Chapter 11
The Senèze Equids

Véra Eisenmann and Eric Delson

Abstract Three genera of Plio-Pleistocene monodactyl equines are recognized and distinguished by cranial proportions: *Equus*, *Plesippus* and *Allohippus*. The rich material of equid fossils from Senèze is not homogeneous. In addition to 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 senezensis*, which by size and proportions is intermediate between *A. senezensis guthi* of La Puebla de Valverde (Spain) and *A. senezensis mygdoniensis* of Gerakarou (Greece). Its relatively short muzzle and deep, not very robust, metapodials are usually found in equids living in rather dry conditions. Two partial skeletons and a few other possibly associated hindlimb elements were recovered in the new excavations close to the bottom of the local sequence, thus ca 2.2 Ma. 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. stenonis vireti* of Saint-Vallier (France) and a few others as small as ?*Allohippus* of Pyrgos (Greece). The affinities and ages of various Pliocene and Pleistocene equid species are discussed and illustrated.

Résumé Grâce aux proportions crâniennes il est possible de reconnaître trois genres d'Equinés monodactyles: *Equus*, *Allohippus* et *Plesippus*. Si l'on prend pour modèles de variation interspécifique les *Equus* actuels, *Allohippus stenonis* et *A. senezensis* sont deux espèces distinctes, chacune comprenant plusieurs sous-espèces, les premières à museau long, les secondes à museau court.

Les fossiles d'équidés de Senèze, pour la plupart issus d'anciennes fouilles et rassemblés dans les collections de Lyon, Bâle et Paris, comprennent de nombreux crânes, squelettes et os des membres isolés sans provenance stratigraphique précise. Le matériel est fortement hétérogène. La présence de quelques spécimens caballins (notamment mandibule et métacarpien du squelette monté FSL 210993, ex 96132) s'explique sans doute par leur caractère intrusif ou par des erreurs de catalogue. Les autres fossiles appartiennent à au moins deux espèces. La plupart peuvent être attribués à *Allohippus senezensis senezensis*, intermédiaire par sa taille et ses proportions entre les *A. senezensis guthi* de La Puebla de Valverde (Espagne) et *A. senezensis mygdoniensis* de Gerakarou (Grèce). La brièveté relative de son museau et les proportions de ses métapodes suggèrent un environnement plutôt sec. Deux squelettes incomplets et quelques os de membre postérieur probablement associés proviennent de fouilles récentes proches du bas de la séquence locale daté d'environ 2,2 Ma. Une P3 supérieure et 16 os des membres (humérus, radius, métacarpien, tibias, astragale, métatarsiens et premières, deuxièmes et troisièmes phalanges) appartiennent à un très grand équidé. Sur la P3 le protocône est court et ne porte pas de sillon, le pli caballin est petit. Sur les métapodes la largeur sus-articulaire est plus grande que la largeur articulaire. Ces caractères rendent plausible une attribution à *Allohippus major*. Deux premières phalanges dépassent la taille moyenne d'*A. stenonis vireti* de Saint-Vallier (ca 2,5 Ma). Un MC III ressemble à *A.*

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stehlini du Valdarno Supérieur (ca. 1,7 Ma). Un MT III et une première phalange ressemblent à *?Allohippus* sp. de Pyrgos (MNQ 18 ou MNQ 19, ca 1,75 Ma). Ces cinq spécimens pourraient provenir d'horizons différents de Senèze ou même d'autres sites. L'âge et les affinités de différentes espèces d'équidés pliocènes et pléistocènes sont discutés. La Fig. 11.51 présente une vue générale de la distribution temporelle des huit taxons ou morphes d'Equidés en question.

Keywords *Allohippus* • *A. senezensis* • *A. major* • *Equus (Suessemionus) suessenbornensis* • *Plesippus* • Late Pliocene • Early Pleistocene • Middle Pleistocene

Mots-clés *Allohippus* • *A. senezensis* • *A. major* • *Equus (Suessemionus) suessenbornensis* • *Plesippus* • Pliocène supérieur • Pléistocène inférieur • Pléistocène moyen

Preliminaries

Before describing and discussing the Senèze equids, it is useful to summarize and explain the general background used here. Figs. 11.1 and 11.2 describe the system of cranial measurements and data used in diagrams illustrating this article. All of the data and almost all of the opinions in this chapter (especially those indicated by "I" or "my") are those of the senior author.

In the Old World, there are three groups of equine crania belonging to the genera *Plesippus*, *Allohippus*, and *Equus*. They have been discussed at length previously (Eisenmann 2004; Eisenmann & Baylac 2000; Eisenmann & Deng 2005; Forsten & Eisenmann 1995; Samson 1975). Although Eisenmann (2022) has used *Allohippus* as a subgenus of *Equus*, we here recognize it as a distinct genus, given the distinguishing features detailed below. Barrón-Ortíz et al. (2019) also accepted all three equids as full genera, following a detailed cladistic analysis. Other authors (e.g., Cirilli et al. 2021, 2024) include species here considered as

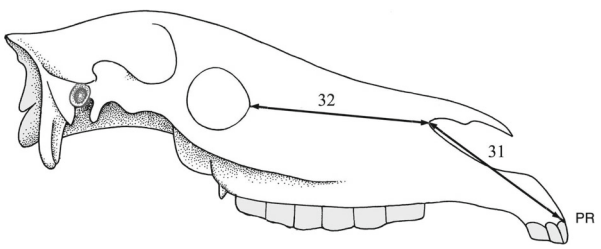

Fig. 11.1 Schematic representation of the profile of an *Equus* cranium. PR: prosthion. 31: length of the naso-incisival notch. 32: cheek length. Measurements defined at https://vera-eisenmann.com/skulls-system-of-measurements

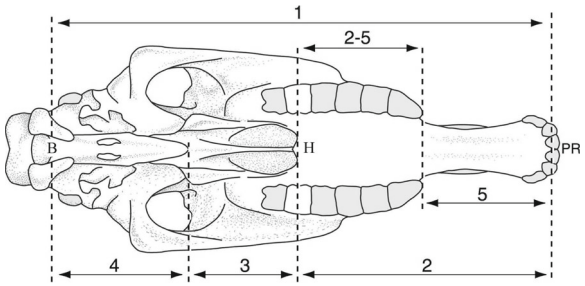

Fig. 11.2 Schematic occlusal view of an *Equus* cranium. B: basion. H: hormion. PR: prosthion. 1: basilar length. 2: overall palatal lengh. 2–5: palatal length sensu stricto. 3: vomerine length. 4: post-vomerine length. 5. muzzle length. Measurements defined at https://vera-eisenmann.com/skulls-system-of-measurements

Allohippus or *Plesippus* in *Equus* without infrageneric division, but importantly, they recognize *senezensis* and *major* as full species present at Senèze.

Equus have a shorter naso-incisival notch relative to cheek length than *Allohippus* (Figs. 11.1, 11.2, 11.3, Table 11.A1). The same is true also in general for *Plesippus* (Fig. 11.4, Table 11.A1). According to this character, the crania of Valdarno (Italy), Saint-Vallier, Senèze, Ceyssaguet (France), La Puebla de Valverde (Spain), Gerakarou (Greece), Kuruksai (Tajikistan), Nihowan, SE Shansi, Locality D (China), East Turkana (Kenya), and Grandview (USA) all belong to *Allohippus*.

To distinguish *Allohippus* and *Plesippus* the Palatal Index (vomerine length relative to the palatal length sensu stricto, Fig. 11.2, higher in *Plesippus*) may be of some help: the ratio of vomerine length to palatal length is generally lower in *Allohippus* (and *Equus caballus*) than in *Plesippus* (and other *Equus*). There is overlap among all three genera, but they are mostly distinguishable (Fig. 11.5). There is some evidence of intermediate forms between *Plesippus* and *Allohippus*, at least at Longdan, China (Qiu et al. 2004 and Wang & Deng 2011).

Equus have longer post-vomerine length relative to overall palatal length than *Plesippus* and *Allohippus* (Fig. 11.6, Table 11.A1). As far as I know it is the only differential diagnostic character of the genus *Equus*. It may be hypothesized that this longer post-vomerine length is related to a larger brain.

There is an unfortunate tendency to refer to *Dolichohippus* any *Equus* with a large cranium. Thus Skinner and Hibbard (1972) referred "*Equus*" *simplicidens* to *Dolichohippus*; Forsten and Eisenmann (1995) showed that it was unacceptable. Churcher and Richardson (1978) and Churcher (1986, 1993) considered that *Equus capensis* was congeneric with *Dolichohippus* while cranial morphology (Eisenmann and Baylac 2000), confirmed later by molecular biology (Orlando et al. 2009), clearly shows its affinity with Quaggas. Following Churcher and Richardson (1978),

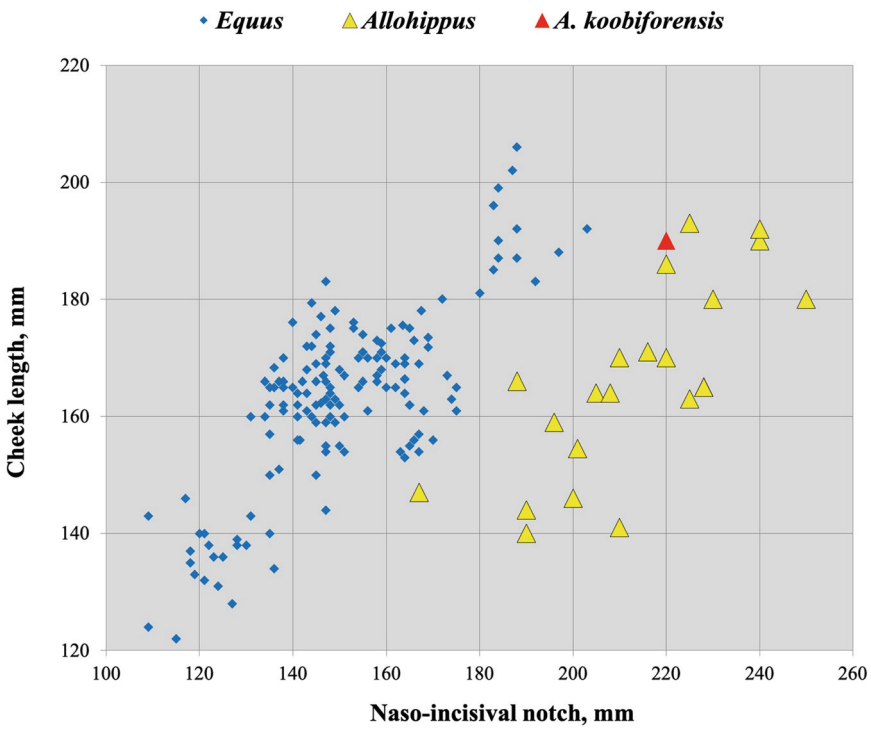

Fig. 11.3 Scatter diagram of the cheek length versus the length of the naso-incisival notch in crania of *Equus* and *Allohippus*. The naso-incisival notch is longer in *Allohippus* than in *Equus*. The East Turkana cranium KNM-ER 1484 (type of *A. koobiforensis*) plots with *Allohippus*, not with *Equus* and therefore should not be included in the subgenus *Dolichohippus*

Bernor et al. (2010) referred '*Equus' koobiforensis* to *Dolichohippus* although its naso-incisival notch is much deeper (red triangle on Fig. 11.3 and Fig. 11.4, Table 11.A1).

The concept of species in paleontology is problematic. Should it be based on osteology, chronology, or geography, or to what exact combination of these factors? My primary guide is the osteological variability in extant wild species of *Equus*. In the case of *Allohippus,* differences in osteological cranial characters, apart from size, are mostly found in the muzzle length (variable 5 in Fig. 11.2). The crania of *A. stenonis* from Valdarno have a long and narrow muzzle (Fig. 11.7, Table 11.A1). So do the crania of Saint-Vallier and Ceyssaguet (France), Liventsovka (Russia), the larger species of Kuruksai (Tajikistan), Nihowan and Fan Tsun, SE Shansi (China). Although similar morphology may indicate conspecificity, I do not think that being as far away in distance and in time as they are, they must all be referred to the single species *A. stenonis*. We refer them to the *A. stenonis* species group. A long muzzle does not give any indication about the ages of taxa, since Saint-Vallier is about 2.4 Ma (Nomade et al. 2014) and Ceyssaguet around 1.2 Ma (Aouadi 1999).

Other crania usually also referred to '*A. stenonis'* have very different proportions: muzzles are shorter and wider at Senèze (France), La Puebla de Valverde (Spain), Gerakarou (Greece), in the smaller species of Kuruksai (Tajikistan), and Localities A and D in China (Fig. 11.8, Table 11.A1). In extant *Equus*, these crania would never be considered conspecific with the preceding. We refer them to the *A. senezensis* species group. According to the available data, short-muzzled skulls seem more restricted in time than long-muzzled ones: between about 2.2–2.1 Ma (Senèze: Nomade et al. 2014; Delson et al. 2024) and the Olduvai subchron (Valdarno). Both morphs seem to coexist at Kuruksai, which may be a little older than Senèze. (Table 11.A2).

In the genus *Allohippus,* there are also differences in limb bone size and proportions, and in relative lengths of limb bone segments. It is not in the scope of this paper to illustrate all relevant data, so I shall only illustrate differences in two characters. The *A. stenonis* species group have more robust and flatter metacarpals (MC) than the *A. senezensis* species group. In extant *Equus* such characters usually correspond respectively to more humid or drier environments (Fig. 11.9, Table 11.A3). Limb segment proportions are also different (Fig. 11.10, Table 11.A4a). Although I do not know why, there again the long-muzzled forms seem to differ from the short-muzzled ones. In consequence I propose to use the following classification and distribution pattern of Table 11.A5 for the taxa discussed in this chapter.

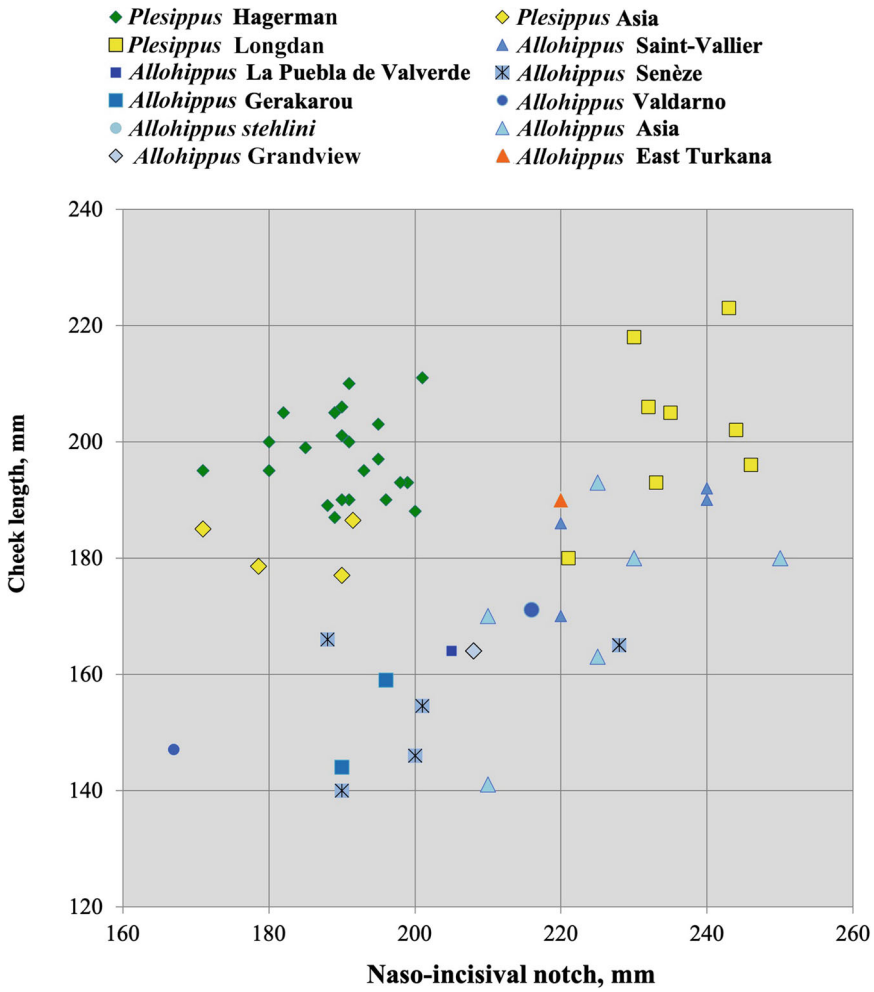

Fig. 11.4 Scatter diagram of the cheek length versus the length of the naso-incisival notch in crania of *Plesippus* and *Allohippus*. The naso-incisival notch is longer in *Allohippus* than in *Plesippus*. The Longdan crania and the East Turkana cranium KNM-ER 1484 plot with *Allohippus*

Material and Methods

Most of the fossil equids from Senèze were collected long ago and are preserved in several institutions: the Université Claude Bernard-Lyon I (UCB-Lyon 1; specimens indicated by the prefix FSL) and Muséum d'Histoire naturelle (now Musée des Confluences, Centre de Conservation et d'Etude des Collections) in Lyon (MHNL Sen), the Laboratoire de Paléontologie (MNHN.F or MNHN.F-AC) of the Muséum national d'Histoire Naturelle in Paris, and the Naturhistorisches Museum in Basel (NMB Se; see, e.g., Schaub 1943, fig. 2) are the richest. Specimens newly recovered by the Franco-American team have not yet been catalogued or deposited formally in any institution (they are stored now in FSL), but they are indicated here by SEN followed by the year of discovery and a field sequence number (e.g., FSL SEN 05–0081). The Senèze sample (combining old collections and new) is rich and comprises crania, mandibles, associated teeth and limb bones, and isolated fossils. The preservation of long bones and teeth is usually good; the crania, however, are often crushed, and some were heavily reconstructed. Abbreviations used for skeletal elements and other terms include: MC, metacarpal; MT, metatarsal; Ph, phalanx. Upper teeth are indicated by uppercase letters, lower teeth by lowercase. A list of other acronyms for museums preserving specimens used in comparative data tables and figures is provided below:

AM: Zoologisch Museum, Amsterdam, Netherlands.

AMNH-P FM (Paleontology, fossil mammals), **-M** (Mammalogy)–American Museum of Natural History, New York, USA;

BE: Naturhistorisches Museum, Bern, Switzerland.

BO: Museum Koenig, Bonn, Germany.

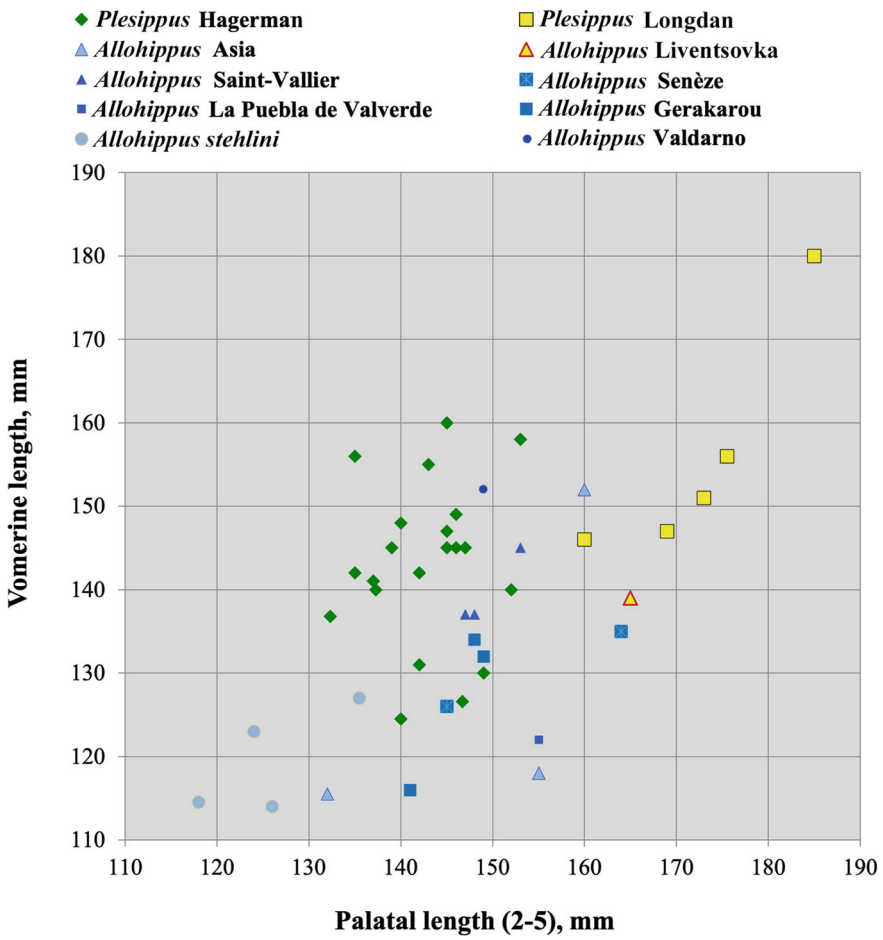

Fig. 11.5 Scatter diagram of the length of the vomer (hormion to posterior border of palate, variable 3) versus the length of the palate (posterior border of palate to anterior borders of P2, variable 2-variable 5) in crania of *Plesippus* and *Allohippus*. The length of the vomer is usually, but not always, larger in *Plesippus*

CRA: Centre de Recherches Archéologiques, Compiègne, France.

