**Abstract  
The rich material of equid fossils from SenÃ¨ze is not homogeneous. Beside a few caballine teeth and limb bones (possibly cataloguing errors or intrusive specimens), there is evidence of at least two species. The bulk of the material may be referred to Allohippus senezensis, which by size and proportions is intermediate between A. pueblensis and A. mygdoniensis. One upper cheek tooth and 16 limb bones belong to a very large ?Allohippus. There are moreover a few fossils larger than the average of A. vireti of Saint-Vallier (France), and a few others as small or smaller than ?Allohippus of Pyrgos (Greece). The affinities and ages of various Pliocene and Pleistocene equid species are discussed and illustrated.  
Keywords  
Allohippus, A. senezensis, A. mygdoniensis. Equus Sussemionus suessenbornensis. Late Pliocene. Early and Middle Pleistocene.**

### 1. Preliminaries

Before describing and discussing the Senèze equids, it may be useful to summarize and explain the general background used here.

****1.1 Chronology and Genera****  
The chronological frame of Figure 1 is based on the article of Nomade et al., 2013. This figure summarizes and emphasizes the uncertainties of generic attributions and/or geological age of many Villafranchian fossil equids. The genera names (columns) do not bear question marks only when the localities yielded crania because only cranial proportions are certain to distinguish *Equus*, *Allohippus*, and *Plesippus*.

As much as we know now:   
 *Plesippus* was found at Locality 32, China, around 2.5 Ma, and at Bajiazui, also in China, which is younger (Eisenmann and Deng, 2005). Therefore it cannot be excluded that some poorly known Villafranchian equids referred to ?*Allohippus* may actually belong to *Plesippus*.   
 *Allohippus* ranges at least from Saint-Vallier LD3 (? 2.4 Ma) to Ceyssaguet (1.2 Ma). A few fossils from Saint-Vallier LD2 seem to belong to a form intermediate between that from El Rincon (? 2.5 Ma) and A. vireti from Saint-Vallier LD3 (Eisenmann, 2004).   
 *Equus* appears in the Old World around 2 Ma (Eisenmann 2006). Therefore, any poorly documented equid dated between 2 and 1.2 Ma may belong either to *Equus* or to *Allohippus*. In particular this is the case of the very large Villafranchian fossils that may belong as well to *E. (Suessemionus)* as to *Allohippus*, especially so when their age is guessed (very large specimens of Senèze, Kislang, Gannat).

Admittedly, many listed â€œ?*Allohippus*â€ are very probably real *Allohippus*, but I wish to make clear that what is probable is not certain. After all was it probable that a survivor of the subgenus *Sussemionus* would be found in deposits of Southwestern Siberia 40 Ky old? (Eisenmann & Vasilev, 2011).

****1.2. Crania****  
In the Old World, there are three groups of crania belonging to monodactyl horses : *Plesippus*, *Allohippus*, and *Equus*. They have been discussed at length previously (Samson, 1975; Forsten and Eisenmann, 1995; Eisenmann and Baylac, 2000; Eisenmann 2004; Eisenmann and Deng, 2005). Schematically, *Equus* have longer post-vomerine length (Basion to posterior border of vomer) relative to overall palatal length (from Prosthion to anterior border of choanae) than *Plesippus* and *Allohippus*; *Allohippus* have a deeper naso-incisival notch relative to cheek length than *Plesippus* (Fig. 2) and a shorter vomerine length relative to the palatal (sensu stricto) length (Fig. 3).

Although most crania from Seneze are poorly preserved, they clearly belong to *Allohippus* (see Table 1).

### ****2. Material and Methods****

Most of the fossil equids from Senèze were collected long ago and are preserved in several institutions: the University Claude Bernard-Lyon I (specimens indicated by the prefix FSL) and Museum d’Histoire naturelle in Lyon (Sen), the Laboratoire de Paléontologie of the Muséum national d’Histoire Naturelle in Paris (PA), and the Museum of Natural History in Basel (NMB Se) are the richest. A few specimens are part of the collections of the Laboratoire d’Anatomie Comparée of the Muséum national d’Histoire Naturelle, Paris (AC). Specimens newly recovered by the Franco-American team have not yet been catalogued or deposited formally in any institution, but they are indicated here by SEN followed by the year of discovery and a field sequence number (e.g., SEN 05-0081).  
Comparisons in this article are based mostly on personal observations and occasionally on data communicated and/or published by: Samson (1975; Oasele, Romania); Mauser (1987; Wà¼rzburg-Schalksberg, Germany); Koufos (1992; Gerakarou, Greece); Azzaroli and Voorhies (1993; Grandview, Idaho, USA); Aouadi (1999; Ceyssaguet, France); Athanassiou (2001; Sesklo, Greece); Koufos personal communication 1990 (Dafnero, Greece); and van Kolfschoten personal communication 1985 (Pyrgos, Greece). Simpson’ s ratio diagrams, scatter diagrams, and variability size indices are given to illustrate differences and similarities between fossil teeth and bones. Tables provide raw measurements. See System of measurements for Equus bones and teeth rubrique <http://www.vera-eisenmann.com/-system-of-measurements-for-equus-bones-and-teeth-english->

