

THE VILAFRANCHIAN EQUINES FROM THE UPPER VALDARNO

JOSEFINA PRIVAT DEFAUS

Key-words: Mammalia, Equidae, Early Pleistocene, Italy.

Resumen. Del análisis morfológico de todos los huesos de las antiguas colecciones florentinas podemos deducir que desde hace aproximadamente 1.7 millones de años hasta hace 1.5–1.4 vivieron en el Valdarno superior dos especies equinas distintas: *E. stenorhis* (forma de talla grande) y *E. stehlini* (forma de talla pequeña).

Dos nuevos yacimientos con ubicación estratigráfica precisa, Matassino y Casa Frata, nos hacen suponer que la forma pequeña y la grande no vivieron en asociación.

El análisis estadístico efectuado sobre los metatarsios y metacarpios de las antiguas colecciones revela que un gran número de ellos poseen longitudes intermedias entre *E. stenorhis* y *E. stehlini*, lo que puede significar una evolución progresiva desde la especie grande a la pequeña.

Los hallazgos fósiles de la Cuenca de Valdichiana nos permiten considerar la posibilidad de coexistencia de las dos especies en la misma cuenca.

Una separación ecológica y una especiación simpátrica parecen explicar el origen de *E. stehlini* desde *E. stenorhis*.

Riassunto. Dall'analisi morfologica di tutte le ossa delle vecchie collezioni a nostra disposizione, risulta possibile affermare che nel Valdarno superiore, tra circa 1.7 e 1.5–1.4 milioni di anni fa, siano vissute due diverse specie equine: *E. stenorhis* (forma di grande statura) ed *E. stehlini* (forma di piccola statura).

Grazie al ritrovamento recente di due faune locali ben ubicate stratigraficamente, Matassino e Casa Frata, possiamo ritenere che la piccola e la grande specie non vissero in associazione.

L'analisi statistica condotta sulla lunghezza dei metatarsi e metacarpi delle vecchie collezioni ci indica che sono presenti un gran numero di campioni con lunghezze intermedie tra *E. stenorhis* e *E. stehlini*; ciò indicherebbe un passaggio graduale fra le due specie.

La documentazione fossile del bacino della Valdichiana ci permette di considerare possibile la coesistenza delle due specie nello stesso bacino.

Una separazione ecologica e una speciazione simpátrica sembrano spiegare l'origine di *E. stehlini* attraverso *E. stenorhis*.

Geological setting.

The fluvio-lacustrine basin of the Upper Valdarno is a typical intermontane basin that has been formed as a result of the post-orogenic extensional tectonic movements that have affected the Northern Apennines since the Up-

per Miocene. The ages of the lacustrine sediments essentially range between Mid Pliocene and Late Pleistocene. Three major phases have been recognized in the evolution of the Upper Valdarno basin (Merla & Abbate, 1967; Azzaroli & Lazzeri, 1977): the first is represented by the Castelnuovo dei Sabbioni Group, the second by the fluvio-lacustrine Montevarchi Group, and the third by the Monticello Group (Magi, 1982). The basin of the Upper Valdarno reached its maximum areal extent in the second lacustrine phase, during the Late Villafranchian. It was at this time that the sediments of the fluvio-lacustrine Montevarchi Group were deposited.

There are three formations in the Montevarchi Group (Merla & Abbate, 1967; Azzaroli & Lazzeri, 1977): the Argille di Figline (Figline Clays), the Sabbie del Tasso (Tasso Sands), and Ciottoli e Sabbie di Colmamento di Conoide (Sands and Gravel Fans).

In the Figline Clays three subunits can be distinguished from bottom to top: Limi di Terranova (Terranova Silts), Argille dell'Ascione (Ascione Clays), and Limi di Oreno (Oreno Silts) (Magi, 1982).

Many fossils, for the most part of vertebrates, have been found in the Montevarchi Group, especially in the Argille dell'Ascione and the Limi di Oreno. The «classic» faunas from the Upper Valdarno come from this group.

As research has progressed over the years, it has become apparent that the so called Fauna del Tasso can be traced to the upper part of the Limi di Oreno rather than the overlying Sabbie del Tasso. Recently, two local faunas have been found which have helped to establish the large scale chronologic succession of the Montevarchi Group. The Matassino Fauna is from the lower half of the Montevarchi Group (Argille dell'Ascione), between 170–180 m above sea level. The Matassino Fauna includes *Archidiskodon meridionalis*, *Equus stenonis*, *Leptobos etruscus*, *Dama nestii*, *Eucladoceros dicranios*, *Sus strozzi*, *Canis etruscus* (De Giuli, 1972). Both the faunistic association and the evolutionary stages reached by the various species correspond closely to those of the Olivola Faunal Unit, typified by a fossiliferous locality of the Val di Magra (Azzaroli, 1977). The composition of the Casa Frata Fauna is very similar to that of the Matassino Fauna, but the type of association is different. It includes *Archidiskodon meridionalis*, *Dicerorhinus etruscus*, *Equus stehlini*, *Leptobos vallisarni*, *Canis etruscus*, *Pachycrouta brevirostris*, *Meganteron cultridens*, *Martes* cf. *martes*, *Lepus valdarnensis*. This faunal association is fairly typical of the Tasso Unit, whose type-locality is not far from Casa Frata, and is also at the same elevation (Borselli et al., 1980).

The transition from the Olivola to the Tasso Faunal Unit seems to have occurred during the period of climatic change that took place in Italy after the Aulla erosional phase, about 1.5 my ago (Arias et al., 1980). This event is characterized by the arrival of new forms (*Canis arnensis*, *Canis falconeri*, *Lep-*

tobos vallisarni, *Hippopotamus antiquus*), as well as the evolution of new species (Azzaroli, 1983).