EV: Ecole Vétérinaire, Maisons-Alfort, France.

FMNH: Field Museum of Natural History, Chicago, USA;

GIN: Geological Institute, Moscow, Russia.

HL: Museum für Haustierkunde, Halle, Germany.

HPM: Hezheng Paleozoological Museum, Hezheng, China.

HUJ-ESE: Section of Ecology, Systematics & Evolution, Hebrew University, Jerusalem, Israel.

IA: Geological Institute, Iakutsk, Russia.

IGF: Istituto di Geologia, Firenze, Florence, Italy.

ISER: Institutul de Speologie Emil Racovitsa, Bucharest, Romania.

IVPP: Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China.

KI: Institut für Haustierkunde, Kiel, Germany.

KNM-P (Palaeontology), **-O** (Osteology): Kenya National Museums, Nairobi, Kenya.

LGPUT: Laboratory of Geology and Paleontology, Aristotle University Thessaloniki, Greece.

MB-Z: Zoologisches Museum der Humboldt Universität, Berlin, Germany.

MGRI: Moscow Geological Research Institute, Moscow, Russia.

MNCS-CSI: Museo Nacional de Ciencias Naturales, Madrid, Spain.

MNHN-ZM-MO: Laboratoire des Mammifères et Oiseaux du MNHN, Paris, France.

MNP-Bonifay: Musée National de Préhistoire, collection of M.F. Bonifay, Les Eyzies, France.

MS: Zoological Museum of Moscow University, Moscow, Russia.

MTA-M: Direction de Recherches Géologiques et Minières, Musée d'Histoire naturelle, Ankara, Turkey.

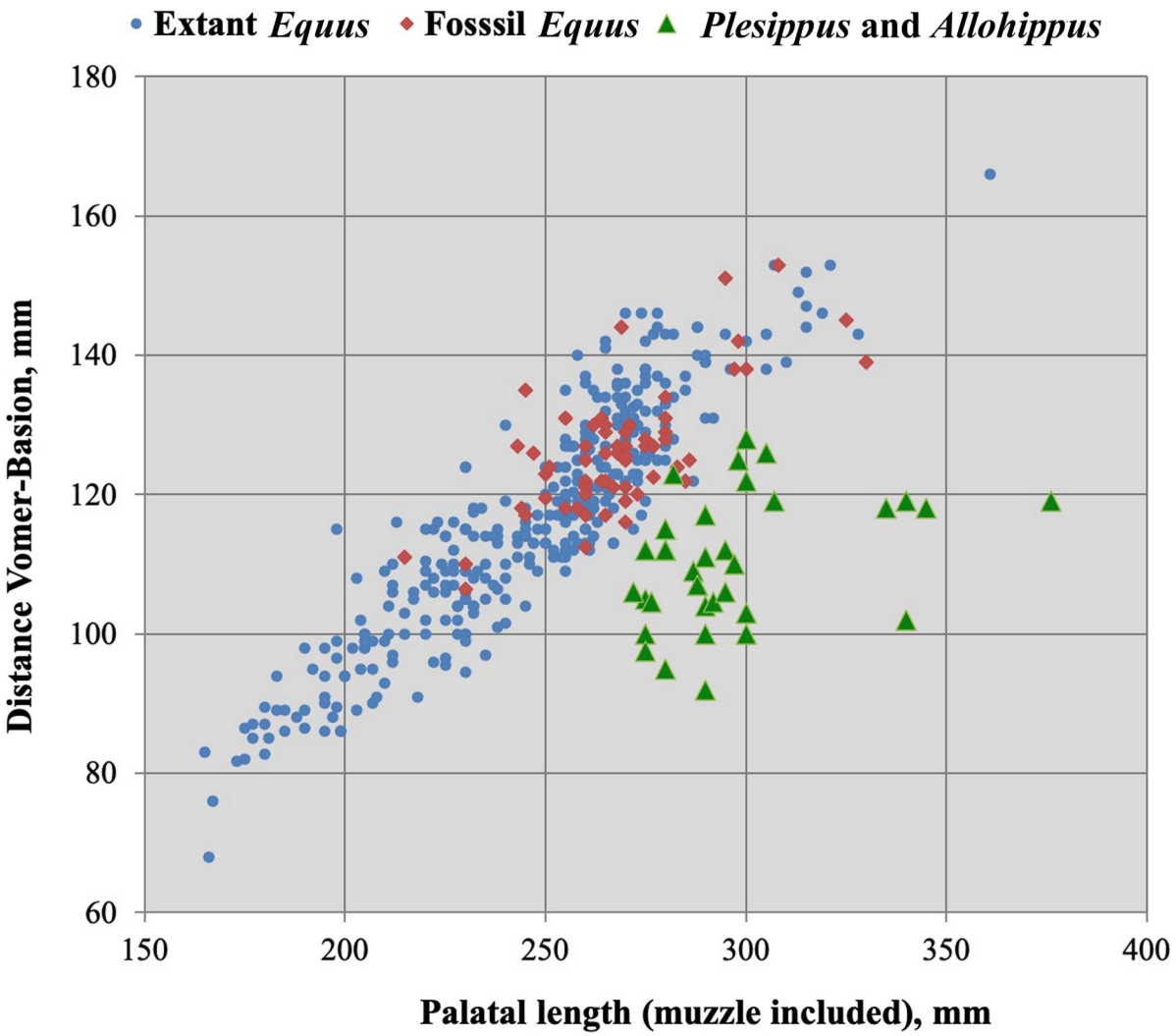

Fig. 11.6 Scatter diagram of the post-vomerine length (hormion to basion, variables 3 + 4) versus the overall palatal length (from posterior border of palate to the I1, variable 2) in crania of *Equus*, *Plesippus*, and *Allohippus*. In spite of some overlaps, *Equus* crania have larger post-vomerine lengths

NHCV: Natural History Collection, Museum of Vrissa, Lesvos, Greece (now mostly located in Athens Museum of Paleontology and Geology).

NHMUK -P (Palaeontology), **-ZD** (Zoology): Natural History Museum [formerly British Museum (Natural History)], London, Great Britain.

NM: Natural History Museum, Windhoek, Namibia.

NMB: Naturhistorisches Museum, Basel, Switzerland.

NMP: Narodni (National) Museum (Natural History), Prague, Czech Republic.

PIN: Paleontological Institite, Moscow, Russsia.

PMU: Paleontological Museum Uppsala University, Sweden.

RGU: State University of Rostov, Rostov on Don, Russia.

RNH-L: Naturalis (formerly Rijksmuseum van Natuurlijke Historie), Leiden, Nederlands.

ROMK: Azov Regional Museum, Rostov on Don, Russia**.**

SAM: Iziko South African Museum, Cape Town, South Africa.

SMF: Naturmuseum und Forschungsinstitut Senckenberg, Frankfurt, Germany.

SMNS: Staatliches Museum für Naturkunde, Stuttgart, Germany.

TMB: Magyar Természettudiomanyi Muzeum, Budapest, Hungary.

TMP: Ditsong (formerly Transvaal) Museum, Pretoria, South Africa**.**

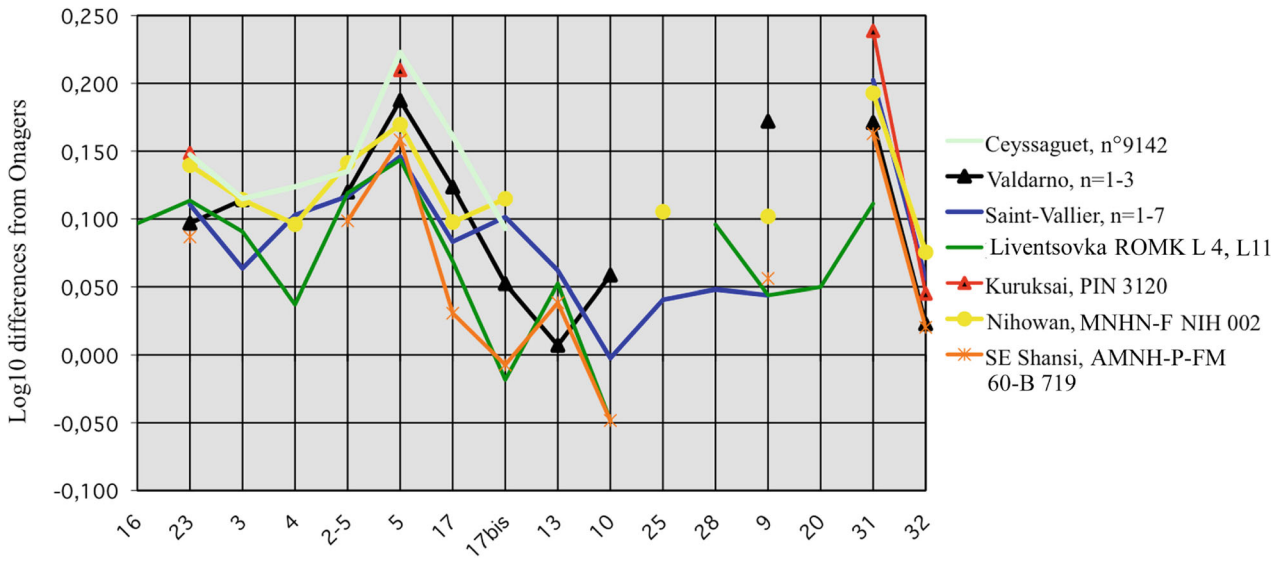

Fig. 11.7 Ratio diagrams of *Allohippus* crania with long muzzles (variable 5). 16: breadth of the supra-occipital crest; 23: anterior ocular line; 3: distance from palate to hormion; 4: distance from hormion to basion; 2–5: palatal length (sensu stricto, without the muzzle); 5: muzzle length; 17: muzzle breadth at the posterior border of the I3; 17bis: least muzzle breadth between the interalveolar borders; 13: frontal breadth: 10: greatest choanal breadth; 25: facial height in front of P2; 28: cranial height behind the orbits; 9: choanal length; 20: height of the external auditory meatus; 31: length of the naso-incisival notch (from prosthion to the back of the narial opening); 32: cheek length (from the back of the narial opening to the most anterior point of the orbit). n: number of specimens. Technique of measurement illustrated defined at https://vera-eisenmann.com/skulls-system-of-measurements

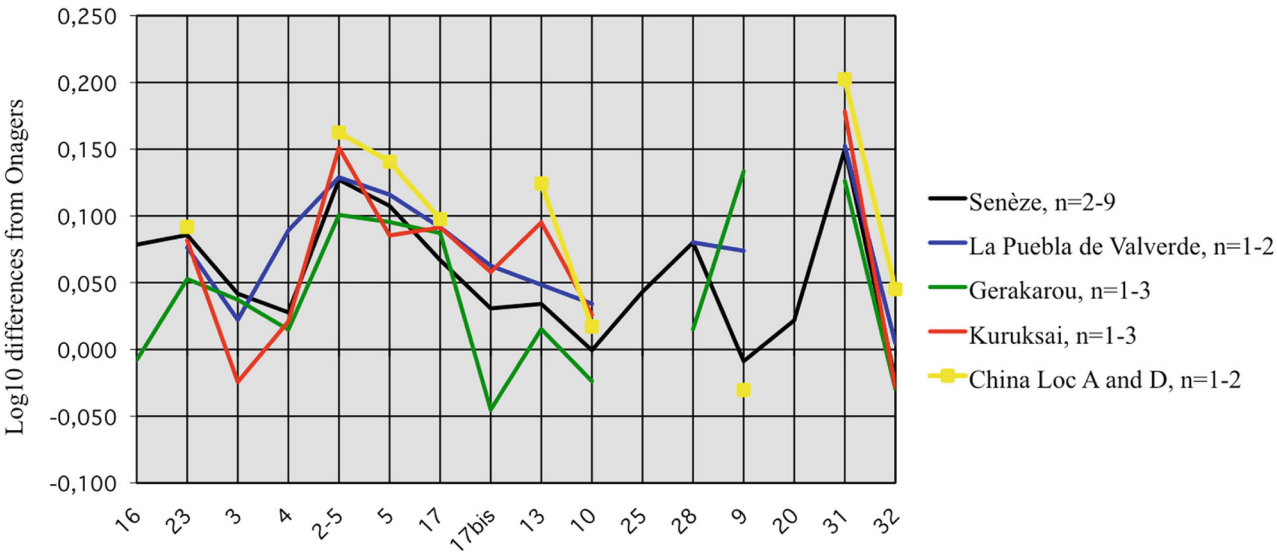

Fig. 11.8 Ratio diagrams of *Allohippus* crania with short muzzles (variable 5). Same variables as in Fig. 11.7

USNM: United States National Museum of Natural History [NMNH], Smithsonian, Washington, DC, USA.

Windhoek: Windhoek Sciences Museum, Namibia.

YPM: Yale Peabody Museum, New Haven, USA.

ZIN: Zoological Institute, Saint Petersburg, Russsia.

ZSM: Zoologische Sammlung des Bayerischen Staats, Munich, Germany.

ZU: Zoologisches Museum der Universität, Zurich, Switzerland.

The detailed system of measurements used in this chapter may be found on my web site at:

https://vera-eisenmann.com/-system-of-measurements-for-equus-bones-and-teeth-english

Click on the element for which measurement details are needed.

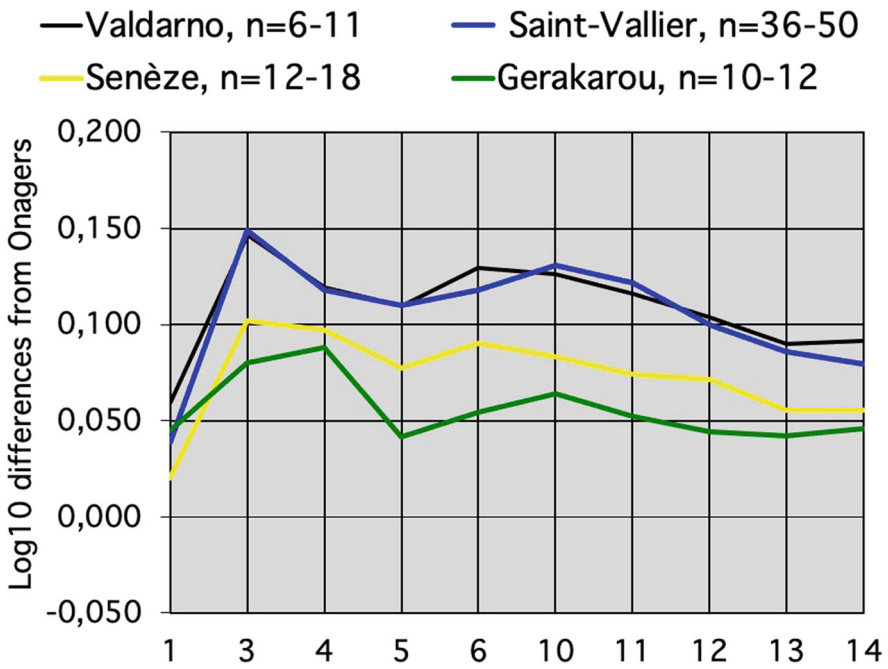

Fig. 11.9 Ratio diagrams of *Allohippus* third metacarpals. 1: maximal length; 3: minimal breadth of the diaphysis; 4: depth of the diaphysis at the same level; 5: proximal articular breadth; 6: proximal articular depth; 10: distal supra-articular breadth; 11: distal articular breadth; 12: depth of the keel; 13: minimal depth of the medial condyle; 14: maximal depth of the medial condyle. Technique of measurement illustrated at https://vera-eisenmann.com/metapodials-system-of-measurements

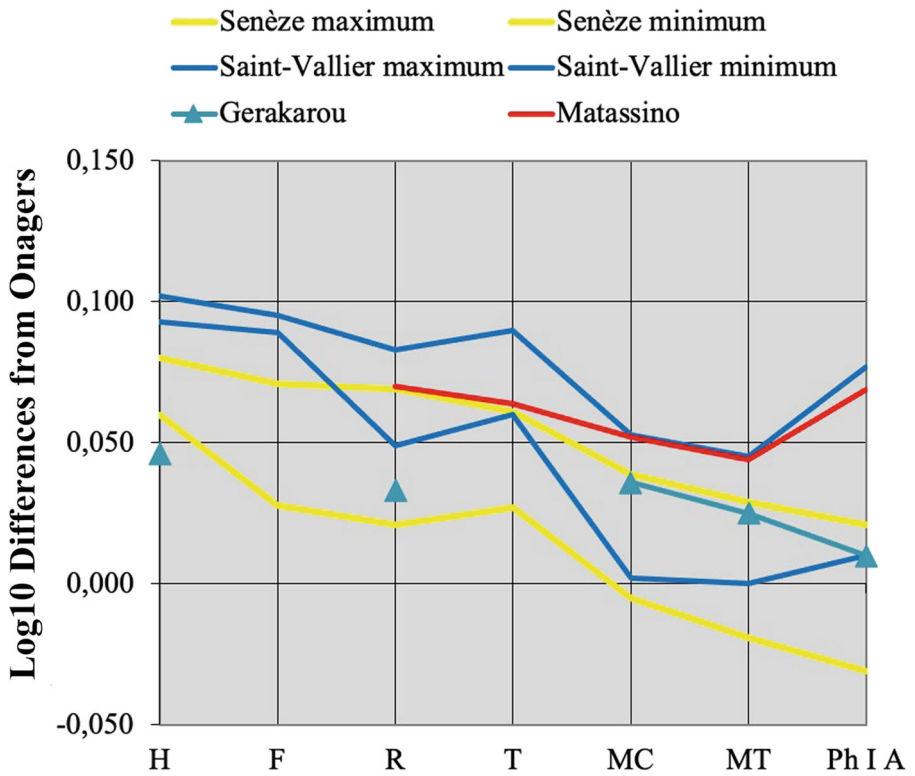

Fig. 11.10 Ratio diagrams of *Allohippus* limb bone segments. Maximal lengths of humerus (H), femur (F), radius (R), tibia (T), third metacarpal (MC), third metatarsal (MT) and first anterior phalanx (Ph1 A). First anterior phalanges are relatively shorter in *A. senezensis senezensis* from Senèze and *A. senezensis mygdoniensis* from Gerakarou than in *A. stenonis stenonis* from Matassino and *A. stenonis vireti* from Saint-Vallier

Comparisons in this article are based mostly on personal observations and occasionally on data communicated and/or published by: Samson (1975; Oasele, Romania); Mäuser (1992; Würzburg-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; Tegelen, Netherlands). Simpson's ratio diagrams, scatter diagrams, and variability size indices (see below) are given to illustrate differences and similarities between fossil teeth and bones. All tables are placed in an Appendix at the end of the chapter.

