, and P4 (same individual as VM 84-C3-E9-52). 5. and 6. VM K-11: Left upper P3 or P4. 5. Oclusal view. 6. Section at mid-crown. 7. VM 84-C3-B9-12: Left lower cheek teeth row. 8. VM 84-C3-J9-16: Right lower M3. 9. VM 84 C3-E8-9: Left lower P2, P3, P4and Ml. IO. Venta Micena: Left lower Ml ad M2.