Historical.

Cocchi first described the species *Equus stenonis* in 1867. Since then Forsyth Major (1877–1880) and Azzaroli (1965) have studied these equines from the Valdarno.

The original skull described by Cocchi and then selected as lectotype by Azzaroli in 1965 came from Terranova Bracciolini, in the Villafranchian basin of the Upper Valdarno. Azzaroli also carefully described other skulls, which had been overlooked because they are crushed and deformed, and distinguished two species. The cranial morphologies are similar, and size and proportions are the major distinguishing characteristics. Azzaroli named the smaller species *Equus stehlini*.

A systematic analysis of the fossils found to date has shown that the dimensions of *E. stenonis* are rather variable, while *E. stehlini* seems more uniform (De Giuli, 1972; Azzaroli, 1982).

Equus stehlini is, cronologically speaking, younger than *E. stenonis*, and its presence is restricted to the upper part of the Late Villafranchian. *Equus stenonis* was already present in the Mid Villafranchian. The larger species was distributed over a wide area that includes Italy, France (the French Villafranchian localities of Senèze and St. Vallier are very important; Prat, in 1964, called *E. stenonis senezensis* the small form from Senèze, and *E. stenonis vireti* the form from St. Vallier), Spain, Central Europe, Great Britain and China (Azzaroli, 1982). *E. stehlini*, on the other hand, is limited to Italy, France and Georgia, U.S.S.R. (Gabunia & Vekua, 1981).

Stratigraphic occurrence of the Valdarno Equines.

The majority of the fossil equines of the Upper Valdarno are from collections made in the last century, and therefore information on their stratigraphic locations is very scant. The precise locations where fossils were found are only known in a few cases, while for the most part the fossils are labelled as being from the «Upper Valdarno», or «Near Terranova», or «Near Figline», or «Near S. Giovanni Valdarno». These terms are completely inadequate for a stratigraphic study.

Fossils have also been found at Infernuzzo, Inferno I, Inferno II, Le Ville, Chiesa delle Ville, Tasso, Vacchereccia, Le Fratte, Le Strette, La Cicogna, Montecarlo, Malpasso and Sammezzano.

In addition to the fact that a place name by itself does not describe a fossil's stratigraphic position, there are different places that have the same name,

and there are old place names that are no longer in use on modern maps and difficult to find on old ones. Because of this, the results of our attempts to trace the stratigraphic position of fossils from the old collections have been uncertain, and there have probably been some errors.

The recent discovery of the local faunas of Matassino and Casa Frata, whose stratigraphic locations are known precisely, has supplied some of the missing pieces of the puzzle which was begun with the fossils from the older collections, though the puzzle has not yet been completely solved.

The Matassino Fauna comes from the Argille di Ascione, at an elevation between 170 and 180 m above sea level, in the lower middle part of the Montevarchi Group. The entire fauna was found in one quarry at Matassino, near Figline, from which clay was taken to make bricks. The equine fossils found at this level belong to the species *E. stenorhis* Cocchi.

The Casa Frata Fauna was found in calcareous muds and iron rich sands at the top of a hill between Casa Frata and C. Inferno I, north of Terranova Bracciolini in the Upper Valdarno (Borselli et al., 1980). The Casa Frata Fauna, which is from a higher elevation (about 210 m a.s.l.) than the Matassino Fauna, also came from the Montevarchi Group. It occurs in the Oreno Silts. Several bones that belong to an equid of the species *E. stehlini* were found here.

Le Ville, L'Inferno, Le Fratte, Tasso, Cicogna and Le Strette all belong to the Tasso Faunal Unit, whose elevation ranges between 210 and 230 m above sea level (Azzaroli, 1977). The fossils found in these localities belong to the same level as those from Casa Frata. In fact, the majority of the fossils from these places are attributed to *E. stehlini*, even though at Tasso, Le Ville and Cicogna remains of the *E. stenorhis* were also found. As we said before, the stratigraphic documentation of these finds is not precise, and in many sites more than one stratigraphic level may be exposed.

At other places such as Malpasso and Sammezzano, which are at lower elevations, large equines, like the ones from Matassino, have been found.

Description.

Skulls.

There are many skulls in the old collections of equines from the Upper Valdarno. They are, for the most part, crushed and distorted, and in many cases we only have fragments, such as tooth rows, or the anterior parts of the jawbones. Because they are almost intact, the type skull of *E. stenorhis* (IGF 560) and the type skull of *E. stehlini* (IGF 563), are the most representative. Detailed descriptions of both can be found in Azzaroli (1965) and Privat

(1984). We were able to separate the skulls of the smaller species from those of the larger one because the skull of *E. stehlini* is smaller and its muzzle is shorter.

Neither Matassino nor Casa Frata produced intact skulls, though they both produced fragments of jawbones and tooth rows.

A comparison of the length of the prosthion—nasal notch of the skulls of *E. stenonis* and *E. stehlini* shows that there are significant differences. Two measurements of the external nares of *E. stenonis* gave lengths of 217 mm (type skull) and 211 mm (IGF 583), while the lengths measured in *E. stehlini* were considerably smaller: 165 mm (type skull) and 162 mm.

This is due to the shorter rostrum of *E. stehlini*; however, in both species the notch extends backwards as far as P³. This unusually deep notch characterises *E. stenonis*, *E. stehlini*, *E. namadicus* and *E. sivalensis*, and together with other features is evidence of close relationship of these species (Azzaroli, 1982).

Comparative analyses between the lengths of the prosthion—nasal notch of the Italian and French forms show that this measurement in *E. stenonis senezensis*, though relatively short, is much longer than that of the Upper Valdarno *E. stehlini*, and that in *E. stenonis vireti* the prosthion—nasal notch reaches its greatest length, which exceeds that of the longest Valdarno skulls.