The Variability Size Index (VSI) is one of the size index scaling techniques used by archeozoologists (Meadow 1999; Uerpmann 1982). A sample including all the bones of one 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:

$$\mathrm{VSI} = 25^{*}(\mathrm{x} - \mathrm{m})/\mathrm{s}$$

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), "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 –25, etc." Some additional details are given at https://vera-eisenmann.com/variability-size-index-vsi.

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. Instead, it appears that some caballine specimens (e.g., the lower premolars MNHL Sen 3982) are present in the Senèze collections, either because they came from as yet unrecognized younger levels or because they were erroneously thought to come from Senèze. Here I will only illustrate the proportions of two probably caballine metapodials. On the MC of the same mounted skeleton FSL 210993, the relative flatness of the proximal end is unusual but a modern Shetland Pony MC (although smaller) has the same proportions (Fig. 11.11, Table 11.A3a). This skeleton thus contains at least two extraneous elements, and the relevance of other bones must be examined with caution. The MT NMB Se 821 although smaller has the same proportions as the "Mindel-Riss" caballine of Lunel-Viel (Fig. 11.12, Table 11.A6a).

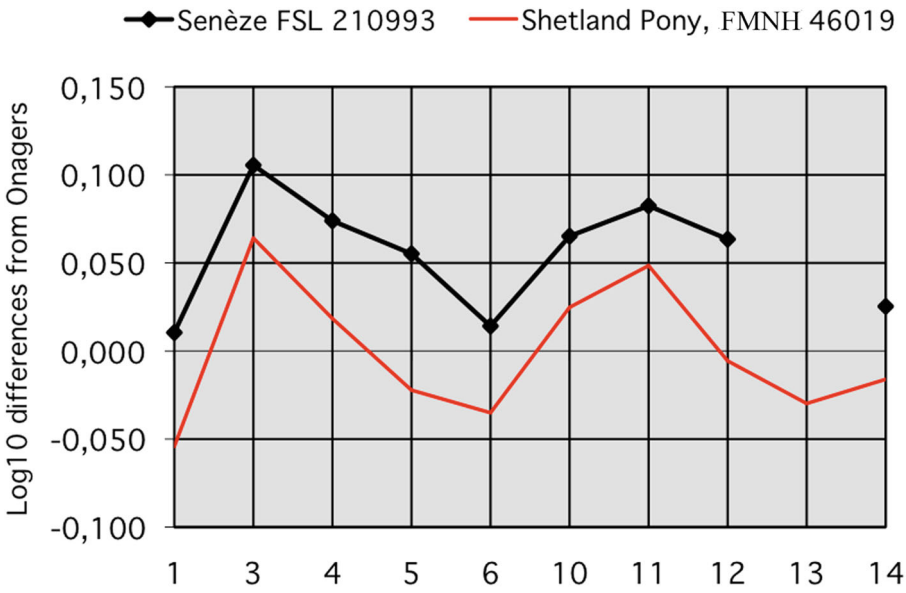

Fig. 11.11 Ratio diagrams of third metacarpals. Same variables as in Fig. 11.9

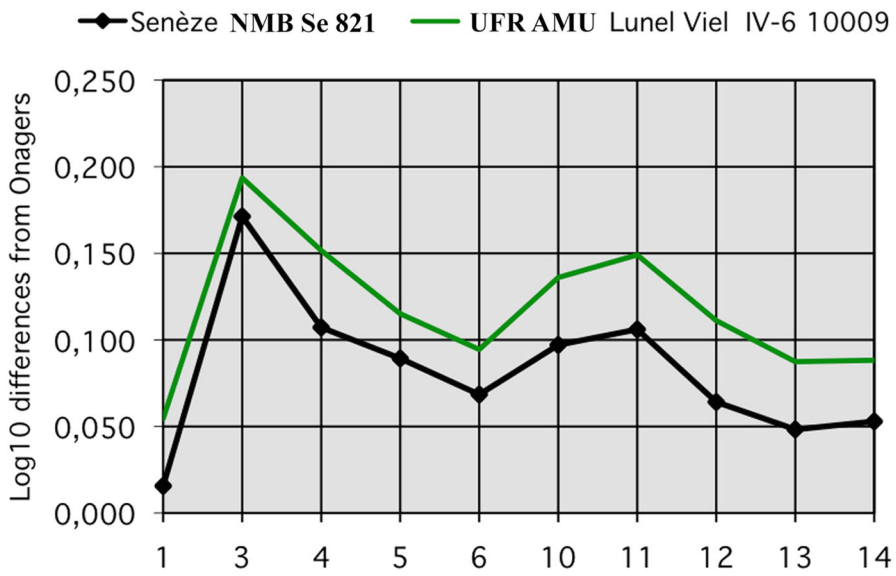

Fig. 11.12 Ratio diagrams of third metatarsals. Same variables as in Fig. 11.9

Cheek Teeth

With their short protocones, all the upper cheek teeth from Senèze are quite typical for *Allohippus*. The development of plis caballin, however, is very variable (see below). One P3, NMB Se 338, is larger than the rest (Fig. 11.13, Table 11.A7). and may be referred to the very large equid discussed below.

Limb Bone Size (Breadths)

Although there are differences in size within the *A. senezensis* sample, almost all fossils (excluding the "caballines" mentioned above) may belong to a single species. This is not the case of 16 considerably larger specimens (see Introduction to "Very Large Villafranchian Equid" below). The difference in size is well illustrated by the Variability

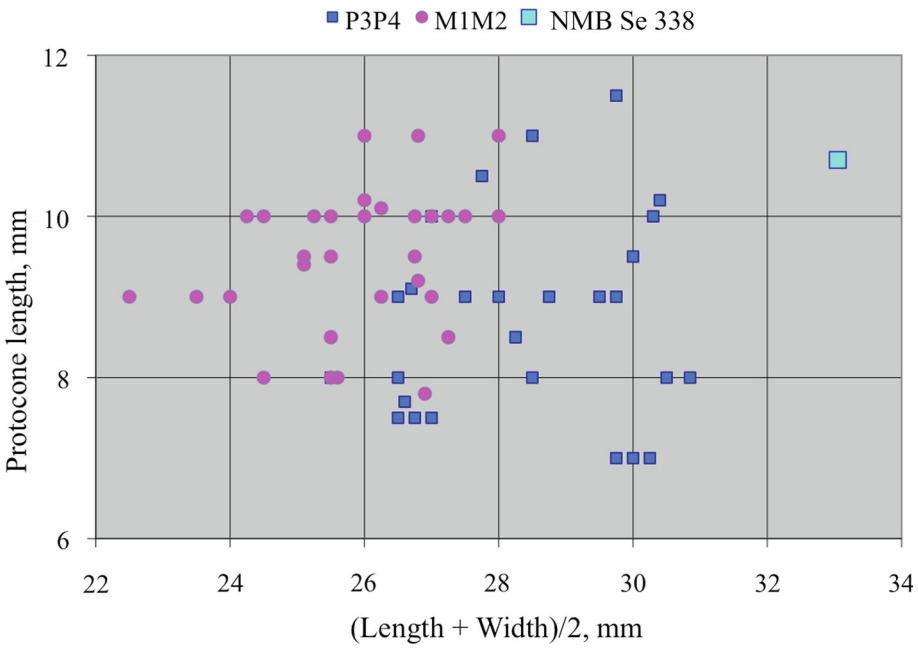

Fig. 11.13 Scatter diagram of protocone lengths versus average occlusal dimensions [(occlusal length + occlusal width)/2] in upper cheek teeth of Senèze

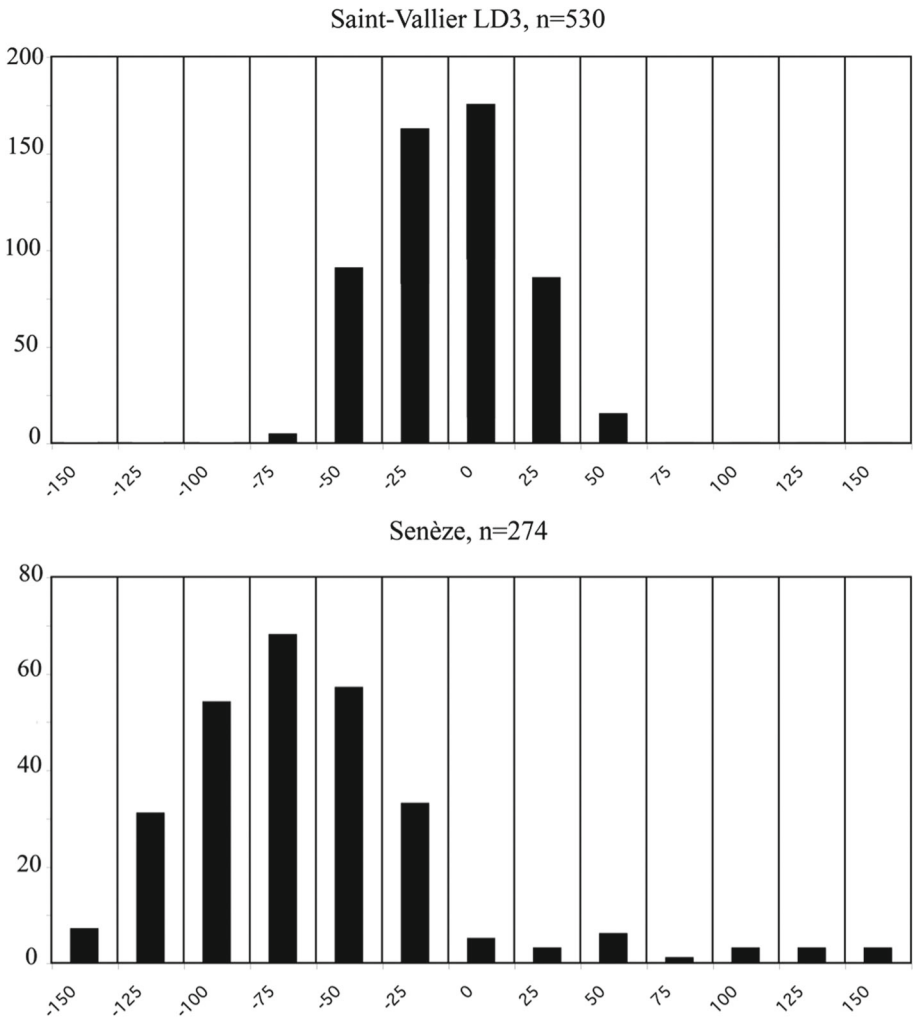

Fig. 11.14 Variability Size Index for 530 breadths of Saint-Vallier LD3 (younger level) and 274 breadths of Senèze limb bones

Size Index (VSI; see the end of the Materials and Methods section above). I have chosen the sample of *A. stenonis vireti* of Saint-Vallier as the reference. I considered only the bone breadths (excluding juvenile specimens). Means and standard deviations for the Saint Vallier reference standard used in Fig. 11.14 are given in Table 11.A8a. Naturally the histogram for Saint-Vallier is centered on 0; it is normally distributed, three standard deviations on each side of 0.

On the histogram for Senèze (Fig. 11.14, Table 11.A8a):

- 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 in Material section of "Very Large Villafranchian Equid") are on the right side of the diagram, all between one and six standard deviations from 0. They may be referred to a very large equid (see "Very Large Villafranchian Equid" below).

Limb Bone Size and Proportions

There is clearly a considerable size difference between *A. senezensis senezensis* and the very large equid Fig. 11.15, Table 11.A4b). I do not know what to make of the other large phalanges.

Very Large Villafranchian Equid

Introduction

The identity of the very large Villafranchian equid which Alberdi et al. (1998) have thoroughly discussed and decided to refer to as *E. major* Depéret, 1893 (rather than *E. robustus* Pomel, 1853 or *E. bressanus* Viret, 1954) is far from resolved, since its precise age is not known, and its main characteristic is its "large" size. I believe that part of the

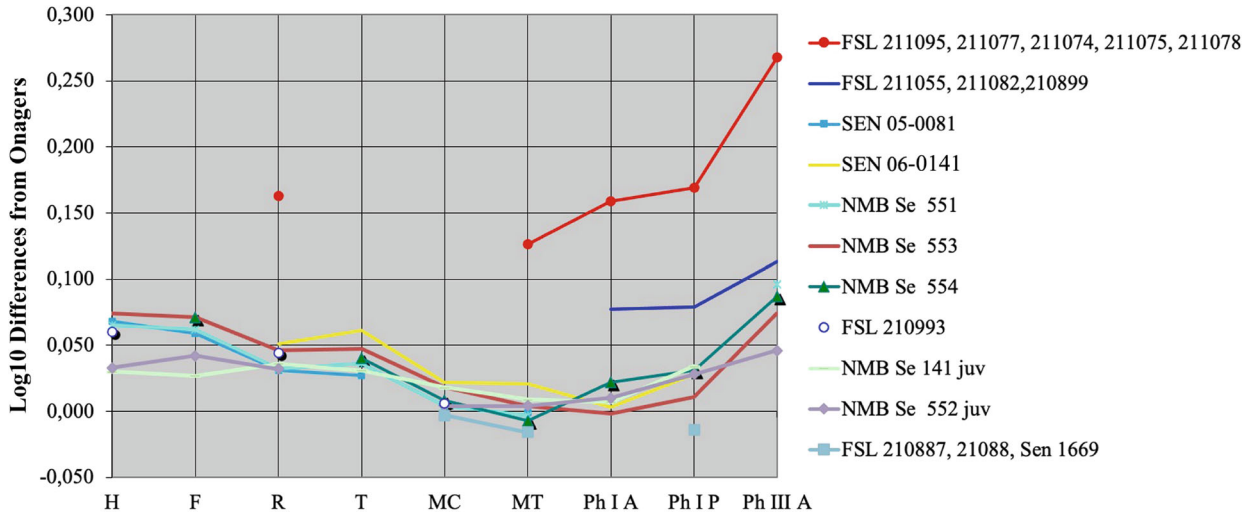

Fig. 11.15 Ratio diagrams of maximal lengths of humerus (H), femur (F), radius (R), tibia (T), first anterior and posterior phalanges (PhIa and PhIp) and plantar width of third anterior phalanx (Ph3a width) from Senèze

fossils referred to *E. major* (Alberdi et al. 1998; Boulbes & Asperen 2019) may belong either to *Allohippus* or to *Equus (Sussemionus*). Others, like the equid of Tegelen illustrated and discussed below, are even more problematic. This "large" size overlaps with two other groups of large and better-documented equids: *Allohippus* (most species) and the large *Equus (Sussemionus)* (from Süssenborn, Akhalkalaki, and Northeastern Siberia, see Eisenmann 2006, 2010). As will be shown below, the large-bodied sample from Senèze can be identified as *Allohippus* on the basis of P3 enamel pattern and metapodial proportions, and due to its size it can be termed *Allohippus major*. (Fig. 11.16).

Material

At Senèze, the large equid is represented by a single tooth, the P3 NMB Se 338 illustrated in Fig. 11.17 below. The other 16 fossils are: humerus FSL 211091; radii FSL 210860 and 211095; MC III FSL 211079; tibiae NMB Se 812 and 813; tali FSL 211073; MT III FSL 211077 and FSL SEN 02–0006 (collected in parcel 164 and presented to the team by the amateur collector A. Consigny, thus essentially of unknown stratigraphic position); 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.

Combined Limb Bone Widths

Based on 41 widths (all available widths) of limb bones from Ceyssaguet (only the largest ones), Chagny, Gannat, Loubières de Pardines, Senèze, Solilhac (France), Schernfeld, Würtsburg-Schalksberg (Germany), Vatera (Greece), Kislang (Hungary), Oesterschelde (Netherlands), Oasele (Romania) and Morozovka (Russia), the VSI histogram of this combined sample overlaps the one of *Allohippus stenonis vireti* (Saint-Vallier) and even more the one of *Allohippus stenonis* subsp. of Ceyssaguet (Fig. 11.16, Table 11.A8, see details at https://vera-eisenmann.com/variability-size-index-vsi).

Upper Cheek Teeth

Figure 11.17 shows the enamel pattern of NMB Se 338 and two other P3s from Senèze compared to patterns of upper premolars of Sussemiones and one upper premolar from Chagny. *Equus (Sussemionus*) teeth from Süssenborn, Akhalkalaki, Liventsovka, and Chukochya have long and grooved protocones, plicated enamel, and very developed plis caballin (Fig. 11.17E, F, H, I). In contrast, NMB Se 338 (Fig. 11.17D) and other upper cheek teeth from Senèze like NMB Se 336 and MNHL Sen 1855 (Fig. 11.17A, G), as well as from Chagny (Fig. 11.17B) have very short, ungrooved protocones, as is usual in *Allohippus*. In *Allohippus* plis caballin are in general small but may be very developed (MNHL Sen 1855). The P3 from Kolyma (Fig. 11.17C), in spite of not having a groove on its rather small protocone, is closer to *E. (Sussemionus*) than to *Allohippus*. In that case, however, the attribution to an *Equus* is certain because of the cranium to which it belongs.

Third Metapodials

In MCs as well as in MTs, the distal articular width (variable 11 in Fig. 11.18 and Fig. 11.19, Table 11.A3a, Table 11.

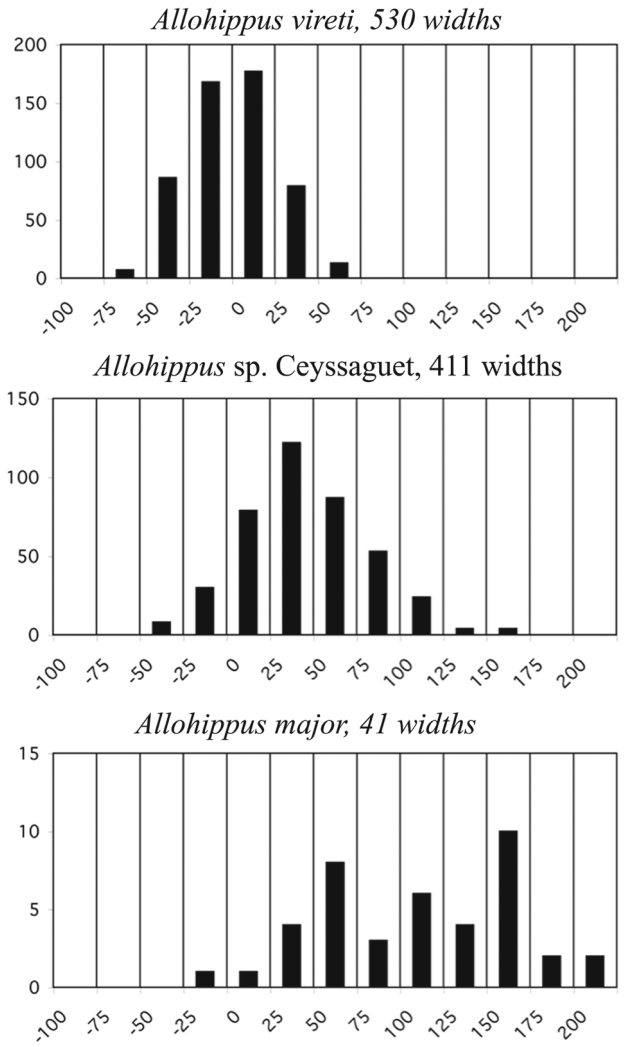

Fig. 11.16 Variability Size Index for Saint-Vallier LD3, Ceyssaguet, and for the *Allohippus major* of Senèze, Gannat, Würzburg-Schalksberg, Oasele, and Kislang

A6a, b, c) is usually larger than the supra-articular width (variable 10) in the large *E.* (*Sussemionus)* from Akhalakalaki, Georgia, and Northeastern Siberia, as opposed to what is seen in *Allohippus*. Using this criterion, I consider that the MCs of Senèze, Gannat (France), Würzburg-Schalksberg (Germany), and Oasele (Romania) belong to *Allohippus*. For the same reason I tentatively refer the gigantic MC from Overstrand (Great Britain) (Fig. 11.19) and the fragmentary MT from Feldioara (Romania) to the large *E. suessenbornensis* group. Although there are several MC morphs at Liventzovka (Fig. 11.20, Table 11.A3b), none qualifies to be *Allohippus major* or *Sussemionus*.