The material is rich and comprises skulls, mandibles, associated teeth and limb bones, and isolated fossils. The preservation of long bones and teeth is usually good, the skulls, however, are often crushed and some were heavily reconstructed.

### ****3. Occurrence of several Equids at Senèze****

I have noted previously (Eisenmann 1981, 1985) that the mandible of the mounted skeleton FSL 210993, ex 96132 cannot belong with the cranium. In consequence the caballine pattern of the lower cheek teeth noted by Viret (1954, p. 145) and commented on by Azzaroli (1965, pp. 2-3) does not mean that Allohippus may have caballine teeth, but instead that some caballine specimens (as the lower premolars Sen 3982) are present inside the Senèze collections, either because they came from younger levels or because they were put there by error. Here I’ll only briefly mention two probably caballine metapodials (Fig. 4).

****3.1 Cheek teeth****  
With their short protocones, the upper cheek teeth of Senèze are quite usual for *Allohippus*. One upper P3, Se 338, is larger than the rest (Figs. 5 and 6) and may be referred to the very large equid discussed below.

****3.2 Limb bone size (breadths)****  
Although there are differences in size inside the A. senezensis sample, all fossils (excluding the "caballines") mentioned above may belong to a single species. This is not the case of 16 considerably larger specimens. The difference in size is well illustrated by the Variability Size Index (VSI) - one of the size index scaling techniques used by archeozoologists (Uerpmann 1982, Meadow 1999). A sample including all the bones of a taxon is chosen as the reference. Mean and standard deviation are calculated for each measurement of this sample. The comparisons are made using the following formula:  
VSI = 25(x-m)/s  
where s is the standard deviation of the mean (m) of the reference measurements to which another measurement (x) is being compared. The obtained values are plotted on a histogram graduated in one, two, three, or more standard deviations from the reference. As phrased by Meadow (1986), Â« Using this formula, the standard dimension is set at zero; a measurement one standard deviation larger than the standard (reference) dimension will be plotted at 25, one standard deviation smaller at â€“25, etc Â».   
I have chosen the sample of *A. vireti* of Saint-Vallier as reference. I considered only the bone breadths (one measure per bone, excluding juvenile specimens). Means and standard deviations for the St. Vallier reference standard are given in Table 22.

Naturally the histogram for Saint-Vallier (Fig. 7) is centered on the 0; it is normally distributed, three standard deviations on each side of the 0. On the histogram for Senèze:   
 Most of the breadths appear on the left side of the histogram, left of one standard deviation from 0, showing that most bones are thinner than those of Saint-Vallier. Their breadths seem normally distributed but less concentrated on the mean than at Saint-Vallier;   
 The breadths of 16 bones (enumerated below) are on the right side of the diagram, all between one and six standard deviations from the 0. They may be referred to a very large equid.  
A rapid description of some specimens is given below.

****3.3 Limb bone size (lengths)****  
Figure 8 shows the size differences of lengths in long limb bones and width in third anterior phalanges from Senèze.

There is clearly a considerable size difference between *A. senezensis*and the very large ?*Allohippus*. I do not know what to make out of the other large first phalanges.

****4. Very large Villafranchian *Allohippus* or *Equus*****

****4.1. Introduction****  
The problem of what was the very large villafranchian equid ("*E. bressanus*", "*E. majo*r", "*E. robustus*") is far from resolved since its precise age is not known, and its main characteristic is its "large" size. However "large", the size overlaps with two other groups of large and better-documented equids: *Allohippus* (most species) and large *Equus (Sussemionus*) (from Sà¼ssenborn, Akhalkalaki, and Northeastern Siberia (*E. coliemensis*, *E. verae*); Eisenmann, 2006, 2010)).

Usually, the metapodials of the latter have larger distal articular widths relative to supra-articular ones. Using this criterion, I consider that the metapodials of Gannat, Wà¼rzburg-Schalksberg, and Senèze belong to the large equid rather than to the E. suessenbornensis group as also do the MC III of Oasele and the MT III of Kislang, Hungary. This could be the only evidence for this "large" species having been an *Allohippus*. Based on 41 widths (all available widths) of limb bones from these sites, the histogram of this species overlaps the one of *Allohippus vireti* (Saint-Vallier) and even more the one of *Allohippus* sp. of Ceyssaguet (Fig. 9).