In comparing the condylobasal length of the *E. stenonis* type skull (approximately 590 mm) to that of the Olivola skull (620 mm), we can see that the latter is slightly longer, and that both are much longer than the skull of *E. stehlini* (IGF 582), which measures 474 mm.

The lengths of the skulls of *E. stenonis vireti* and *E. stenonis* from the Valdarno are almost exactly the same, while the skulls of *E. stenonis senezensis* are shorter than those of *E. stenonis vireti*, but much longer than those of *E. stehlini* from the Valdarno.

From the comparisons of the above mentioned cranial lengths we can deduce that:

- 1) the dimensions of the skull of *E. stehlini* are much smaller than those of all the varieties of the species *E. stenonis*;
- 2) the dimensions of the skull of *E. stenonis* are highly variable, but quite distinct from those of *E. stehlini*.

Jawbones.

There are many jawbones in the Florentine collections, although with exception of two, which are almost intact, they are for the most part fragmentary. No complete lower jawbones were found at either Matassino or Casa Frata. Detailed descriptions of the individual fossils can be found in Azzaroli (1965), De Giuli (1972), Privat (1984).

Teeth.

In the Florentine collections of fossils from the Upper Valdarno there are considerable numbers of teeth, both as isolated fossils and as components of tooth rows.

Lower Incisors.

There are many lower incisors, and they can be divided into three categories: incisors with well formed infundibula, incisors with poorly formed or rudimentary infundibula and incisors without infundibula. It is difficult to decide whether isolated incisors belong to the larger or the smaller species; only those which are attached to the jawbone can be assigned with certainty. Though the number of satisfactory samples is small, we can see that there are considerable differences between the incisors of *E. stenonis* and *E. stehlini*. *E. stenonis* incisors never lack the infundibulum, which also is never rudimentary; the infundibulum is only partly open in the third incisor. On the other hand, in *E. stehlini* the infundibulum may be rudimentary in the second incisor, and may be lacking altogether in the third (Fig. 1).

All this is in substantial agreement with the fact that the lack of the infundibulum indicates evolutionary progress, according to this criterion *E. stehlini* seems to be more specialised than *E. stenonis*.

The Upper Tooth Row.

As regards the study of premolars and molars, we must point out that the stenonian forms exhibit a fair amount of variation in the morphology of the enamel from individual to individual, and for this reason the only criterion used to distinguish between *E. stenonis* and *E. stehlini* is size. The tooth row of *E. stenonis* is longer than that of *E. stehlini*.

There are only three samples of *E. stenonis* in the Florentine collections upon which the entire length of the tooth row can be measured. The length varies from 178 mm (IGF 560) to 185 mm (IGF 535). IGF 583 is an old animal and consequently the tooth row is shorter (175 mm). The ratio between the length of the molars and the premolars varies between 76.91 (IGF 535) and 86.17 (IGF 583).

In the maxillaries of the type skull and IGF 535, the tooth row is preceded by the first premolar, which is missing in IGF 583.

The protocone length of *E. stenonis* is variable and changes with wear.

There are more samples from the small species in the Florentine collections, and we were able to measure the tooth rows of nine individuals (IGF 563 was excluded because of its age). The length of the tooth row varies between a minimum of 156 mm (IGF 543), and a maximum of 173 mm (IGF 564), while the average length, 165 mm, is much shorter than in *E. stenonis*.

The molar–premolar ratio varies between 76.28 (IGF 523) and 93.82 (IGF 534). A comparison between *E. stehlini* and *E. stenorhis* ratios shows that the premolars of the former tend to be larger, and, as a result, the length of the premolars with respect to molars is less in *E. stehlini*. Before this conclusion can be confirmed, further study of larger samples is necessary.

The protocone, in all of the teeth that can be attributed to *E. stehlini*, is short, with the exception of one isolated tooth with a long protocone found at Casa Frata. In *E. stehlini* the first premolar is consistently missing.

Upper jawbones with complete tooth rows were not found either at Casa Frata or at Matassino.