Since the same distingishing characters seem as true for the third metatarsals as for the metacarpals, I refer the MTs from Kislang (Hungary), Würtzburg-Schalksberg, Gannat, and Senèze (FSL 211,077) to *Allohippus major*. Although smaller, I believe that the MTs from Chagny, Vatera (Lesvos, Greece), Liventsovka L-778 and Tataourova (Russia) may also belong to *Allohippus major* (Fig. 11.21, Table 11.A6c).

First Phalanges

Apart from a larger size, anterior first phalanges of the large equid do not seem to differ from those of Sussemiones (Fig. 11.22, Table 11.A12a). The morphology of the posterior first phalanges is more distinct (Fig. 11.23, Table 11.A12b). In specimens from both Chagny and Senèze, the distal supra-articular width is small relative to the proximal depth (variables 6 and 5 on the diagram, respectively). In Sussemiones from Süssenborn and from NE Siberia, the distal supra-articular width is large relative to the proximal depth. At Akhalkalaki, however, only a few phalanges have these proportions, so that the mean for Akhalkalaki is not typical.

Other Limb Bones

According to my data, there are no important differences in the proportions of the other limb bones of the large equids, whether they belong to *Allohippus major* or to the *E.* (*Suessemionus*) group.

Allohippus senezensis senezensis: Material, Description, and Comparisons

Skeletons

–FSL 210993 (ex 96,132) is a mounted skeleton at UCB-Lyon 1. As is usual for mounted skeletons, the data for FSL 210993 are poor. Moreover as mentioned before this skeleton is composite with a caballine mandible and MC.

–FSL SEN 05–0081 + is a nearly complete skeleton of an adult male with a crushed skull (Fig. 11.24, see also Fig. 2.7), excavated in 2005. There are many elements with different field numbers, but as 0081 is the cranium, the specimen can be termed 0081 + .

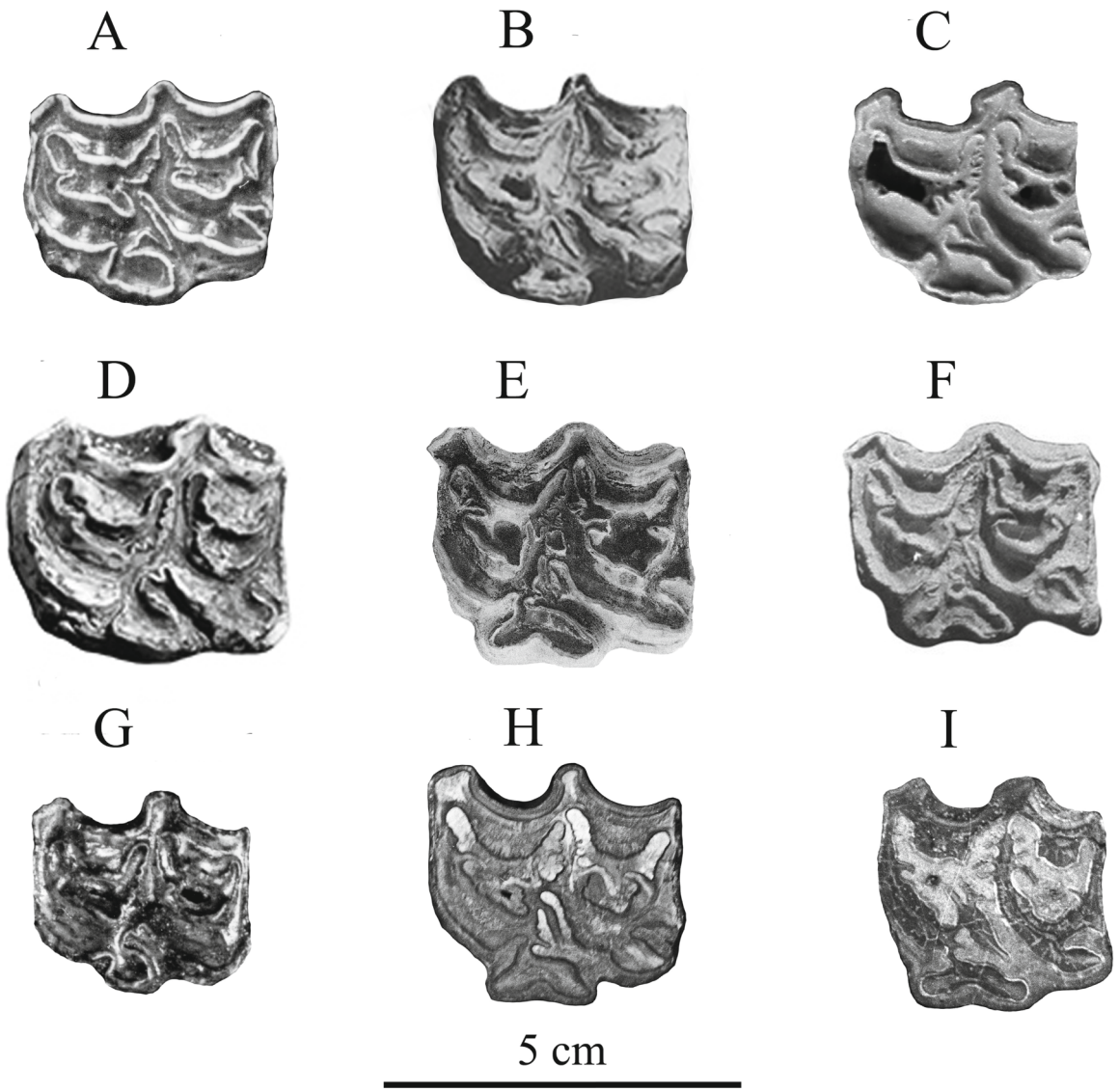

Fig. 11.17 Occlusal views of upper premolars. A. *Allohippus senezensis senezensis,* MNHL Sen 1855. B. *A. major*, Chagny no number. C. *E. (Sussemionus) coliemensis*, Kolyma IA 1741. D. *A. major*, Senèze NMB Se 338. E. *E. (Sussemionus) suessenbornensis,* Süsenborn P4 of the type series figured by Wüst (1910 Plate IV-9). F. *E. (Sussemionus)* cf. *suessenbornensis,* Akhalkalaki AKHA 1289. G. *A. senezensis senezensis,* NMB Se 336. H. *E. (Sussemionus)* sp., Liventsovka ROMK L 131. I. *E. (Sussemionus) verae,* Chukochya PIN 2998–243

–FSL SEN 06–0137 + , recovered in 2006, is less complete, including radius, tibia, metapodials, and first phalanges among other elements (Fig. 11.25).
–NMB Se 141 is a juvenile skeleton.
–NMB Se 551 is a mounted skeleton (the data are therefore poor) of an old female.
–NMB Se 552 is a juvenile skeleton.
–NMB Se 553 is the complete mounted skeleton of a male a little less than 4 years old.
–NMB Se 554 is a nearly complete skeleton of an old male.

Cranial Material

–NMB Se 336, very well preserved cranium of an adult male Fig. 11.26.
–NMB Se 551 is the skull of the above-mentioned mounted skeleton (Fig. 11.27). The cranium shows a malar depression, probably due to the shortness of the very worn crowns of the upper cheek teeth.
–NMB Se 553 is the fragmentary and badly preserved cranium (Fig. 11.28A, B) of another mounted skeleton.

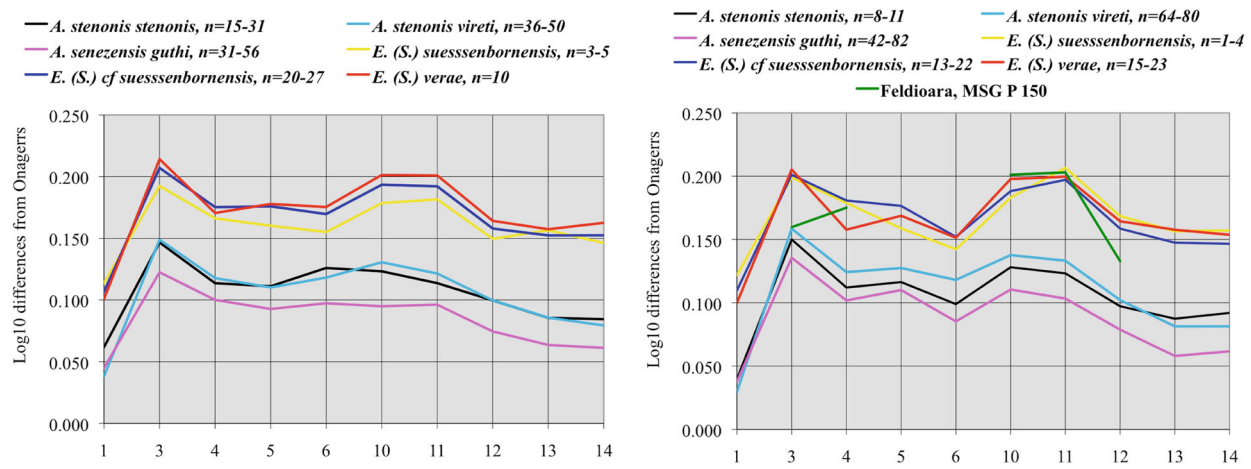

Fig. 11.18 Ratio diagrams of third metacarpals (left panel) and metatarsals (right panel) of *Allohippus* compared to *E. (Sussemionus)*. n: number of specimens. Same variables as in Fig. 11.9. In *Allohippus* the distal articular breadths are relatvely smaller

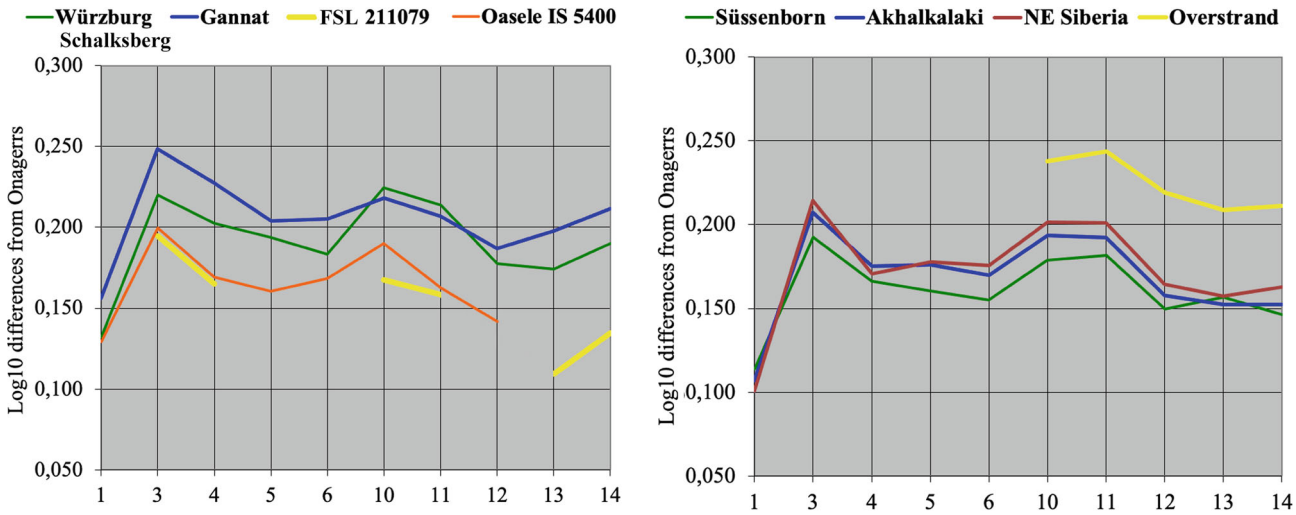

Fig. 11.19 Ratio diagrams of third metacarpals of *Allohippus major* (left panel) compared to Sussemiones (right panel). Same variables as in Fig. 11.9

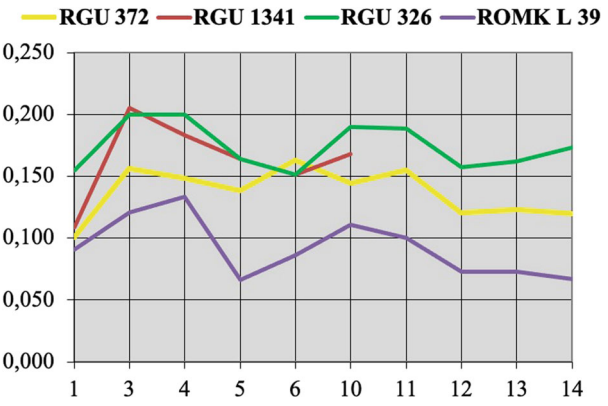

Fig. 11.20 Ratio diagram of some third metacarpals from Liventsovka. Same variables as in Fig. 11.9

–NMB Se 554 is the very badly preserved cranium (Fig. 11.28C) of a nearly complete skeleton.
–NMB Se 796 is the skull of a ca. 1 year old juvenile (Fig. 11.29).
–NMB Se 803, very old and very damaged fragmentary cranium.
–MNHL Sen 5233, adult male skull (Fig. 11.30).
–FSL 210887, crushed cranium of an adult female (Fig. 11.31)
–FSL 210993 (ex 96,132) is the cranium (Fig. 11.32) of the mounted skeleton discussed in Sect. 5.1.
–FSL SEN 05–0081/82 is the skull (Fig. 11.33) of the skeleton excavated in 2005 (see Fig. 1.27 for specimen before cleaning).

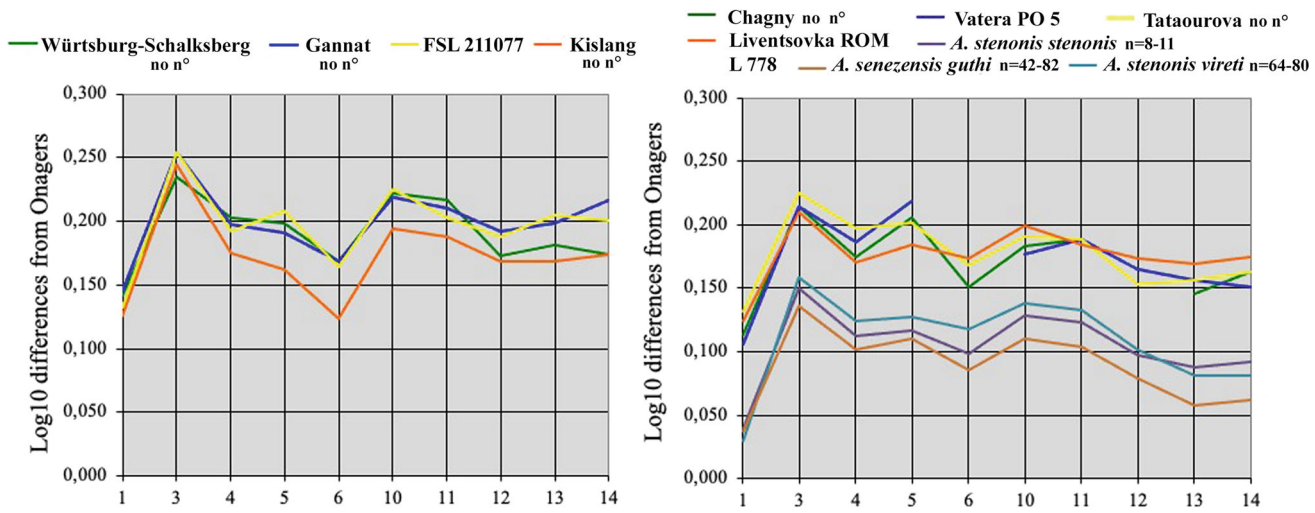

Fig. 11.21 Ratio diagrams of some third metatarsals of *Allohippus major* (left panel) compared to other *Allohippus* (right panel). n: number of specimens. Same variables as in Fig. 11.9

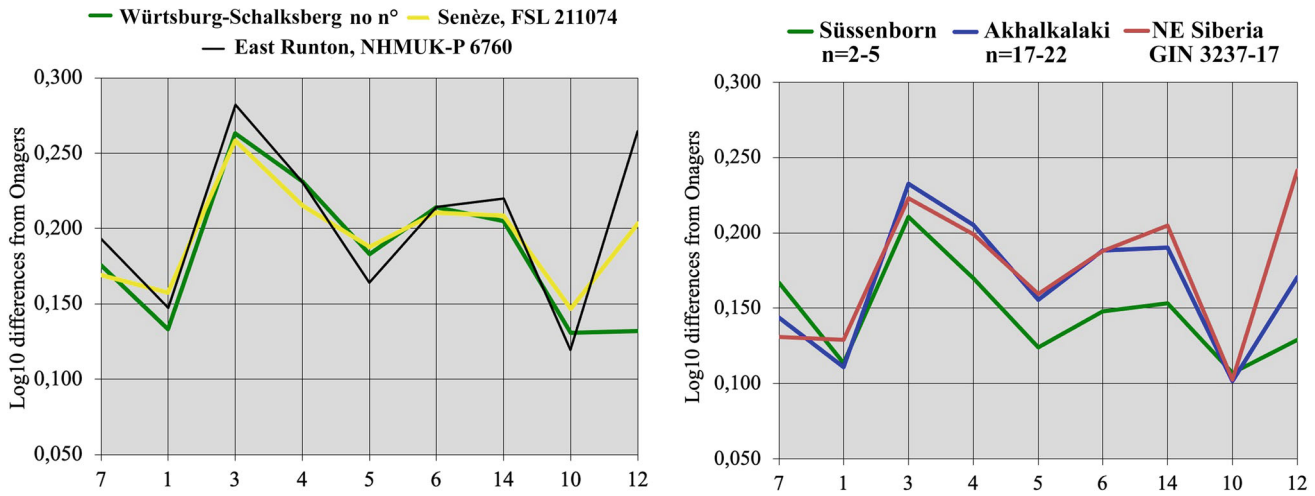

Fig. 11.22 Ratio diagrams of first anterior phalanges of *Allohippus major* from Senèze and other sites (left panel) compared to Sussemiones (right panel). n: number of specimens. 7. Maximal length of trigonum phalangis, 1. Maximal length, 3. Minimal breadth, 4. Proximal breadth, 5. Proximal depth, 6. Distal breadth at the tuberosities, 14. Distal articular breadth, 10. Medial supratuberosital length, 12. Medial infratuberosital length. Technique of measurement illustrated at https://vera-eisenmann.com/first-phalanges-system-of-measurements

Crania Description and Comparisons

In spite of some differences in size and shape, all crania (Table 11.A2) may be referred to a single form. As noted before they have relatively shorter muzzzles and are smaller in size than the 'long-muzzled' *Allohippus*: the average basilar length of Senèze skulls (523 mm) is smaller than in many other samples [545 mm in *Allohippus senezensis guthi* of La Puebla de Valverde (Spain), 554 mm in *A. stenonis vireti* of Saint-Vallier (France), 560 mm in *A. stenonis stenonis* of Olivola (Italy)], but larger than in *A. senezensis mygdoniensis* of Gerakarou, Greece (488 mm). Alberdi et al. 1998 suggested that a close relationship existed between *A. senezensis* and *A. stehlini*, the latter being a subspecies of the former. In spite of the results of their multivariate analyses of limb bones and the resulting phylogenetic tree, I cannot agree with this conclusion given the morphological differences betwen the crania of *A. senezensis* and *A stehlini* (Fig. 11.34, Table 11.A9a).