****4.2. Material****  
At Senèze, the large equid is represented by a single tooth, an upper premolar illustrated above (Fig. 15). The other 16 fossils are: humerus FSL 211091; radii FSL 210860 and 211095; MC III FSL 211079; tibiae Se 812 and 813; talus FSL 211073; MT III FSL 211077 and SEN 02-2006 (collected in parcelle 164 and presented to the team by amateur collectors); first phalanges FSL 211074 and 211075; second phalanges FSL 210919, 211075, and 211078; and third phalanges FSL 211078 and 211082. Their measurements are included in the general tables.

****4.3 Third metacarpals****  
As mentioned above, the differences between the MC III of the large form from Senèze, Gannat, Wà¼rzburg-Schalksberg, and Oasele, Romania ("*E. euxinicus*") versus *E. suessenbornensis*and closely related forms from Akhalakalaki, Georgia, and North-Eastern Siberia are not so much in size (although MCs of E*. suessenbornensis* s.l. seem shorter) but in proportions of the distal ends. The distal articular widths (variable 11 on Fig. 10) relative to supra-articular ones (10 ibidem) seem larger in *E. suessenbornensis*. For this reason I tentatively refer the specimen from Overstrand, Great Britain, to the *E. suessenbornensis* group.   
I do not know to which group to refer specimen 326 of Livenzovka (Fig. 11).

****4.4. Third metatarsals****  
The same distingishing characters seem true for the third metatarsals. Moreover, the smaller depth of the medial condyle relative to the depth of the sagittal crest (respectively 13 and 12 on Fig. 31) is smaller in *E. suessenbornensis* s.l. For these reasons I have placed the MT III of "*E. bressanus*" from Chagny and a large specimen from Vatera, Greece, together with the *E. suessenbornensis* group.

****4.5 First phalanges****  
Anterior first phalanges of the large equid do not seem to differ from those of from those of Sussemiones (Fig. 13).

The morphology of the posterior first phalanges is variable (Fig. 14). The specimens from Chagny and Senèze resemble each other (unlike the metatarsals); in both, the distal supra-articular width is small relative to the proximal depth (respectively 6 and 5 on the diagram). In Sussemiones from Sà¼ssenborn and from NE Siberia, the distal supra-articular width is large relative to the proximal depth. But at Akhalakalaki, only a few phalanges have these proportions so that the mean for Akhalakalaki is less typical.

****4.6 Other limb bones****  
There are no important differences in the proportions of the other limb bones of the large equids whether they belong to *Allohippus* or to the *Sussemionus* group.

### ****5. Allohippus senezensis: Material****

A rapid description of some specimens is given below.

****5.1 Apparently isolated skulls and crania****:

Se 336, very well preserved cranium of an adult male (Figs. 15, 16),  
Se 796, ca. 1 year old associated skull (Fig. 17),  
Se 803, very old and very damaged fragmentary cranium,  
Se 804, associated fragmentary mandible and upper cheek teeth series (Fig. 18),  
Se 806, associated upper and lower cheek teeth series (Fig. 19),  
Sen 1855, fragments of palate associated with a fragmentary female mandible (Fig. 20),  
Sen 5233, adult male associated skull (Figs. 21, 22),  
FSL 210887, crushed cranium of an adult female (Figs. 23, 24).

****5.2 Skeletons****

There are several more or less complete skeletons (the actual association of the bones is sometimes doubtful). They will be briefly reviewed below.

Se 141 is a juvenile skeleton.  
Se 551 is a mounted skeleton (the data are therefore poor) of an adult female (Fig. 25).   
Se 552 is a juvenile skeleton.  
Se 553 is the complete skeleton of a male a little less than 4 years old. The cranium is fragmentary and badly preserved (Fig. 26).  
Se 554 is a nearly complete skeleton of an old male with a very badly preserved skull (Figs. 27, 28).  
SEN 05-0081 is a recently excavated nearly complete skeleton of an adult male with a crushed skull (Fig. 29, 30).

In 2006, the Seneze team recovered an associated radius, tibia, metapodials and first phalanges. Several other, previously recovered phalanges are probably also associated (first anterior: FSL 211055, first posterior: FSL 211082, and third anterior: FSL 210899).

Finally, there is the mounted skeleton (FSL 210993, ex 96132) at the Faculty of Sciences, Lyon mentioned above (Fig. 31,32). As usual for mounted skeletons the data for FSL 210993 are poor.