The lengths of the tooth rows of *E. stenorhis* from Olivola are somewhat

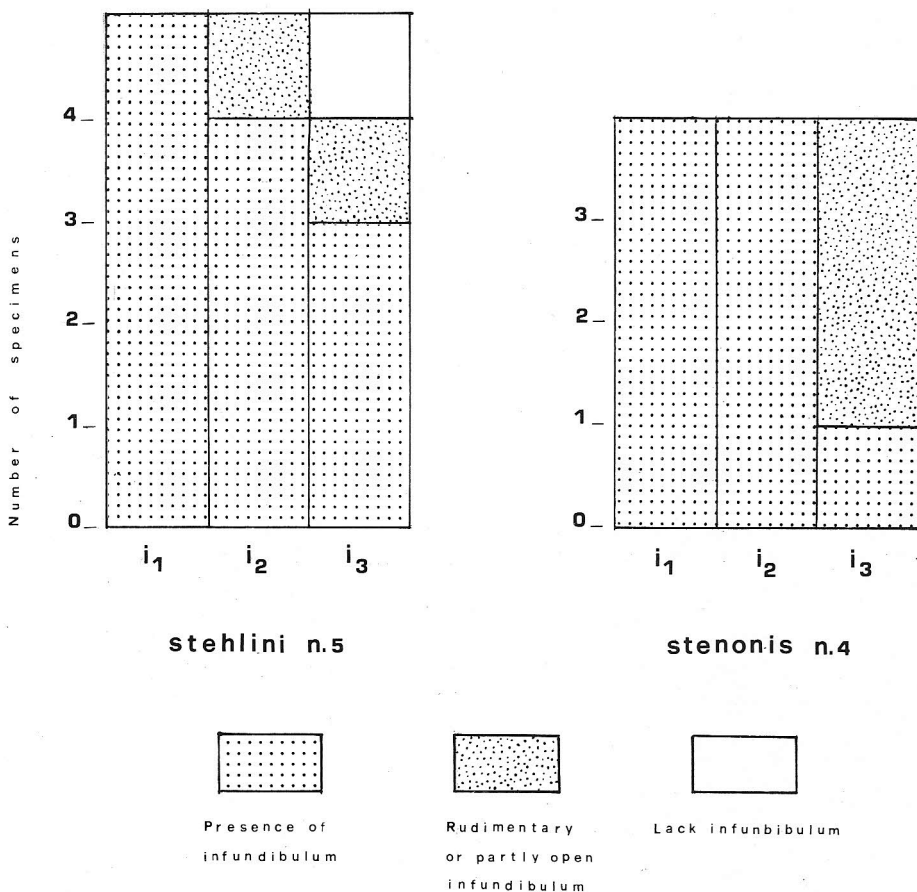


Fig. 1 — Differences between incisors of *E. stenonhis* and *E. stehlini*. The incisors of *E. stenonhis* never lack the infundibulum, which is also never rudimentary; the infundibulum is only partly closed in the third incisor. (I_3). In the *E. stehlini* the infundibulum may be rudimentary in the second incisor, and may be lacking altogether in the third.

greater than those of *E. stenonis* from the Valdarno, while the greatest values are reached by *E. stenonis vireti*. In *E. stenonis senezensis* the range of tooth row lengths overlaps, to a certain degree, the range of *E. stehlini*, and though it does not reach the minimum *E. stehlini* values, it does include the entire range of *E. stenonis*.

In comparing the molar–pre-molar length ratios of all the samples we have considered until now, we can see that they are more or less constant, though they seem to be somewhat larger in *E. stehlini*. A higher ratio indicates that the premolars are smaller with respect to the molars. We can attribute this characteristic to the shortening of the muzzle that the smaller species underwent, which resulted in a shortening of the premolars with respect to the molars.

Lower Tooth Rows.

There are four lower jawbones that are well preserved enough to allow us to measure the tooth row length of *E. stenonis*, which varies between 168 mm (IGF 508), and 182 mm (IGF 526). The average is 175.5 mm. The molar–pre-molar ratio varies between 90.32 (IGF 563) and 96.62 (IGF 525). As was the case with the upper teeth, there are extreme variations in enamel morphology.

We measured the tooth rows of nine lower jaws from the Valdarno attributable to *E. stehlini*, and found that the length varies between 155 mm (IGF 522) and 166 mm (IGF 582); the average is 161 mm. This average is much shorter than in *E. stenonis*, though some of the lower tooth rows fall between the ranges of the two species. The molar–pre-molar ratio varies between 91.86 (IGF 542) and 110 (IGF 511).

Neither Matassino nor Casa Frata produced lower jawbones with intact tooth rows.

Comparative analyses of the lower tooth rows from Olivola, Senèze and St. Vallier with those from the Florentine collections of Valdarno fossils reach the same conclusions as comparisons of the upper tooth rows.

Post–Cranial Skeleton.

The Florentine collections have a wide assortment of limb bones, as well as some vertebrae, scapulae and pelvis fragments. The majority of the fossils are from separate individuals, and only rarely have articulated bones been found. This is probably due, in part, to lack of care in collecting, but, more importantly, to the conditions that prevailed during deposition.

Descriptions of all the post–cranial fossils can be found in Azzaroli (1965), De Giuli (1972) and Privat (1984).

Complete statistical analyses were only possible for those bones which were found in large quantities, such as metacarpals and metatarsals.

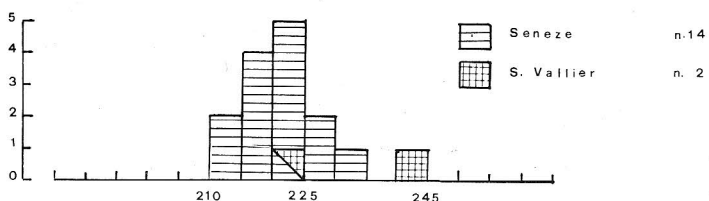
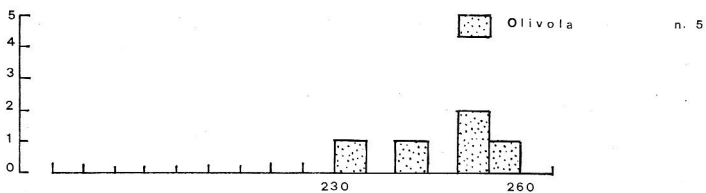
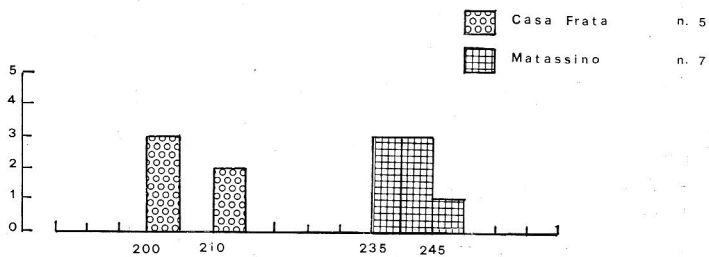
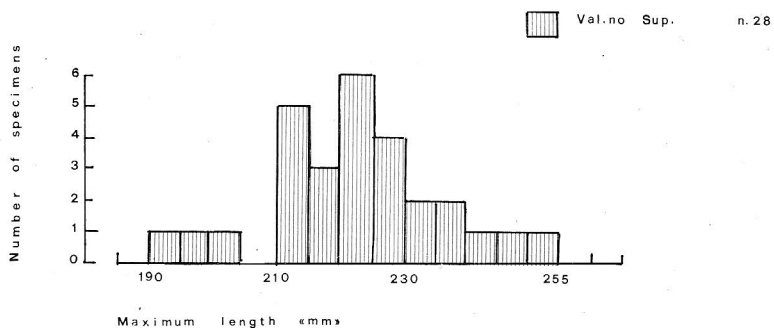


Fig. 2 – Comparative histograms between the lengths of metacarpals of the Italian and French Villafranchian forms.