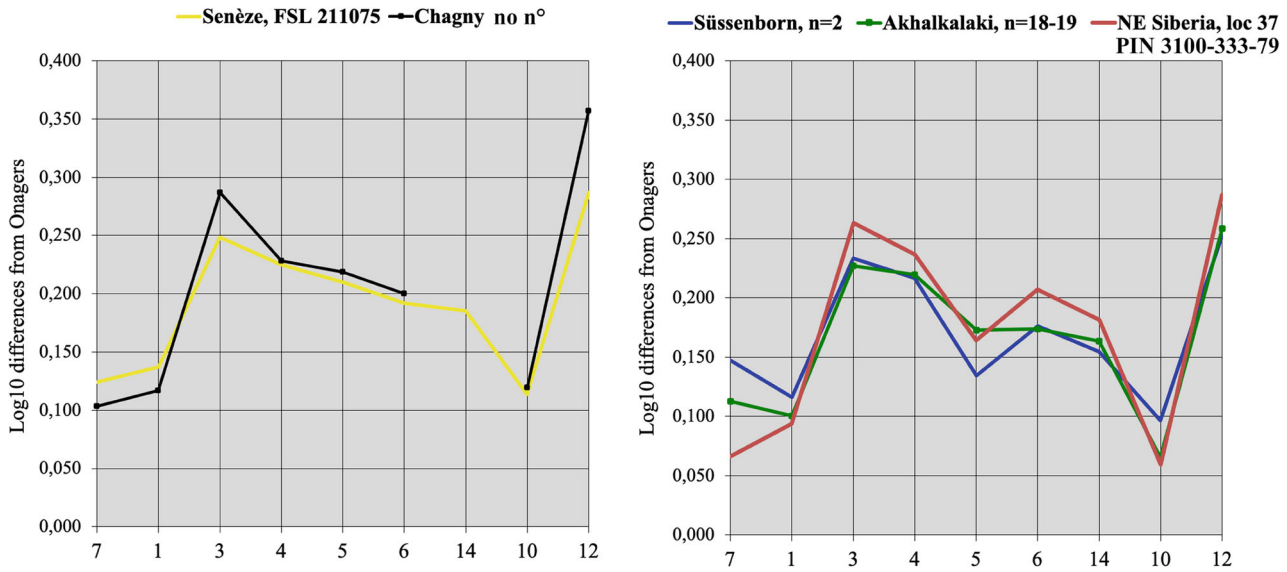

Fig. 11.23 Ratio diagrams of first posterior phalanges of *Allohippus major* (left panel) compared to Sussemiones (right panel). Same variables as in Fig. 11.22

Mandibles (Figs. 11.27, 11.29, 11.30, 11.33)

Mandibles are not very informative elements. Usually they just mirror cranial characters such as size and muzzle proportions (Table 11.A10). Figure 11.35 shows differences between extant *Equus* mandibles and among *A. stenonis vireti*, *A. senezensis senezensis* and *A. senezensis guthi*. The three *Allohippus* mandibles do not differ very much; they resemble those of extant *E. grevyi*.

Cheek Teeth–Specimens

–NMB Se 336, upper cheek teeth (Fig. 11.36A), associated with lowers.
–NMB Se 554, upper cheek teeth (Fig. 11.36F), associated with lowers.
–NMB Se 804, upper cheek teeth (Fig. 11.36B), associated with lowers.
–NMB Se 806, upper cheek teeth (Fig. 11.36C), associated with lowers.
–MNHL Sen 5233, upper cheek teeth (Fig. 11.36D), associated with lowers.
–FSL 210993 (ex 96132), upper cheek teeth (Fig. 11.36E).
–MNHL Sen 1855, upper cheek teeth associated with lowers (Fig. 11.37).
–FSL SEN 05–0081 upper cheek teeth associated with lowers -0082 (Figs. 11.38, 11.39).
–NMB Se 336, lower cheek teeth (Fig. 11.40A), associated with uppers.
–NMB Se 554, lower cheek teeth (Fig. 11.40F), associated with uppers.
–NMB Se 804, lower cheek teeth (Fig. 11.40B). associated with uppers.
–NMB Se 806, lower cheek teeth (Fig. 11.40C) associated with uppers.

Upper Cheek Teeth

As noted above, the short protocones of the upper cheek teeth are quite typical for *Allohippus stenonis*, but the development of the plis caballin is very variable. It is exceptionally long and wide at its base in MNHL Sen 1855 (Fig. 11.37); this is not a usual character. Figure 11.39 shows that most of the Senèze teeth are smaller than *Allohippus stenonis stenonis* from Olivola and Matassino (see measurements in Table 11.A7 and Table 11.A13).

Fig. 11.24 *A. senezensis senezensis* from Senèze. Skeleton SEN 05–0081 +

Fig. 11.25 *A. senezensis senezensis* from Senèze. Partial skeleton SEN 06–0137 +

Lower Cheek Teeth and Incisors

They are typical for *Allohippus*: rounded metaconid and metastylid, pointed liguaflexid, deep ectoflexid on the molars (Figs. 11.37, 11.38, 11.40); cups on incisors, at least on I1 and I2. Measurements are given in Table 11.A11.

Third Metacarpals

FSL 210887 is absolutely similar to *A. stehlini* from Valdarno (Fig. 11.41, Table 11.A3 a and c.). Even excluding the *E. caballus* mentioned above (Fig. 11.11) and the *A. major* FSL 211079, the MCs apppear very polymorphic (Figs. 11.42, Table 11.A3c). Many have deep proximal ends, not usual in *Allohippus stenonis stenonis*. The average MC is smaller and has a deeper diaphysis and proximal epiphysis than *A. senezensis guthi* (La Puebla de Valverde) (Fig. 11.43, Tables 11.A3, 11.A14, 11.A15).

Third Metatarsals

The smallest of them (FSL 210868b) resembles metatarsals of ?*Allohippus* sp. from Pyrgos, Greece (Fig. 11.44, Table 11.A16 a). Apart from the *Allohippus major* specimens and the small FSL 210868b, the morphology (Fig. 11.45 Table 11.A6d) of the MTs seems more homogeneous than for the MCs (even so, the coefficients of variation are larger than usual for one species). Their mean is intermediate in size between the larger *A. senezensis guthi* (La Puebla de Valverde) and the smaller *A. senezensis mygdoniensis* (Gerakarou, Greece) (Fig. 11.46, Table 11.A6b), differing from all of these by a deeper proximal end (measure 6).

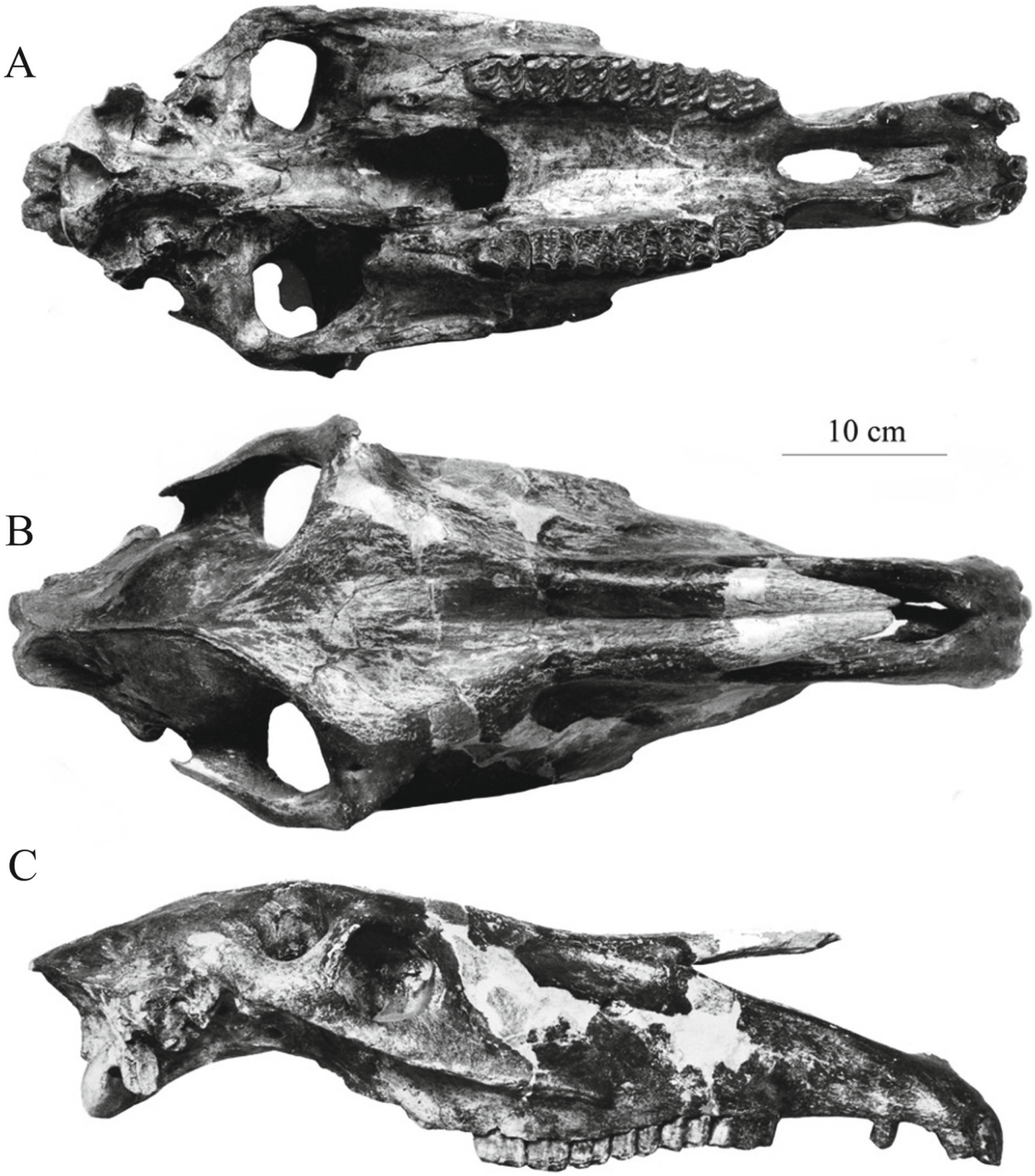

Fig. 11.26 *A. senezensis senezensis* from Senèze. Cranium NMB Se 336. A. Occlusal view. B. Dorsal view. C. Lateral view

Fig. 11.27 *A. senezensis senezensis* from Senèze. Skull NMB Se 551, occlusal view

First Phalanges

First anterior phalanx FSL 211055, first posterior FSL 211082, and third anterior FSL 210899 are probably associated with each other. They are quite a bit larger than the rest but not as large as those of *Allohippus major* (Fig. 11.15). Ten anterior first phalanges which are alike in size and proportions are referred to *A. senezensis senezensis*. They are slightly smaller than those of *A. senezensis guthi* of La Puebla de Valverde. Three others are quite a bit larger: NMB Se 554, NMB Se 828, and FSL 211055, the last being even longer (variable 1) than the average of *A. stenonis vireti* (Fig. 11.47, Table 11.A12).

Among the first posterior phalanges, nine are relatvely similar. Two (NMB Se 554 and FSL 211090) are close to the average of *A. stenonis vireti* and two (MNHL Sen 1689 and FSL 211083) are as small as the specimens from Pyrgos (Fig. 11.48, Table 11.A12). The average dimensions of the nine posterior Ph1s which can be referred to *A. senezensis senezensis* are slighly smaller than in *A. senezensis guthi*; one of them (FSL 211085bis) overlaps the mean of the latter.

Other Limb Bones (Tables 11.A14, 11.A15, 11.A16, 11.A17, 11.A18, 11.A19, 11.A20, 11.A21, 11.A22).

Except for the large and small specimens already discussed, other Senèze elements are intermediate in size between those of *A. senezensis guthi* and smaller forms like *A. senezensis mygdoniensis*.

Conclusions

Tentative Identification of Selected Villafranchian Equids

A better understanding of Villafranchian equids cannot be achieved without a combination of detailed morphology and dating, at least for key localities, i.e., where the material is varied, abundant, homogeneous, and well preserved and/or where fossils are especially interesting by their “originality”

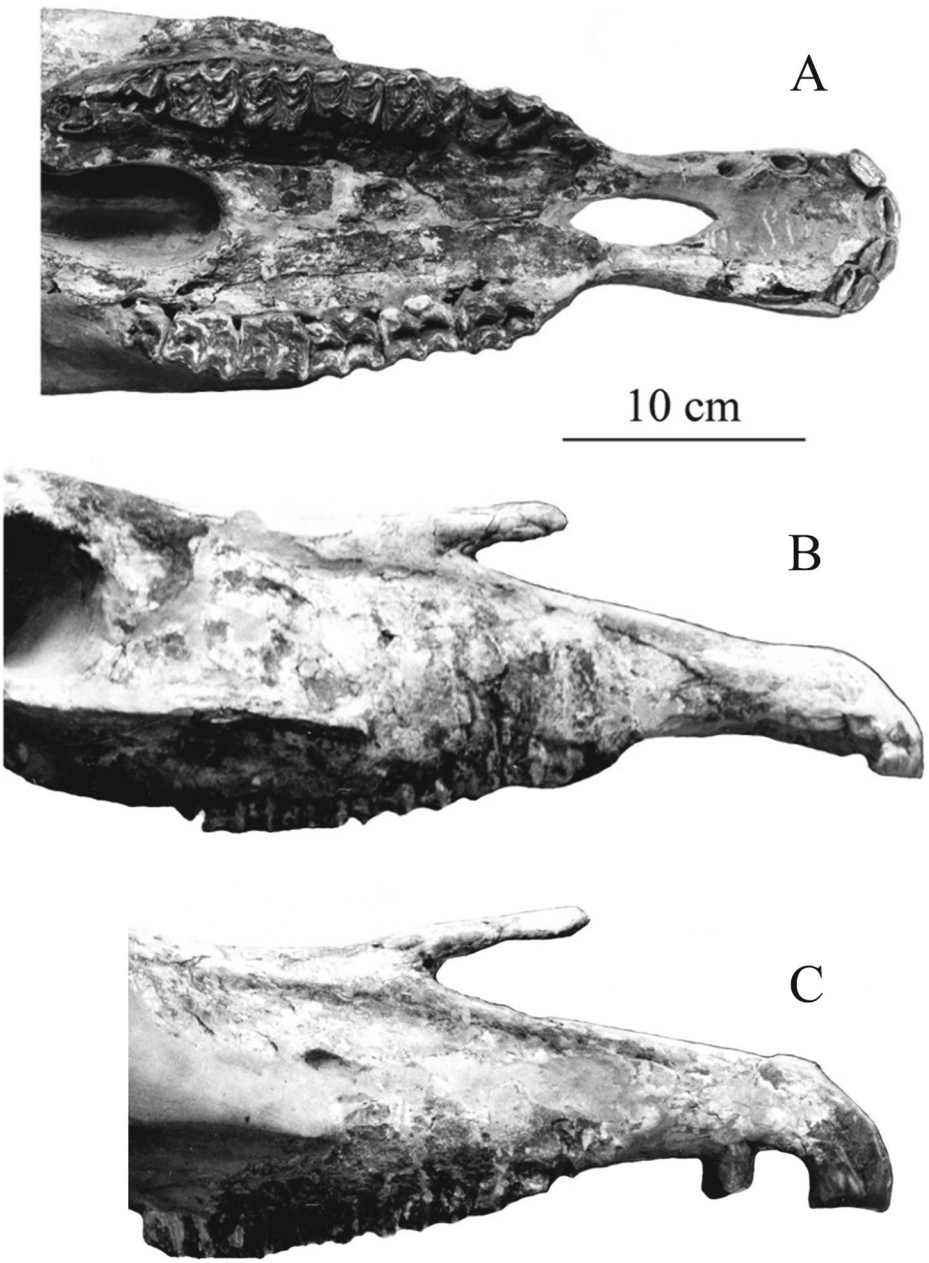

Fig. 11.28 *A. senezensis senezensis* from Senèze. Anterior fragment of cranium NMB Se 553. A. Occlusal view. B. Lateral view. Anterior fragment of cranium NMB Se 554. C. Lateral view

Fig. 11.29 *A. senezensis senezensis* from Senèze. Juvenile skull NMB Se 796, lateral view

(unusual size or morphology). The age may help to distinguish morphologically similar populations which differ widely in time. But progress also depends 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 definitive classification. The size of an equid cannot be used as chronological evidence: large equids occur just above the Gauss-Matuyama boundary (Montopoli) as well as around the Brunhes-Matuyama boundary (Würzburg-Schalksberg). 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 (Fig. 11.49, Table 11.A3d).

- Figure 11.49A. ?*Allohippus* sp. 1 from Montopoli (Italy), Sarikol Tepe (Turkey), and Loubières de Pardines (France). Metacarpals are robust and have shallow distal keels (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 this genus.
- Figure 11.49B.?*Allohippus* sp. 2: two metacarpals from Vatera (Greece) and Huelago (Spain) are slender, with distal supra-articular breadth large relative to articular breadth (variables 10 and 11), as is usually the case in *Allohippus*. Their slenderness, however, is not typical for *Allohippus*, their proportions being more onager-like. Both localities are believed to be about 2 Ma or more (Alberdi & Ruiz-Bustos 1989; Alberdi et al. 1998; Eisenmann 2002).
- Figure 11.49C. ?*Allohippus* sp. 3: four metacarpals are larger than the preceding and very similar in size and morphology, being slender and with relatively large proximal depths and distal articular breadths (measures 6, 11). One is from Tegelen (Netherlands) believed to be 1.8 Ma (Westerhoff et al. 1998); the other three are from Morskaja, Liventzovka, and Khapry (from the Khapry complex, Russia) believed to be ca. 2.5 Ma.
- *Allohippus stenonis* ssp. from Ceyssaguet: According to the data kindly provided by N. Aouadi, the sample of MCs 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. By their proportions, they resemble the average MC from Sainzelles (France) but are quite a bit larger (Fig. 11.50). Sainzelles 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).

Keeping all those caveats in mind, Fig. 11.51 presents the various taxa (and selected populations or individuals) and their distributions in time.

A. senezensis senezensis

- As illustrated above (Fig. 11.6, Table 11.A9 a), the average skull of *A. senezensis senezensis* belongs to the short-muzzled group and is intermediate in size between *A. senezensis guthi* and *A. senezensis mygdoniensis*.
- The average MC III of *A. senezensis senezensis* is smaller than *A. senezensis guthi* and larger than *A. senezensis mygdoniensis* (Fig. 11.43, Table 11.A3). As in *A. senezensis mygdoniensis*, the diaphysis is deep relative to its width (variables 4 and 3).
- Short muzzles and deep, not very robust, metapodials are usually found in equids living in rather dry conditions like extant *Equus hemionus* and *E. przewalskii* (Eisenmann 1984; Eisenmann & Guérin 1984).