### ****6. *Allohippus senezensis*: Description and Comparisons****

*6.1. Crania*

*Allohipus* is best defined by its cranial morphology, in particular the depth of the naso-incisival notch (see above). According to this character, the skulls of Valdarno (Italy), Saint-Vallier, Senèze, Ceyssaguet (France), La Puebla de Valverde (Spain), Gerakarou (Greece), Kuruksai (Tadjikistan), Livenzovka (Russia), Nihowan, SE Shansi, Locality D (China), Grandview (USA) all belong to *Allohippus*. The size of the skull is variable, as is the relative length of the muzzle (variable 5, Table 1).

The average basilar length of Senèze skulls (523mm) is smaller than usual (545mm in *A. pueblensis* of La Puebla de Valverde (Spain), 554mm in *A. vireti* of Saint-Vallier (France), 560mm in *A. stenonis* of Olivola (Italy) but larger than in *A. mygdoniensis* of Gerakarou, Greece (488mm).

Muzzles are relatively long in *A. stenonis* (Valdarno), *A. vireti* (Saint-Vallier), *A. livenzovensis* (Livenzovka) and *A*. cf. *livenzovensis* of SE Shansi, *A. sanmeniensis* (Nihowan), *Allohippus* sp. of Ceyssaguet and the largest species of Kuruksai, Tadjikistan (Fig. 33).   
This character does not give any indication about the taxa ages since Saint-Vallier is about 2.5 Ma old (Nomade et al. 2013) and Ceyssaguet around 1.2 Ma (Aouadi 2000).

Muzzles are short in the smaller species of Kuruksai, *Allohippus* sp. of Locality D (and probably A) of China, *A. senezensis*, *A. pueblensis* (La Puebla de Valverde), *A. mygdoniensis* (Gerakarou), and especially *A. stehlini*, Valdarno (Fig. 34). According to the available data, short-muzzled skulls seem more restricted in time: between about 2.1 Ma (Senèze, Nomade et al. 2013) and Olduvai (Valdarno).

Both morphs seem to coexist at Kuruksai.

****6.2. Mandibles****

Measurements are given in Table 2.

****6.3. Upper cheek teeth****

With their short protocones, the upper cheek teeth are quite usual for Allohippus. Se 1855 (Fig. 20) has exceptionally long plis caballins.   
Figure 35 shows that most of the Senèze teeth are about the size of those of Dmanisi, Georgia, and smaller than *Allohippus stenonis* from Olivola and Matassino (see measurements in Table 3 and 4).

****6.4. Lower cheek teeth and incisors****

They are typical for *Allohippus*: rounded metaconid and metastylid, pointed liguaflexid, deep ectoflexid on the molars; cups on incisors. Measurements are given in Tables 5 and 6.

****6.5 Third metacarpals****

One of them (Se 552, juvenile) resembles metacarpals of *Allohippus stehlini*from Valdarno (Fig 36). The mean of the rest is close in size and proportions to *A. pueblensis* (Spain), *A. mygdoniensis* (Greece), and *Allohippus* sp. of Dmanisi, Georgia (Fig. 36). Measurements are provided in Table 7.

****6.6. Third metatarsals****

One of them (FSL 210868b) resembles metatarsals of ?*Allohippus* sp. from Pyrgos, Greece (Fig.37). The mean of the rest is close in size and proportions to *A. pueblensis*(Spain), *A. mygdoniensis* (Greece), and *Allohippus* sp. of Dmanisi, Georgia (Fig. 37). Measurements are in Table 8.

****6.7. First phalanges****

Measurements are in Tables 9 and 10.   
Nine anterior first phalanges are alike in size and proportions; they are referred to *A. senezensis*. They are slightly smaller than those of *A. pueblensis*. Three are quite a bit larger: Se 554, Se 828 and FSL 211055, the last being even longer than the average of A. vireti (Fig. 38). The individual ratio diagrams of the first anterior (and posterior: see below) phalanges document this distinction.

Among the first posterior phalanges, ten are again slightly smaller than in *A. pueblensis*, one (FSL 211082) is longer than the average of *A. vireti*(Fig. 39).

****6.8. Other limb bones****

Except for the large specimens already discussed, they are intermediate in size between those of *A. pueblensis* and smaller forms like *A. mygdoniensis* and *Allohippus* sp. from Dmanisi (see Tables 11-21).

### ****7. Discussion and Conclusions****

****7.1 Limits in possibilities of Villafranchian equids determination****

A better understanding of Villafranchian equids cannot naturally be achieved without precise datations, at least for key localities, i.e. where the material is varied, abundant, and well preserved and/or where fossils are especially interesting by their "originality" (unusual size or morphology). But it depends also very much on the discovery of crania associated with limb bones.