Metacarpals.

Of the 37 metacarpals in the Florentine collections, 28 are intact and nine are fragmentary. Their greatest length varies between 190 and 250 mm, with an average of 221.6 mm. The range of variation is wide (Fig. 2).

Even though we had little difficulty in sorting out the other bones that were represented by small numbers of intact specimens, we were less certain

Third Metacarpal of U. Valdarno	Total length mm	Breadth of the diaphysis (mm)	Slenderness Index
IGF 11.055	190	29	15,26
" 11.047	198	29	14,64
" 11.059	202	30	14,85
" 11.046	210	32	15,23
" 11.054	211	30	14,85
" 10.995	211	33	15,63
" 11.060	212	30	14,15
" 11.062	212	30	14,15
" 11.065	215	31	14,41
" 11.053	215	34	15,81
" 11.048	216,5	35	16,16
" 11.049	220	34	15,45
" 11.058	220	30	13,63
" 11.051	221	37	16,74
" 11.057	222	35	15,76
" 11.045	222	38	17,11
" 11.061	223	33,5	15,02
" 11.043	225	31	13,77
" 545	227	36,5	16,07
" 11.044	229	32	13,97
" 547	231	32	13,85
" 568	235	38,5	16,3
" 11.039	237	36	15,18
" 11.040	238	37	15,54
" 11.041	241	35	14,52
" 543	246	37,5	15,24
" 11.038	250	38	15,2
" 11.050	226	33	14,60

Tab. 1

about the metacarpals. In fact, after sorting out the long ones, which certainly belong to *E. stenonis*, from the short ones, which come from *E. stehlini*, we were left with several specimens of intermediate length.

Seven intact metacarpals and four fragmentary ones were found at Matassino. Their maximum length varies between 236 and 248 mm while the average

Third Metacarpal of Matassino	Total length (mm)	Breadth of the diaphysis (mm)	Slenderness Index
IGF 12.825	236	39	16,38
" 12.827	237	39	16,45
" 12.826	238	36	15,52
" 12.826	243	36,5	14,98
" 12.829	242	39	16,11
" 12.828	244	35,5	14,54
" 12.830	248	36	14,51

Tab. 2

is 240.86 mm. Figure 2 clearly shows that the size range of the Matassino metacarpals is the same as that of the larger specimens from the Florentine collections.

At Casa Frata five intact metacarpals and two fragmentary ones were found. Their lengths vary between 201 and 215 mm, with average of 206.8 mm.

Third Metacarpal of Casa Frata	Total length (mm)	Breadth of the diaphysis (mm)	Slenderness Index
IGF 606 V	201	32	15,92
" 605 V	203	30,5	15,02
" 609 V	204,5	32	15,64
" 691 V	211	32	15,16
" 608 V	215	34,5	16,06

Tab. 3

Figure 2 shows that the metacarpals from Casa Frata are longer than those of the smallest animals from the Valdarno in the Florentine collections.

The second and third histograms of Figure 2 show that the metacarpals from Olivola are slightly longer than those attributed to *E. stenonis* from the Valdarno, and even though there are some slight statistical differences, they can be correlated with the Matassino metacarpals (De Giuli, 1972).

The histograms of the lengths of the metacarpals of the French equines show that limbs of *E. stenonis vireti* were shorter than those of *E. stenonis* from both Olivola and the Upper Valdarno, and longer than those of *E. stenonis senezensis*.

The metacarpals of the small species from Senèze are longer than those from the Valdarno that have been attributed to *E. stehlini*. Their mean length coincides with the peak of the mixed sample histogram of Upper Valdarno. The metacarpals from St. Vallier seem to be the strongest of all the stenonian forms, followed by those from Senèze. In any case, the slenderness index of the metacarpals varies considerably within each form.

Metatarsal.

There are 42 intact metatarsals and 19 fragmentary ones, in many of which the proximal end is preserved, in the Florentine collections. Their maximum length varies between 224 and 287 mm, the average is 253.8 mm.

As was the case with the metatarsals, even though the large range of metapodial sizes indicates that there are probably two different species present, it is not possible to separate them sharply, because there are a number of metatarsals whose lengths fall between the extreme values (Fig. 3).

Three intact metatarsals and a few fragmentary ones were found at Matassino. Their maximum length varies between 273 and 280 mm, and averages 277.6 mm.

Four fragments and eight intact metatarsals were found at Casa Frata. Their average length is 243 mm, while the maximum is 254 mm and the minimum is 239 mm.