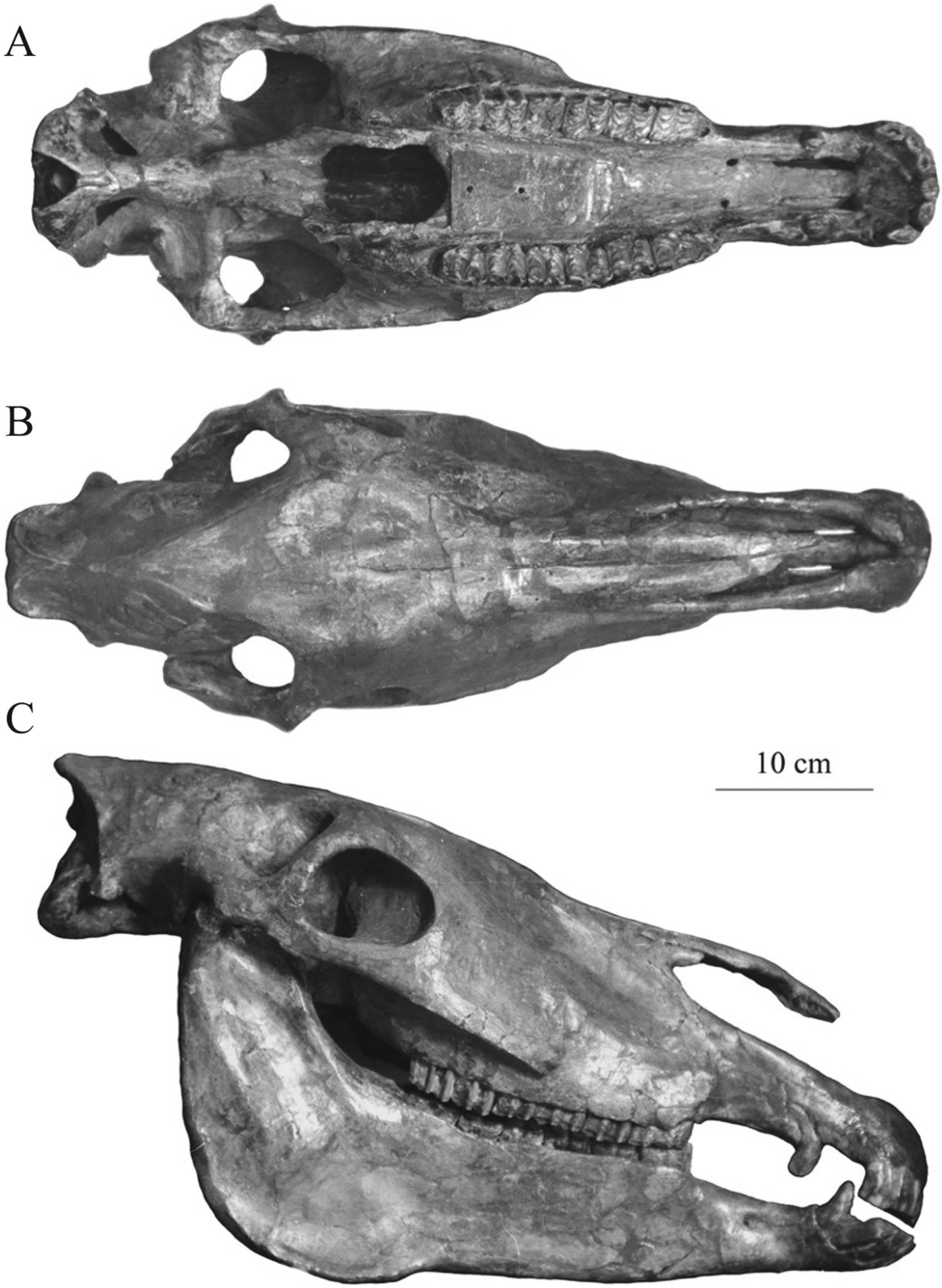

Fig. 11.30 *A. senezensis senezensis* from Senèze. Skull MHNL Sen 5233. A. Occlusal view. B, Dorsal view. C. Lateral view

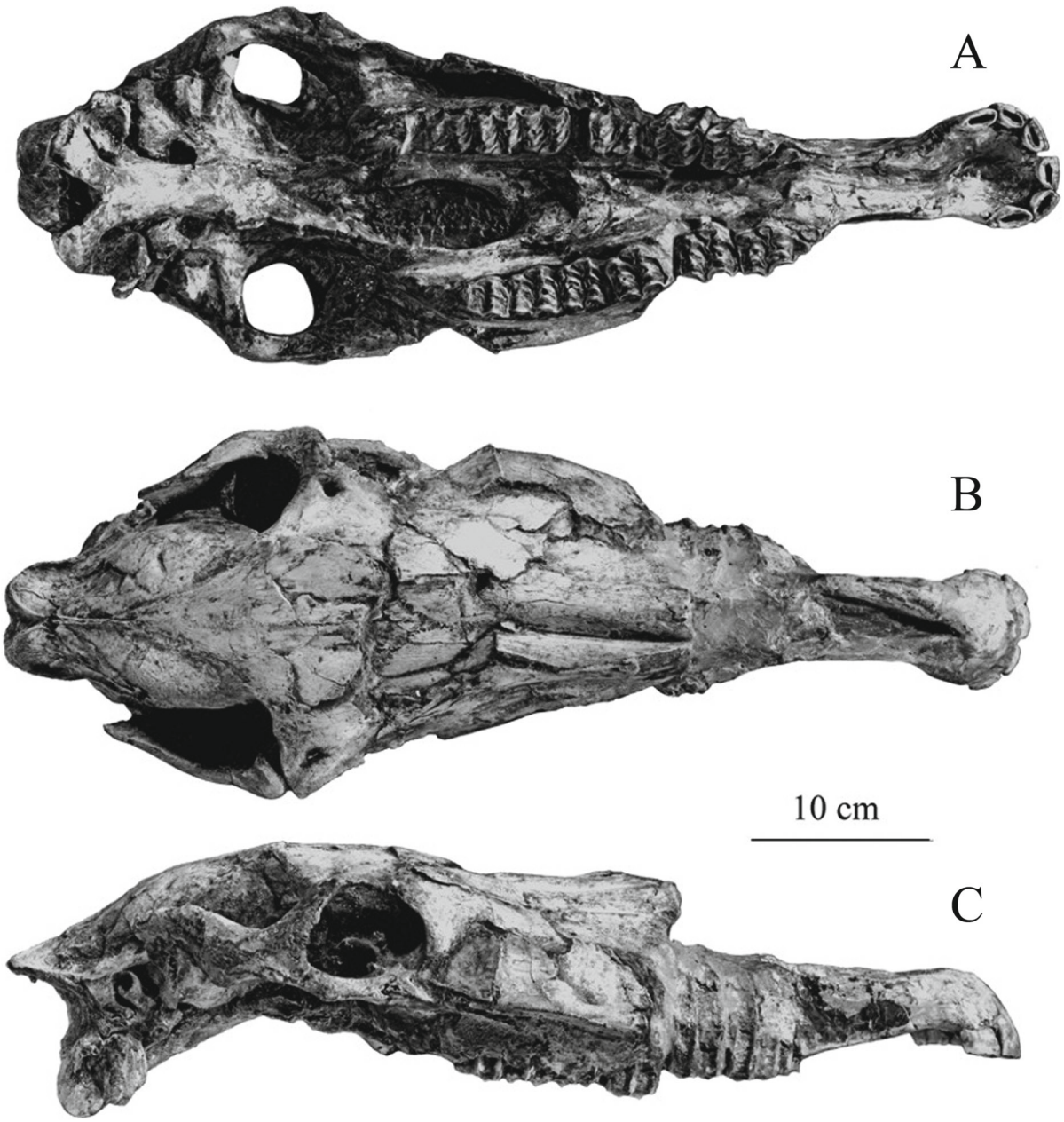

Fig. 11.31 *A. senezensis senezensis* from Senèze. Cranium FSL 210887. A. Occlusal view. B. Dorsal view. C. Lateral view

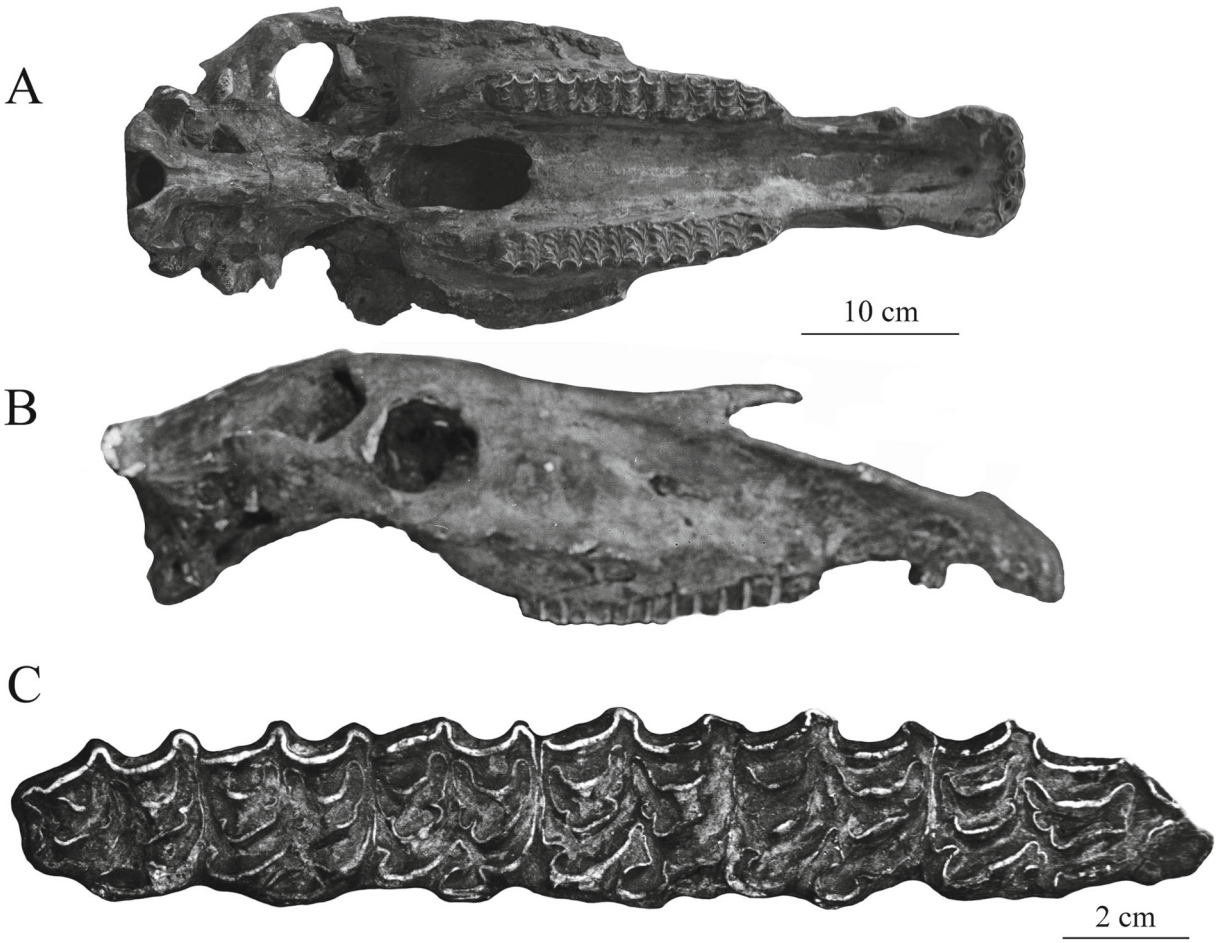

Fig. 11.32 *A. senezensis senezensis* from Senèze. Cranium FSL 210993. A. Occlusal view. B. Lateral view. C. Right P3-M3, occlusal view

Allohippus major *from Senèze and Other Localities*

From the enamel pattern of the P3 as well as the proportions of the metapodials, the large equid from Senèze is almost certainly an *Allohippus*, although we cannot be certain so long as its cranial proportions remain unknown. It can be referred to *A. major* although the upper cheek series from Chagny chosen as lectotype by Alberdi et al. (1998) is not completely typical for *Allohippus.* According to the proprtions of metapodials and first phalanges, the similarly-sized specimens from Gannat (France), Würtsburg-Schalksberg (Germany), East Runton (Great Britain), Vatera PO 5 (Greece), Kislang (Hungary), Oasele (Romania), and Tataourova (Russsia) also belong to *Allohippus major*.

Are there Age Indications for the Senèze Equids?

The occurrence of caballine fossils has already been discussed above. (See "Occurrence of several equids at Senèze"). Assuming that they do not actually belong to the primary Senèze collections, there still remains evidence for more than one species of equid at Senèze.

– *A. senezensis senezensis* is the most frequent equid. Both partial skeletons and other elements were found below the oldest dated level (SEN 98, 2.18 ± 0.03 Ma in Trench 5); the more complete FSL SEN 05–0081 + may be one of the oldest of all Senèze fossils, around 2.2 Ma (Delson et al. 2024). *A. senezensis senezensis* is similar to *A senezensis guthi* of La Puebla de Valverde (Spain),

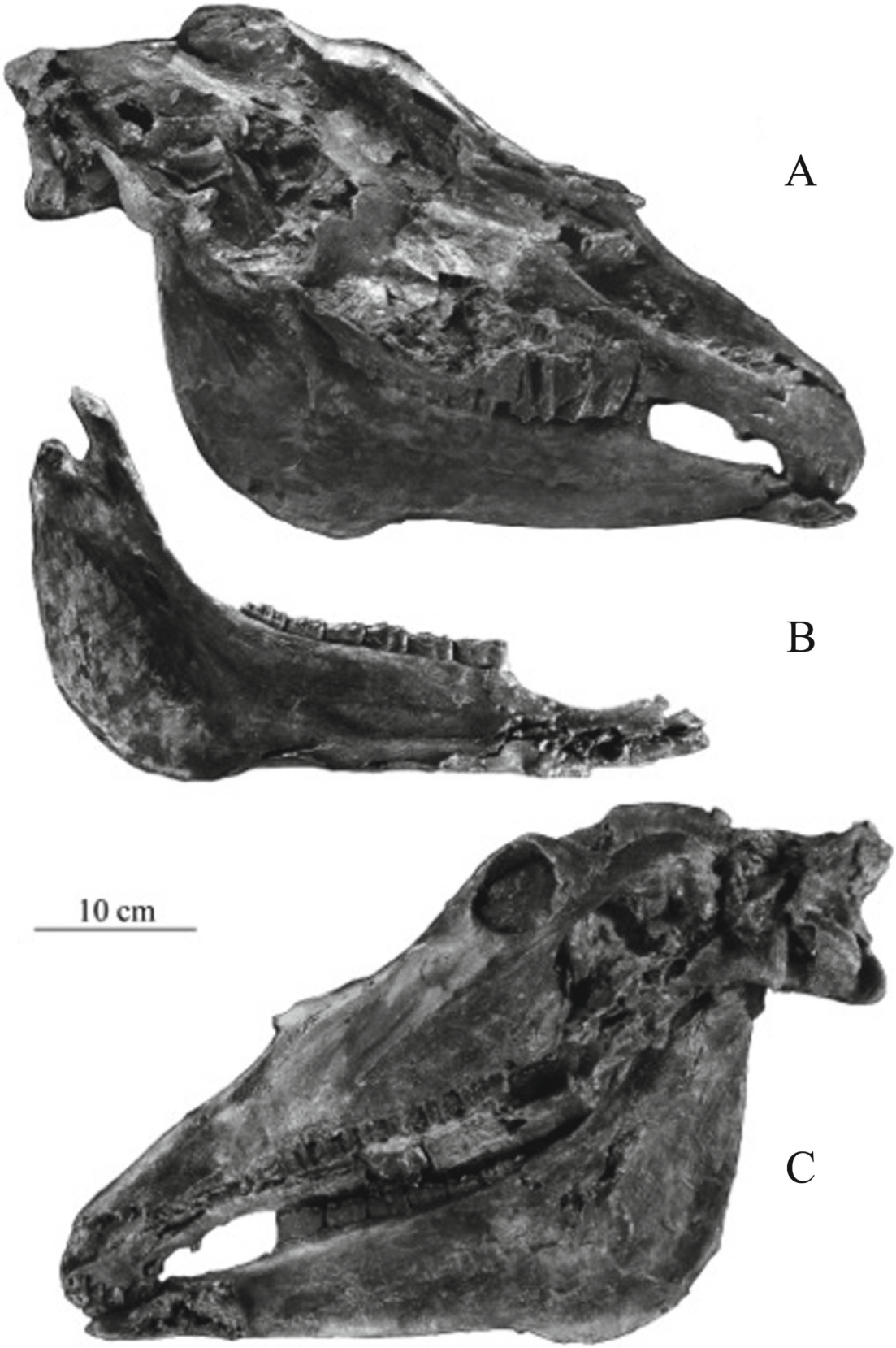

Fig. 11.33 *A. senezensis senezensis* from Senèze. Skull SEN 05–0081/82. A. Right lateral view. B. Internal view of the left mandibular corpus (05-0082). C. Left lateral view

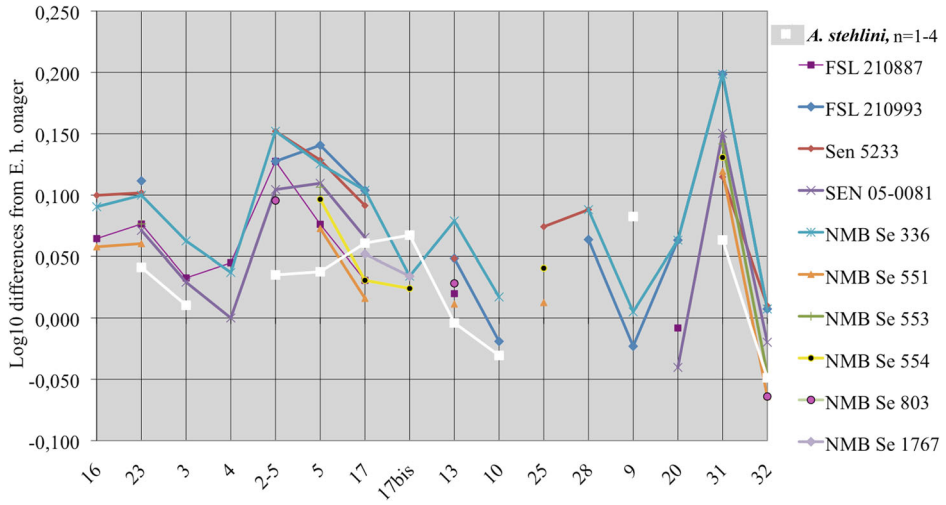

Fig. 11.34 Ratio diagrams of *Allohippus senezensis senezensis* (10 individuals) and *Allohippus stehlini* crania. Same variables as in Fig. 11.7. In addition to their smaller size, the crania of *A. stehlini* differ from those of *A. senezensis senezensis* by a wider muzzle breadth between the interalveolar borders (variable 17bis) and by longer choanae (variable 9)

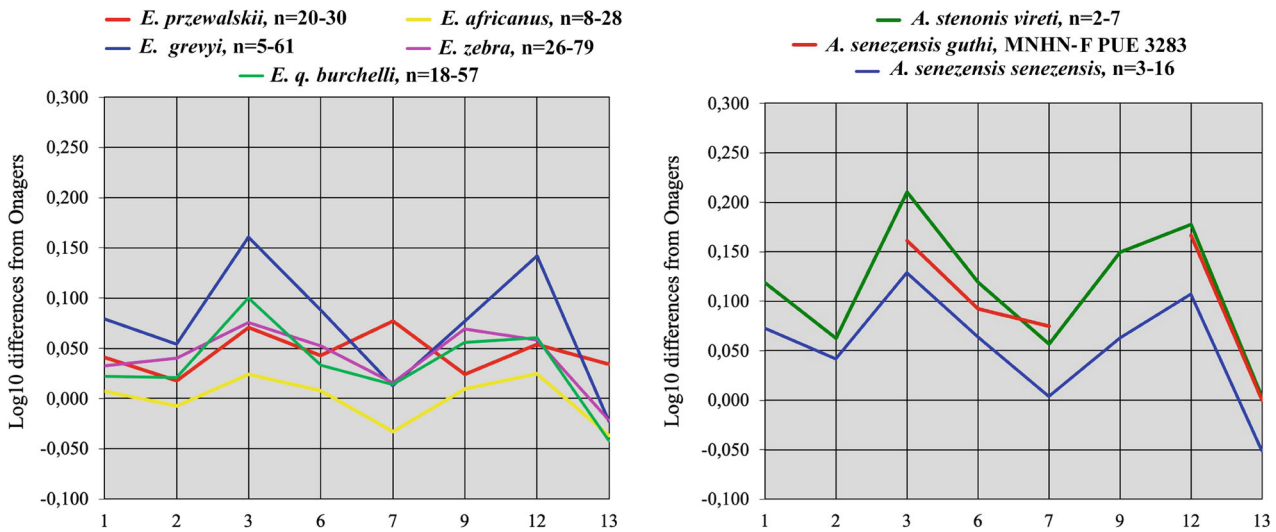

Fig. 11.35 Ratio diagrams of extant *Equus* (left panel) and *Allohippus* (right panel) mandibles. 1. Maximal length; 2. Radius of the mandibular angle; 3. Diastema; 6. Symphysis length; 7. Breadth at the posterior borders of i3; 9. Height in front of p2; 12. Muzzle length; 13. Least symphysis breadth. n: number of specimens. System of measurements illustrated at https://vera-eisenmann.com/mandibles-system-of-measurements