The diversity of sizes and proportions of limb bones as well as their overlaps discourages attempts at any reliable classification. The size of an equid cannot be used as chronological evidence: large equids occur just above the Gauss-Matuyama limit (Montopoli) as well as around the Brunhes-Matuyama limit (Wà¼rzburg). The first may belong to *Allohippus* and/or *Plesippus*; the second - to *Allohippus* and/or *Equus*.

In fact, when crania are missing, geologically old fossils may possibly belong to *Plesippus* as well as to *Allohippus*: A few examples will show some of the problems in these cases.

 ?*Allohippus* 1. from Sarikol Tepe, Turkey, and Loubières de Pardines, France. Metacarpals are robust and have shallow distal ends (measures 12, 13, 14) as in *Allohippus*, but the distal articular breadth (11) is large relative to the supra-articular one (10), - which is not typical for that genus (Fig. 40).

 ?*Allohippus* 2. Two metacarpals of the same age are slender, with distal supra-articular breadths large relative to the articular one (Fig. 41, 10 and 11) - usually the case in *Allohippus*. Their slenderness, however, is not typical for *Allohippus*, their proportions being more Onager-like. They come from Vatera, Greece, and Huelago, Spain; both localities are believed to be very old, about 2 Ma or more (Alberdi and Ruiz-Bustos, 1989; Alberdi et al., 1998; Eisenmann, 2002).

 ?*Allohippus* 3. Two further metacarpals are very similar in size and morphology: they are slender and have relatively large proximal depths and distal articular breadths (Fig. 42, measures 6, 11). They were collected at Tegelen, Holland, and Morskaja, Russia. Tegelen is believed to be 1.8 Ma (Westerhoff et al. 1998). Morskaja is one of the localities near Livenzovka and belongs in the Khapry complex.

 Ceyssaguet. According to the data kindly provided by N. Aouadi, the sample of MC from Ceyssaguet is very rich but not homogeneous. Three specimens belong to some kind of slender and large equid. Four more (especially 9012) resemble a MC from El Rincon (12440). Another 15 are even larger, robust specimens with variable morphologies. The bulk of the material (n=41-47) probably belongs to a large, robust *Allohippus*, with deep diaphyses and epiphyses (Fig. 43). By its proportions, it resembles the average MC from Sinzelles (France) but is quite a bit larger. Sinzelles is believed to be about 1.3 Ma (Lacombat, 2005), which fits well with the supposed age of Ceyssaguet, about 1.2 Ma (Aouadi, 1999).

****7.2 Senèze****

Position of *A. senezensis*

 As illustrated above (Fig. 35), the average skull of *A. senezensis* belongs to the short-muzzle group and is intermediate in size between *A. pueblensis* and *A. mygdoniensis*.   
 The average MC III of *A. senezensis* is smaller than *A. pueblensis* and larger than *A. mygdoniensis* (Fig.36). As in *A. mygdoniensis*, the diaphysis is deep relative to its width (4 and 3) as in (Fig. 42).   
 Short muzzles and deep, not very robust, metapodials are usually found in equids living in rather dry conditions.

What age(s) for Senèze equids?

The occurrence of caballine fossils has already been commented above. Assuming that they do not actually belong to Senèze collections, there still remain evidences for more than one species of equid at Senèze.   
 *A. senezensis*, is the most frequent equid. Its similarities with *A. pueblensis* and *A. mygdoniensis* would point to a younger age than the now accepted dates of 2.1-2.2 MA.   
 One upper cheek tooth and 16 limb bones belong to a very large Villafranchian equid. I refer them to ?*Allohippus* (see above the comparison of metapodials) but they could belong to a Late Pliocene species like at Oasele (Montopoli faunal unit?), or to an Early Pleistocene form like at Gannat (where it is associated with a Merck Rhinoceros and a peculiar Megaceros (C. Guérin, 1995, pers. com.)).   
 Two first phalanges are larger than the average for *A. vireti* (2.5Ma).   
 One MC III resembles *A. stehlini*of Valdarno (younger than Olduvai).   
 One MT III and one first phalanx resemble the small ?*Allohippus* sp. of Pyrgos (MNQ 18?).

### ****Conclusions****

The equid material of Senèze is not homogeneous. The bulk belongs to *A. senezensis*, intermediate in size between *A. pueblensis* and *A. mygdoniensis*. It was probably adapted to drier conditions than A*. vireti*. A few fossils give evidence for an younger age and even drier conditions. A very large equid (?*Allohippus*) is represented mostly by limb bones.