Figure 3 shows that the metatarsals from Matassino correspond, more or less, to the larger ones from the older collections. While the metacarpals from

	Third Metatarsal of U. Valdarno	Total length (mm)	Breadth of the diaphysis (mm)	Slenderness Index
IGF	11.306	224	27	12,05
"	11.012	229	29	12,66
"	11.032	231	29,5	12,77
"	546	231	28	12,12
"	11.020	233	29	12,44
"	11.010	233	29	12,44
"	11.002	233	30	12,87
"	10.994	234	28	11,96
"	11.021	234	30	12,82
"	11.019	237	31	13,08
"	11.016	239,5	30	12,52
"	11.031	240	29	12,08
"	11.009	241	29,5	12,24
"	11.018	244	30	12,29
"	10.992	247	36	14,57
"	11.015	247	31,5	12,75
"	11.029	250,5	28,5	11,37
"	11.030	250	31,5	12,60
"	11.017	252	30,5	12,10
"	11.028	254	32	12,59
"	579	254	32	12,59
"	11.034	257	30	11,67
"	11.011	258	34	13,17
"	11.008	258	29	11,24
"	11.033	260,5	32	12,28
"	11.005	260	34	13,07
"	10.993	261	28	10,72
"	11.006	261	29	11,11
"	11.007	261	29	11,11
"	11.014	261	34	13,02
"	11.035	261	30	11,49
"	11.003	262	30	11,45
"	567	268	32	11,94
"	11.001	268	35,5	13,24
"	548	272	36	13,23
"	569	274	35	12,77
"	544	274	36	13,13
"	11.036	279	35	12,54
"	1316 V	276	39,5	14,31
"	11.383	280	33	11,78
"	11.013	286	34	11,88
"	11.037	287	38	13,24

Tab. 4

Matassino correspond to those from Olivola', the metatarsals are shifted to the right with respect to the smaller forms from the Valdarno. In other words, they are longer. A comparison of the histograms of the French and the Valdarno metatarsals leads to conclusions that are analogous to those reached for the metacarpals, though with the metatarsals we can see that the dimensions of those from Casa Frata and Senèze partially overlap.

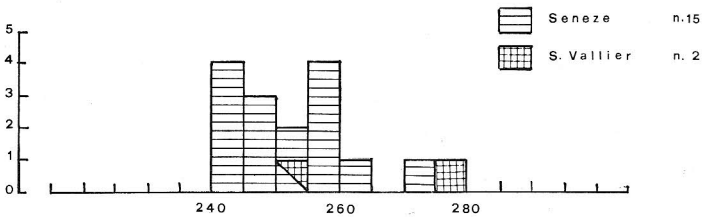
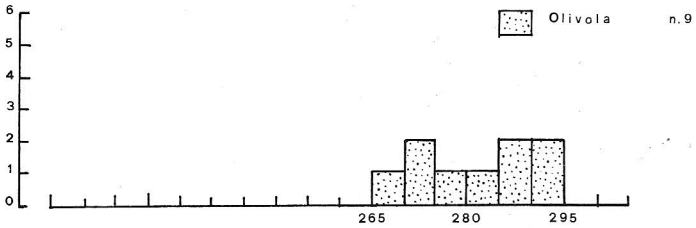
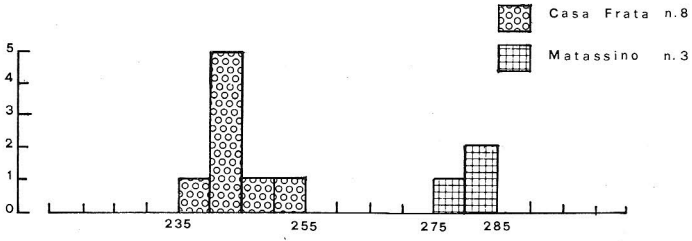
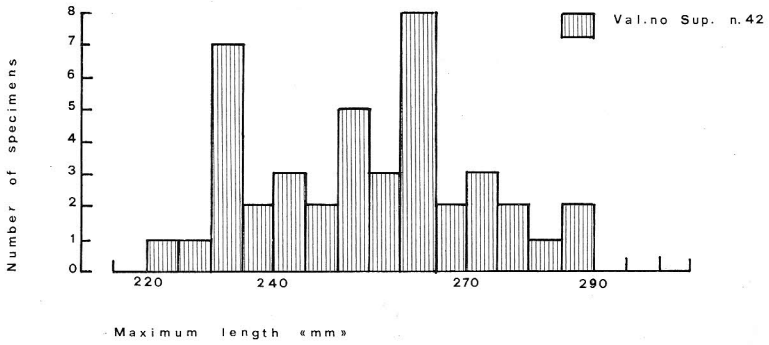


Fig. 3 — Comparative histograms between the lengths of metatarsals of the Italian and French Villafranchian forms.

Third Metatarsal of Matassino	Total length (mm)	Breadth of the diaphysis (mm)	Slenderness Index
IGF 12.833	280	34	12,14
" 12.834	280	34	12,14
" 15.231	273	39	14,28

Tab. 5

Third Metatarsal of Casa Frata	Total length (mm)	Breadth of the diaphysis (mm)	Slenderness Index
IGF 611 V	243	30,5	12,55
" 612 V	239	30,5	12,70
" 613 V	242	31	12,80
" 614 V	239	31,5	13,17
" 616 V	243	30	12,34
" 617 V	240	29,5	12,29
" 618 V	246	29	11,78
" SMT 2	254	31,5	12,40

Tab. 6

Conclusions.

On the basis of the morphological analysis conducted on the bones in the Florentine collections it seems safe to conclude that two different species lived in the Upper Valdarno between about 1.7 and 1.5–1.4 million years ago.

Several different hypotheses have been advanced to explain the origin of *E. stehlini*. One suggests that *E. stehlini* probably migrated from eastern Europe, and then replaced *E. stenonis*, who lived in Europe at the beginning of the Pleistocene (De Giuli, 1972).

A detailed study of cranial features, carried out by Azzaroli in 1982, has brought to light new data that suggest that *E. stehlini* is closely related to *E. stenonis*. The fact that in both North America and Eurasia small species co-existed with large, similar species further supports the idea that the smaller species may have been derived from the larger one. This would indicate that speciation (divergent evolution) occasionally led to reduction in size.

Geographic isolation combined with allopatric speciation are usually thought to be the conditions necessary for this type of evolutionary divergence. In our case, however, it seems unrealistic to say that the two populations of *E. stenonis* and *E. stehlini* remained topographically isolated for a relatively long period of time in such a small area, and therefore the possibility of sympatric speciation must be considered.