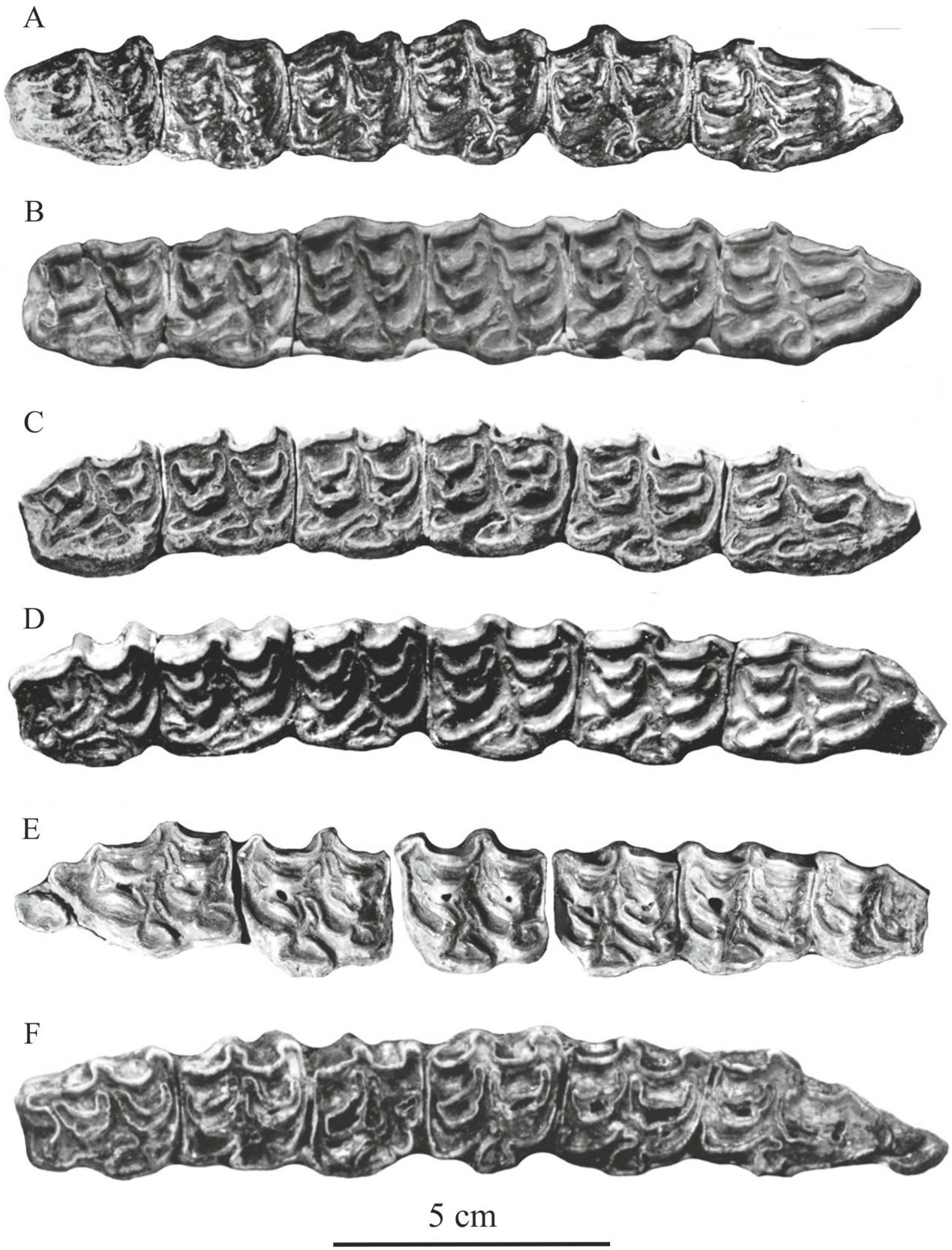

Fig. 11.36 *A. senezensis senezensis* from Senèze. Uppper cheek teeth: A. Right P2-M3 NMB Se 336. B. Right P2-M3 NMB Se 804. C. Right P2-M3 NMB Se 806. D. Right P2-M3 MHNL Sen 5233. E. Left P2-M3 FSL 210887. F. Right P2-M3 NMB Se 554

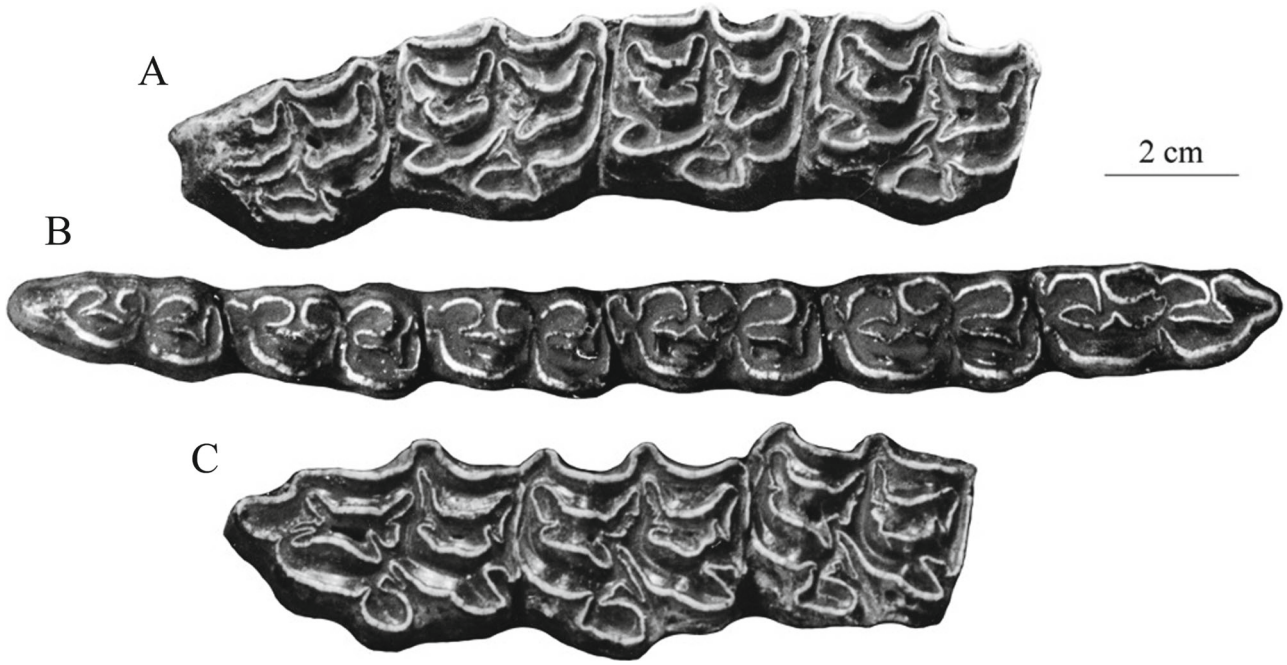

Fig. 11.37 *A. senezensis senezensis* from Senèze. Upper and lower cheek teeth of MNHL Sen 1855. A. Right P4-M3. B. Right p2-m3. C. Left P2-P4

Fig. 11.38 *A. senezensis senezensis* from Senèze. A. SEN 05–0081 right P2-M3. B. SEN 05–0082 right p2-m3

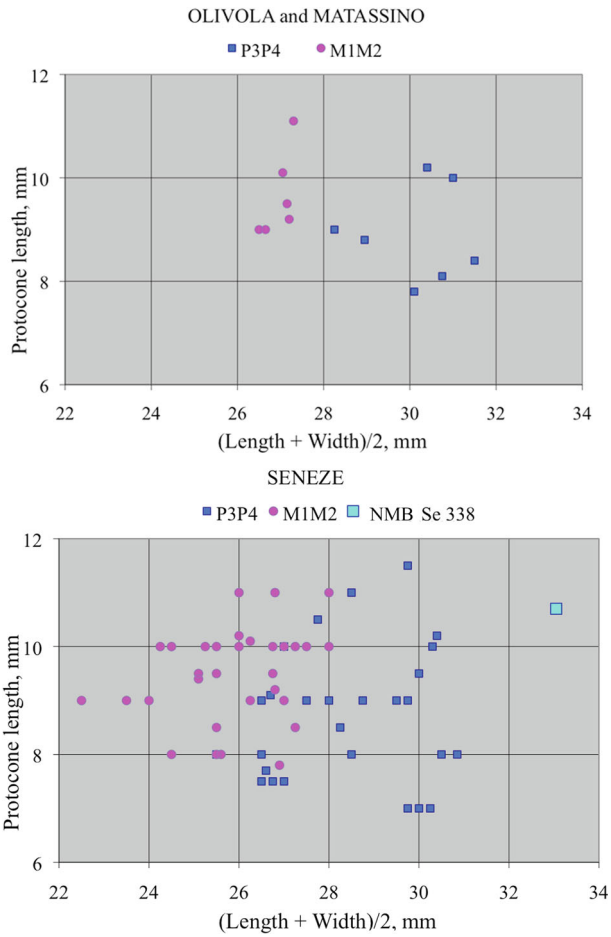

Fig. 11.39 Scatter diagrams of protocone lengths versus average occlusal dimensions [(occlusal length + occlusal width)/2] in *A. senezensis* of Senèze and *A. stenonis* of Olivola and Matassino

which is generally considered to be biochronologically closer to St. Vallier than to Senèze, suggesting that La Puebla de Valverde is older than 2.2 Ma. *A. senezensis mygdoniensis* of Gerakarou (Greece) is also similar and may thus be older than its estimated age of ca. 1.8 Ma shown on Fig. 11.51.

- One upper cheek tooth and 16 limb bones belong to a very large Villafranchian equid. I refer them to *Allohippus major* (see above the comparison of metapodials and first phalanges). They could belong to an earliest Pleistocene species like the one from Oasele (Montopoli faunal unit?) or to a mid-Early Pleistocene form as at Gannat (where it is associated with a Merck's Rhinoceros and a peculiar *Megaceros* [C. Guérin, 1995, pers. comm.]).
- Two first phalanges are larger than the average for *A. stenonis vireti* (ca. 2.5 Ma).
- One MC III resembles *A. stehlini* of Valdarno (younger than the Olduvai subchron).
- One MT III and one first phalanx resemble the small ?*Allohippus* sp. of Pyrgos (late MNQ 18 or early MNQ 19).

The last five specimens seem to be significantly different from typical *A. senezensis senezensis*. They might indicate additional rare equids at Senèze, in which case they would extend the known ranges of these taxa, or they might potentially be intrusive or erroneous (as with the caballine material).

Summary

Three genera of Plio-Pleistocene monodactyl equines are recognized and distinguished by cranial proportions: *Equus*, *Plesippus* and *Allohippus*. *Equus* (and generally *Plesippus*) have a shorter naso-incisival notch relative to cheek length than *Allohippus*, while the ratio of vomerine length to palatal length is generally lower in *Allohippus* than *Plesippus* (and *Equus caballus*). All *Equus* also have longer post-vomerine length compared to overall palatal length than either *Plesippus* or *Allohippus*. Using variation in extant wild species of *Equus* as a model, *Allohippus stenonis* is distinguished from *A. senezensis* at the species level based on relative

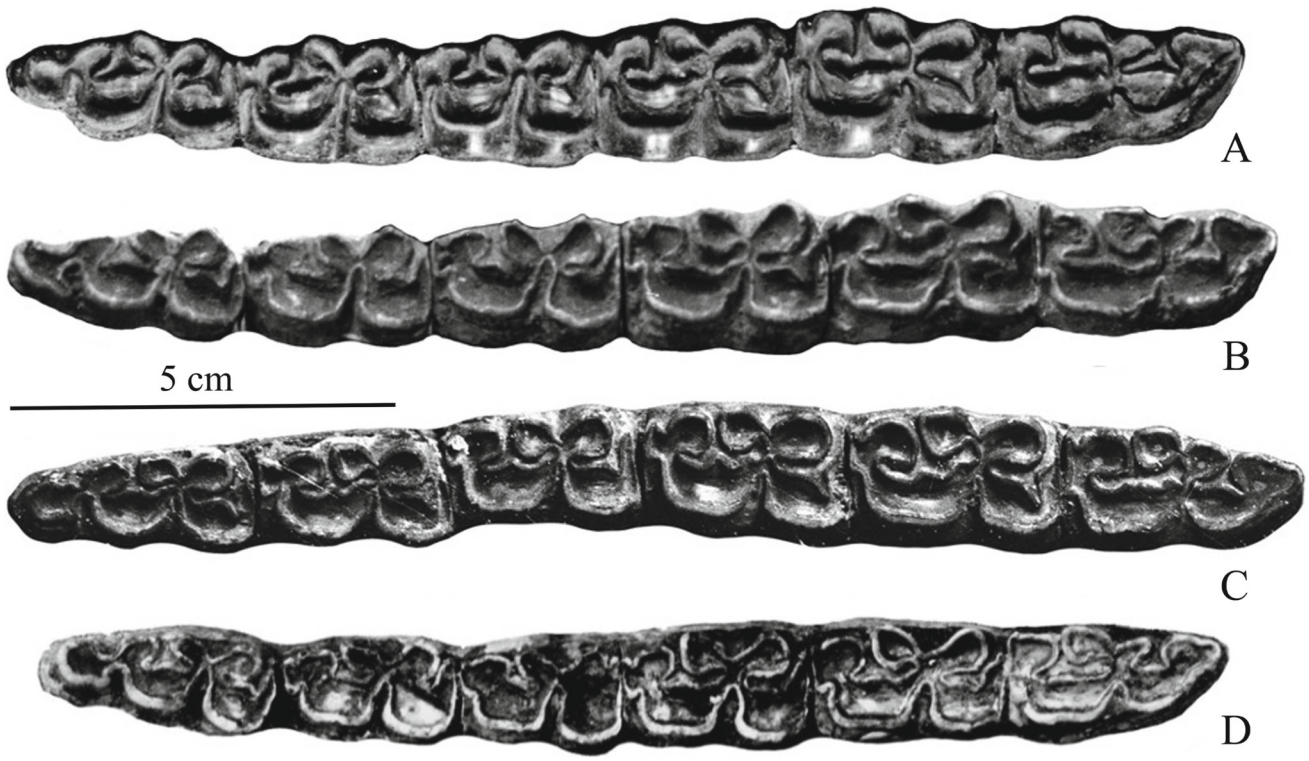

Fig. 11.40 *A. senezensis senezensis* from Senèze. Lower cheek teeth. A. NMB Se 804. B. NMB Se 806. C. Sen 5233. D. NMB Se 554

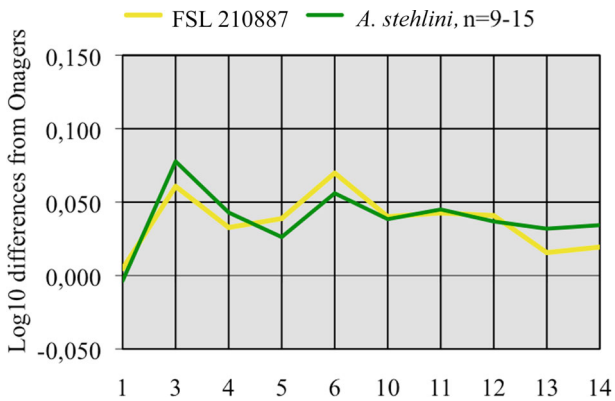

Fig. 11.41 Ratio diagrams of third metacarpals of *Allohippus stehlini* from Valdarno and of FSL 210,887 from Senèze. n: number of specimens

muzzle length (and some postcranial features), with several subspecies in each (see Table 11.A5).

The numerous equid fossils from Senèze were mostly collected in the first half of the twentieth century without detailed stratigraphic provenance. At least two and possibly up to six different taxa can be distinguished in the material catalogued as coming from Senèze in the Lyon, Basel and Paris collections. The mandible and metacarpal of a mounted skeleton, an isolated metatarsal and some isolated lower cheek teeth are clearly caballine and may be erroneously labeled or derived from an otherwise unknown younger horizon at Senèze.

The vast majority of the finds are identified as *Allohippus senezensis senezensis*, which is intermediate in size and proportions between *A. senezensis guthi* of La Puebla de Valverde (Spain) and *A. senezensis mygdoniensis* of

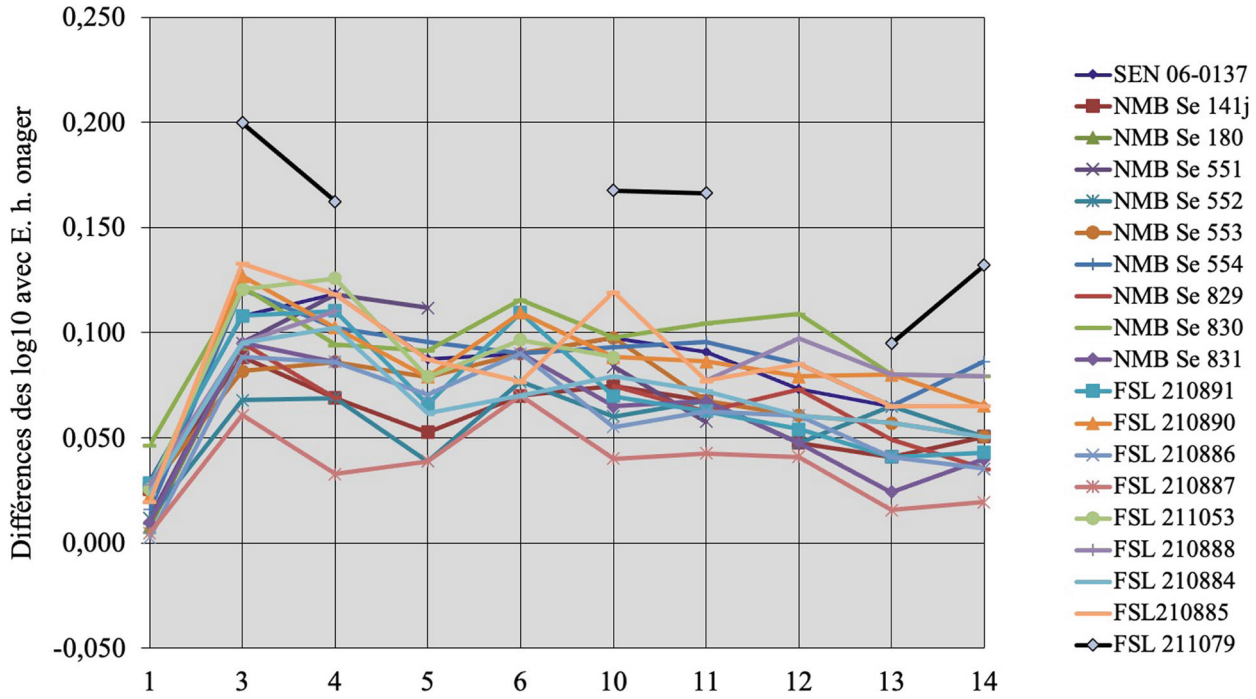

Fig. 11.42 Ratio diagrams of third metacarpals from Senèze. Same variables as in Fig. 11.9