Statistical analyses of the better represented types of bones in the Floren-

tine collections show that there was a great number of individuals whose size was intermediate between *stenonis* and *stehlini*.

On the other hand, species with considerable individual variation, like *E. stenonis*, can be the starting points for divergent evolution. Therefore our hypothesis of a gradual speciation within a faunal province (Italy and France) is supported by our statistical analyses.

On the basis of this hypothesis we can postulate that there are three types of equids in the Florentine collections: *E. stenonis* (the parent species), transitional forms, and the new smaller species. This scheme does, however, raise the following questions:

a) Is it correct to affirm that with the appearance of *E. stehlini*, *E. stenonis* gradually became extinct?

b) What relation, if any, exists between *E. stehlini* and the form from Senèze, which was also a small animal?

The answer to the first question will become apparent when we will have precise information about the Farneta Fauna. Until now fossils of *E. stehlini* have been collected at Farneta (Valdichiana). Gioiella, which is another locality in the same basin whose precise stratigraphic position is uncertain, has yielded fossils of *E. stenonis* which indicate that the animal was smaller and stronger than the one from the Valdarno. Much of the material from Gioiella is fragmentary and its age is unclear. Therefore, though the fossils from the Valdichiana Basin cannot give us the answer we had hoped for, they do show that *E. stenonis* survived beyond the Tasso Faunal Unit, and the possibility that the two species coexisted therefore exists.

Diversification, coupled with the progressive ecological separation could explain the coexistence, in some regions, of the parent with the daughter species.

The answer to the second question is also difficult because, unfortunately, the fauna from Senèze is probably heterogeneous both in terms of its composition and its age. Part of the fauna could be intermediate in age between those of St. Vallier and Olivola, while the more recent part of the fauna could be of the same age as the Farneta Fauna Unit. Unfortunately, the two age groups cannot be separated. Prat, in 1964, assumed that *E. stenonis senezensis* (a small animal) was derived from *E. stenonis vireti* (a large, strong animal).

Following a line of reasoning analogous to the one applied to the Villafranchian fauna of the Upper Valdarno, we can assume that *E. stenonis vireti*, who lived in the Rhone valley (Drôme), diversified and brought forth a new, smaller species: *E. stenonis senezensis*. The latter species, however, occupied a new ecological niche in the highlands of the region (Central Massif).

It seems therefore safe to conclude, on the basis of the fossil remains, that ecological separation and sympatric speciation took place during the Villafranchian.

R E F E R E N C E

- Abbate E., Bartolini C., Billi P., Cicali F., De Giuli C., Ferrini G., Magi M. & Sagri M. (1983) - I depositi fluvio-lacustri del Valdarno Superiore. *Guida Escursioni Gruppo Informale Sedimentologia CNR*, 27-28 maggio 1983, pp. 1-29, Firenze.
- Alberdi M.T., Arias C., Bigazzi G., Bonadonna F.P., Leone G., Lopez N., Michaux J., Morales J., Robles F. & Soria D. (1982) - Nuevo yacimiento de moluscos y vertebrados del Villafranchiense de la cuenca del Júcar (Albacete, España). *Act. Coll. "Le Villafranchien Méditerranéen"*, Lille 9-10 déc. 1982, pp. 255-271, Lille.
- Alberdi M.T. & Bonadonna F.P. (1983) - El *Equus stenonis* Cocchi como indicador biostratigráfico del Plio-Pleistocene en Italia y España. *VI Reunión Grupo Español de trabajo del Cuaternario*. Santiago Ocasto Vigo. (in the press).
- Ambrosetti P., Azzaroli A., Bonadonna F.P. & Follieri M. (1972) - A scheme of Pleistocene chronology for the Tyrrhenian side of central Italy. *Boll. Soc. Geol. Ital.*, v. 91, pp. 169-184, Roma.
- Arias C., Azzaroli A., Bonadonna F.P. & Bigazzi G. (1980) - Magnetostratigraphy and Pliocene-Pleistocene Boundary in Italy. *Quaternary Research*, v. 13, pp. 65-74, New York.
- Azzaroli A. (1950) - Osservazioni sulla formazione villafranchiana di Olivola in Val di Magra. *Att. Soc. Tosc. Sc. Nat., Mem.*, v. 57, pp. 104-111, Pisa.
- Azzaroli A. (1965) - The two villafranchian horses of the Upper Valdarno. *Palaeont. Ital.*, v. 59, pp. 1-12, 10 pl., Pisa.
- Azzaroli A. (1966) - Pleistocene and Living Horses of the Old World. *Palaeont. Ital.*, v. 61, pp. 1-15, 46 pl., Pisa.
- Azzaroli A. (1977) - The Villafranchian stage in Italy and the Plio-Pleistocene Boundary. *Giorn. Geol.*, v. 41, pp. 61-79, Bologna.
- Azzaroli A. (1979) - On a Late Pleistocene Ass from Tuscany; with notes on the History of Asses. *Palaeont. Ital.*, v. 71, pp. 27-47, 9 pl., Pisa.
- Azzaroli A. (1982) - On Villafranchian palaeartic Equids and their allies. *Palaeont. Ital.*, v. 72, pp. 74-95, 4 pl., Pisa.
- Azzaroli A. (1982) - Remarques sur les subdivisions chronologiques du Villafranchien. *Act. Coll. "Le Villafranchien Méditerranéen"*, Lille 9-10 déc. 1982, pp. 7-14, Lille.
- Azzaroli A. (1983) - Quaternary Mammals and the "end Villafranchian" dispersal event - a turning point in the history of Eurasia. *Palaeogeogr., Palaeoclim., Palaeoecol.*, v. 44, pp. 117-139, Amsterdam.
- Azzaroli A. & Lazzeri L. (1977) - The lakes of the Upper Valdarno. *Publ. 28 "Centro per la geologia dell'Appennino in rapporto alle Geosinclinali Mediterranee"*, pp. 1-4, Firenze.
- Azzaroli A., De Giuli C., Ficarelli G. & Torre D. (1982) - Table of the stratigraphic distribution of terrestrial mammalian faunas in Italy from the Pliocene to the early middle Pleistocene. *Geogr. Fis. Dinam. Quat.*, v. 5, pp. 55-58, Torino.
- Borselli V., De Giuli C., Ficarelli G. & Mazzini M. (1980) - Casa Frata: una località fossilifera del Villafranchiano Superiore presso Terranuova Bracciolini (Arezzo) nel Valdarno Superiore. *Boll. Soc. Paleont. Ital.*, v. 19, n. 2, pp. 254-258, 2 fig., Modena.
- Cocchi I. (1867) - L'uomo fossile nell'Italia centrale. *Mem. Soc. It. Sc. Nat.*, v. 2, n. 7, pp. 1-80, 4 pl., Milano.
- De Giuli C. (1972) - On the type form of *Equus stenonis* Cocchi. *Palaeont. Ital.*, v. 68, pp. 35-49, 11 pl., Pisa.

- Eisenmann V. (1975) - Nouvelles interprétations des restes d'équidés de Nihowan (Pléistocène inf. de la Chine du nord): *Equus teilhardi*. *Géobios*, v. 8, pp. 125–134, Lyon.
- Eisenmann V. (1979) - Etude des cornets des dents incisives inf. des *Equus* actuels et fossiles. *Palaeont. Ital.*, v. 71, pp. 55–75, 2 pl., Pisa.
- Eisenmann V. (1979) - Les métapodes d'*Equus* sensu lato. *Géobios*, v. 12, pp. 863–886, Lyon.
- Eisenmann V. (1980) - Les chevaux fossiles et actuels: crânes et dents jugales sup. *Ed. CNRS, Cahiers Paléont.*, pp. 1–186, 22 pl., Paris.
- Eisenmann V. (1981) - Etude des dents jugales inf. des *Equus* actuels et fossiles. *Palaeovertebrata*, v. 10, pp. 127–226, Montpellier.
- Eisenmann V. & De Giuli C. (1974) - Caractères distinctifs des I–phalanges ant. et post. chez les équidés actuels et fossiles. *Bull. Soc. Géol. France*, s. 7, v. 16, pp. 352–361, Paris.
- Forsyth Major C.J. (1877–1880) - Beiträge zur Geschichte der fossilen Pferde, insbesondere Italiens. *Abh. Schweiz. Pal. Ges.*, v. 4–7, 144 pp., 7 pl., Basel.
- Gabunia L.K. & Vekua A.K. (1981) - Terrestrial mammals of the Pliocene and early Pleistocene and boundary between Neogene and Quaternary in Georgia, USSR. Field Conference, Neogene–Quaternary Boundary, India 1979, Proceedings, pp. 45–48.
- Gromova V. (1949) - Histoire des chevaux (genre *Equus*) de l'Ancien Monde. *Trav. Inst. Paléont. Acad. Sc. URSS*, v. 17, pp. 1–373, (French translation Centr. Etud. Docum. Paléont., 13, Paris 1965).
- Howe J.A. (1970) - The range of variation of *Equus (Plesippus) simplicidens* Cope from the Broadwater Quarries of Nebraska. *Journ. Paleont.*, v. 44, pp. 958–968, Tulsa.
- Magi M. (1982) - Indagini stratigrafiche e sedimentologiche sui terreni fluvio–lacustri nell'area centro meridionale del Valdarno Superiore. Tesi di Laurea, Univ. Firenze.
- Marcucci M. (1970) - Notizie Paleobotaniche sul Valdarno. *Guide Escursioni 65° Congr. Soc. Geol. Ital.*, pp. 139–140, Roma.
- Merla G. & Abbate E. (1967) - Note illustrative della carta geologica d'Italia a 1:100000 (Foglio 114 «Arezzo»). *Serv. Geol. Italia*, pp. 1–52, Roma.
- Prat F. (1964) - Contributions à la classification des Equidés Villafranchiens. *P.V. Soc. Linn. Bordeaux*, v. 101, pp. 14–32, 2 pl., 3 tab., Bordeaux.
- Prat F. (1966) - «Les Equidés». In Lavocat R. Ed. — Faunes et Flores préhistoriques de l'Europe occidentale, pp. 195–215, N. Boubée et C. ie, Paris.
- Prat F. (1980) - Les Equidés villafranchiens de France, Genre *Equus*. *Ed. CNRS, Cahiers Quatern.*, v. 2, pp. 1–290, Paris.
- Privat J. (1984) - Gli Equidi villafranchiani del Valdarno Superiore. Tesi di Laurea, Univ. Firenze.
- Torre D. (1967) - I cani villafranchiani della Toscana. *Palaeont. Ital.*, v. 63, pp. 113–138, Pisa.
- Venturini P. L. (1977) - I ciottoli del gruppo fluvio–lacustre di Montevarchi. Tesi di Laurea, Univ. Firenze.
- Viret J. (1954) - Le loess à bancs durcis de Saint–Vallier (Drôme) et sa faune de Mammifères villafranchiens. *Nouv. Arch. Mus. Hist. Nat. Lyon.*, v. 4, pp. 1–200, 33 pl., Lyon.
- Von den Driesch Angela (1976) - A Guide to measurement of animal bones from Archeological sites. *Peabody Mus. Bulletin*, n. 1, Peabody Mus. Archeol. Ethnol., Harvard University, pp. 1–137, Harvard.