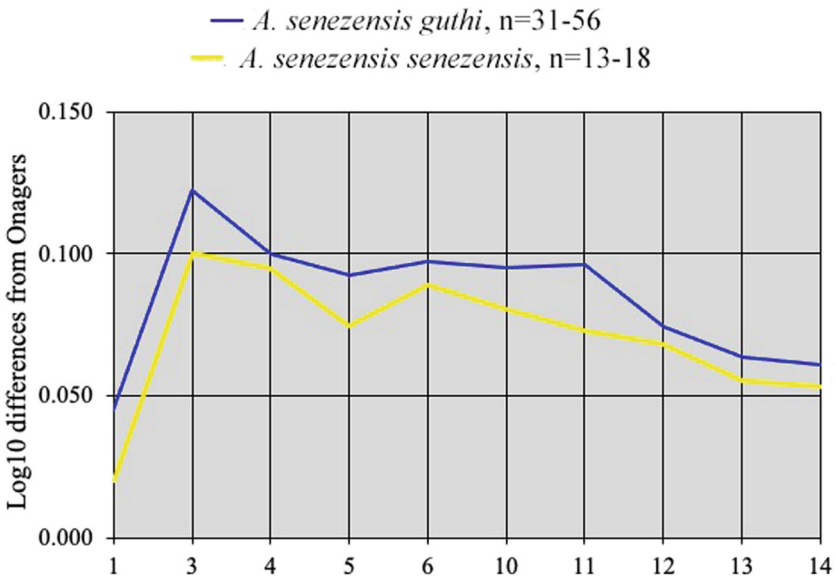

Fig. 11.43 Ratio diagrams of mean of third metacarpals of *A. senezensis senezensis* from compared to those of other equids. Same variables as in Fig. 11.9

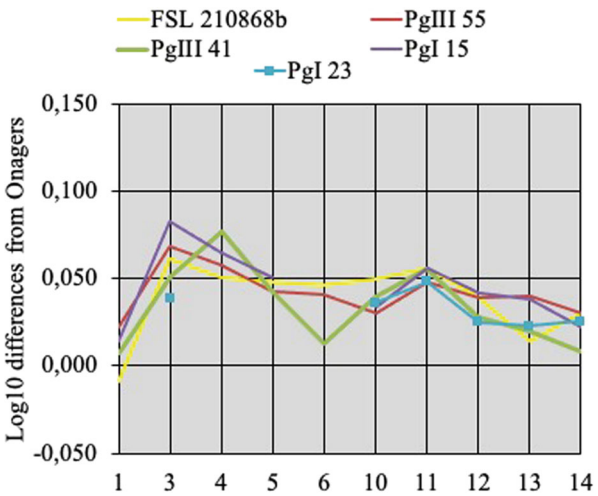

Fig. 11.44 Ratio diagrams of third metatarsals from Pyrgos and of FSL 210868b from Senèze. Same variables as in Fig. 11.9

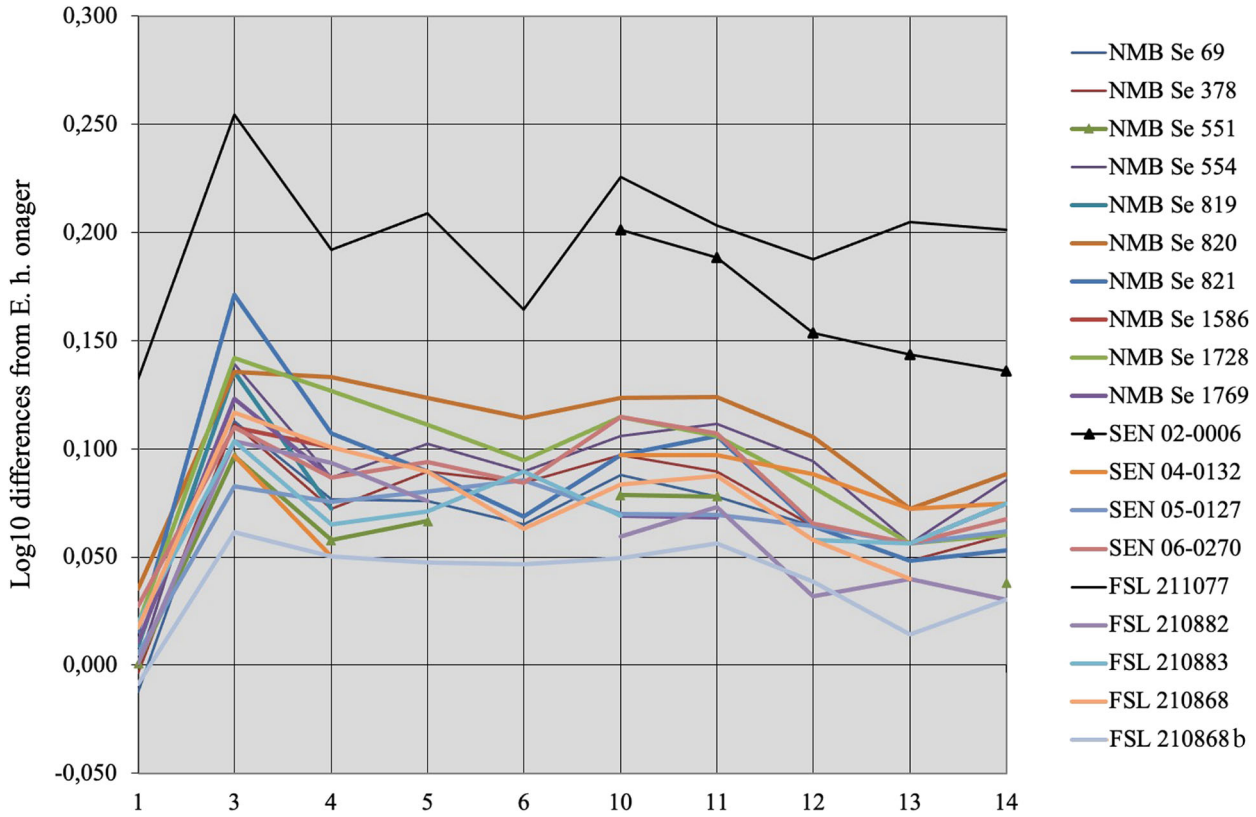

Fig. 11.45 Ratio diagrams of third metatarsals from Senèze. Same variables as in Fig. 11.9

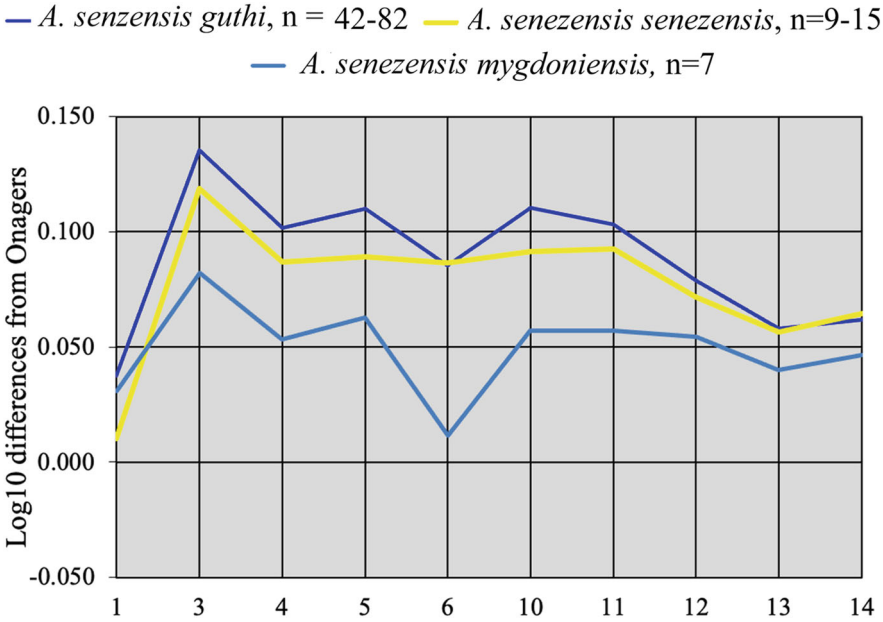

Fig. 11.46 Ratio diagrams of mean of third metatarsals of *A. senezensis senezensis* from Senèze compared to those of other equids. n: number of specimens. Same variables as in Fig. 11.9

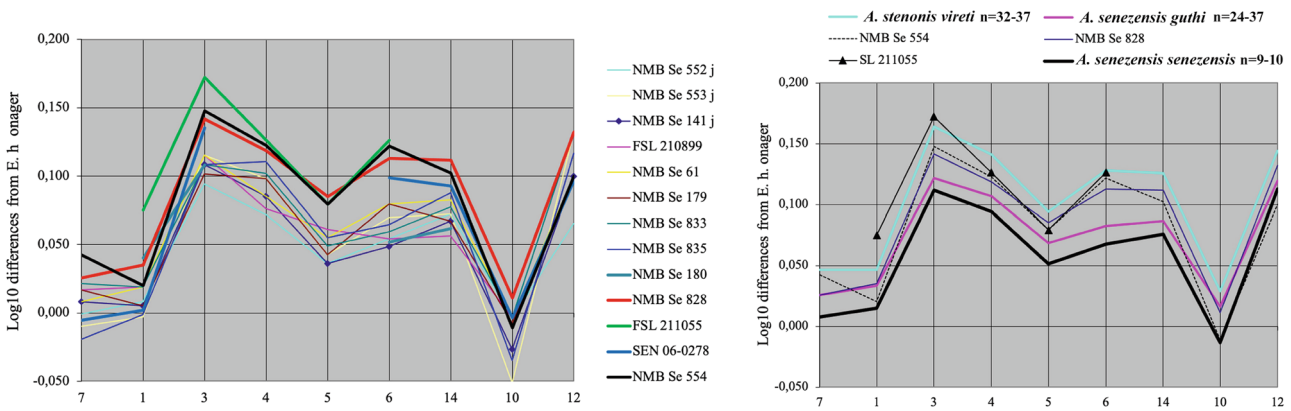

Fig. 11.47 Ratio diagrams of first anterior phalanges from Senèze (left panel) and of the mean of *A. senezensis senezensis* compared to those of other equids and three large Ph1A from Senèze (right panel). n: number of specimens. Same variables as in Fig. 11.22

Gerakarou (Greece). It has a relatively short muzzle and deep, not very robust, metapodials, comparable to those of extant equids living in rather dry conditions. Two partial skeletons and a few other possibly associated hindlimb elements were recovered in the new excavations close to the bottom of the local sequence, thus ca 2.2 Ma.

One isolated P3 and 16 limb bones (humerus, radii, metacarpal, tibiae, tali and first, second and third phalanges) belong to a very large ?*Allohippus*. The tooth has a short, ungrooved protocone and small pli caballin; on the metapodials, the distal articular width is larger than the supra-articular width; on the anterior first phalanx the distal supra-articular width is small relative to the proximal depth; these features are common for *Allohippus*. This sample can be identified as *Allohippus major*, and samples from other localities referred to this species are also discussed.

In addition to these clearly distinguishable samples, there are five specimens which appear to be beyond the variation range of either *Allohippus* population and might possibly represent additional taxa which are similar to larger samples

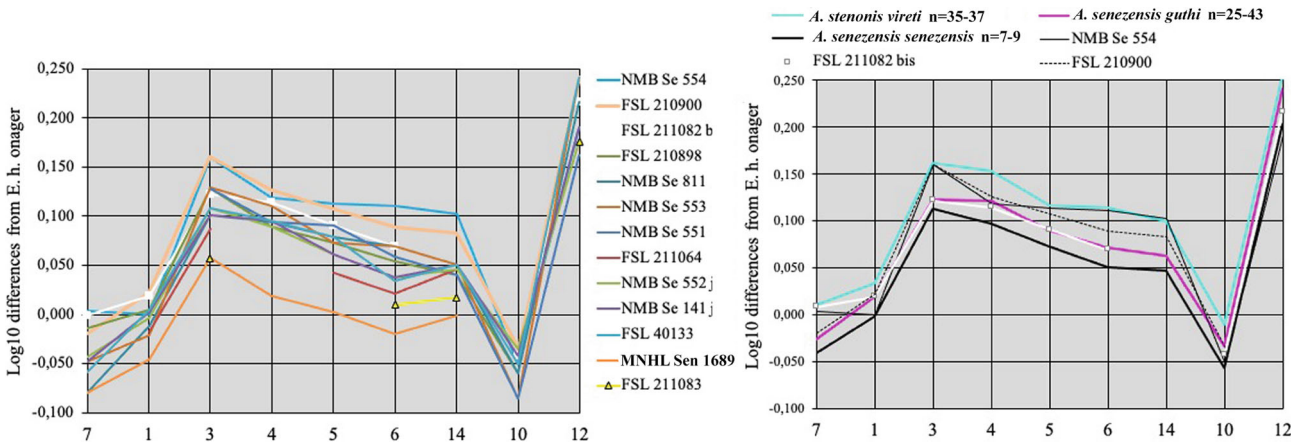

Fig. 11.48 Ratio diagrams of first posterior phalanges from Senèze (left panel) and of the mean of *A. senezensis senezensis* compared to those of other equids and three large Ph1P from Senèze (right panel). n: number of specimens. Same variables as in Fig. 11.22

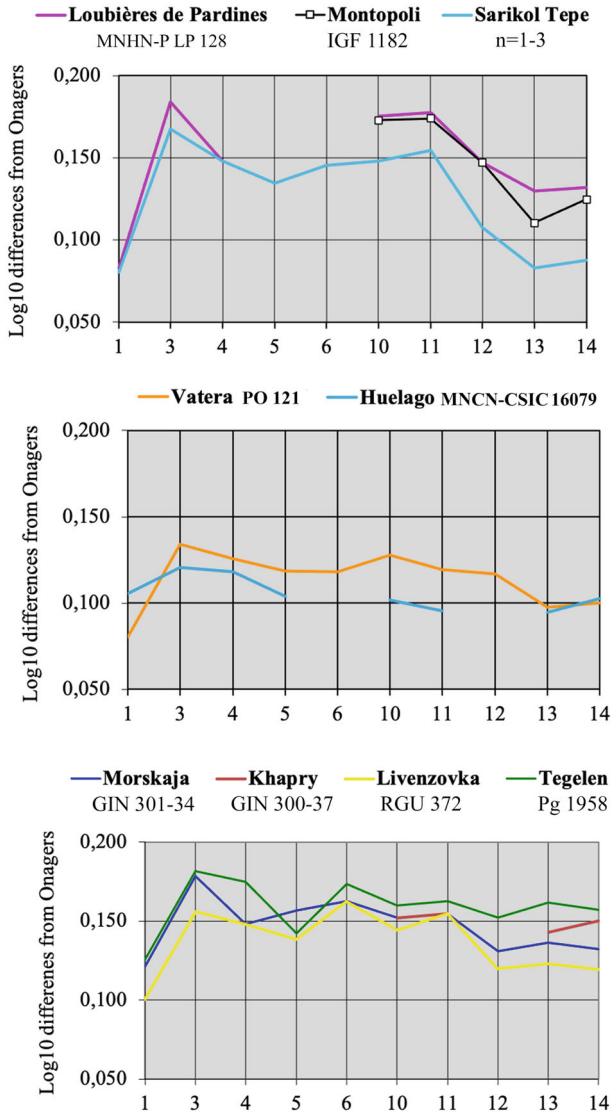

Fig. 11.49 Ratio diagrams of third metacarpals of A ?*Allohippus* sp.1, B ?*Allohippus* sp. 2, C ?*Allohippus* sp. 3. Same variables as in Fig. 11.9

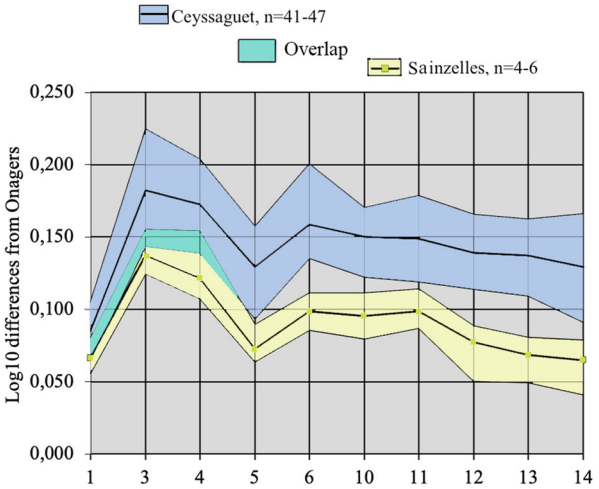

Fig. 11.50 Ratio diagrams of third metacarpals from Ceyssaguet and Sainzelles. n: number of specimens. Same variables as in Fig. 11.9

from sites older or younger than Senèze: two first phalanges are larger than the average for *A. stenonis vireti* (ca. 2.5 Ma); one MC III resembles *A. stehlini* from the Upper Valdarno (ca. 1.7 Ma); and one MT III and one first phalanx resemble the small ?*Allohippus* sp. of Pyrgos (late MNQ 18 or early MNQ 19, ca 1.75 Ma). These five specimens could document rare Senèze taxa or could be either cataloguing errors from another site or derived from different Senèze horizons, as noted for the caballine specimens.

Various other equid fossils from Plio-Pleistocene sites are identified where possible. Figure 11.51 presents an overview of the distribution of eight taxa or morphs of mainly Villafranchian equids from Old World localities.

chrons	Ma	MNQ units	*EQUUS* (*Suessemionus*)	*?ALLOHIPPUS* LARGE and ROBUST	*?ALLOHIPPUS* LARGE and SLENDER	*?ALLOHIPPUS* SMALL,SLENDER	*ALLOHIPPUS major*	*ALLOHIPPUS* LONG MUZZLES	*ALLOHIPPUS* SHORT MUZZLES	*PLESIPPUS*
								A. stenonis stenonis *A. stenonis vireti* *A. koobiforensis* *A. sanmeniensis*	*A. senezensis senezensis* *A. senezensis guthi* *A. senezensis mygdoniensis* *A. stehlini*	
BRUNHES	0.6		Overstrand Süssenborn Akhalkalaki							
Matuyama										
Jaramillo	1		NE Siberia Liventsovka (L-131?)				Würtzburg			
MATUYAMA	1.2	MNQ 19				Libakos		Ceyssaguet		
	?					Pyrgos?	Gannat?		Upper Valdarno	
Olduvai					Tegelen		Kislang? Tataourova?	Nihowan Upper Valdarno	Gerakarou	
	2	MNQ 18					Chagny?			
	2.1									
Feni							Senèze		Senèze	
MATUYAMA	2.2							Fuentenueva	Dafnero	
								Kuruksai	Kuruksai, Sesklo	
		MNQ 17b			Vatera F (PO 121)		Vatera (PO 5	Tetoiu	Chilhac, La Puebla de Valverde	Bajiazui
				Sarikol Tepe	Huelago (16079)		Electric site)	St Vallier LD3 (classic)		
					St Vallier LD2					
	2.5	MNQ 17a		Montopoli	El Rincon		Liventzovka (L778)	Liventzovka (L4-11)		Loc 32
				Loubières de Pardines	Liventzovka (RGU 372)		L. de Pardines			
	2.6				Morskaja, Khapry (300-37)		Oasele			

Fig. 11.51 Selected *Plesippus*, *Allohippus*, and *Equus* taxa and samples from the Early and Middle Pleistocene and their approximate temporal distribution. "?" indicates uncertainty about age. Individual specimens include: Liventsovka, ROMK L-131 P3 or P4; Sarikol Tepe, mean of three MC; Montopoli, distal fragment of MC IGF 1182; Loubières de Pardines, distal fragment of MC MNHN.F LP 128; Vatera, MC NHCV PO 121; Huelago, MC MNCS-CSI 16079; Liventsovka MC RGU 372; Morskaja, MC GIN 302–34; Khapry, MC fragment GIN 300–37; Tegelen, MC Pg 1958; Oasele, MC ISER 5400; Liventsovka, MT ROMK L-178; Vatera, MT NHCV PO 5; Senèze, upper premolar and various limb bones of *Allohippus major*; Chagny, upper cheek teeeth, MT and Ph1 post no n°s; Kislang, MT no n°; Gannat, MC and MT no n°s; Würtsburg-Schalksberg, MC 76–500, MT no n°; Liventsovka, cranium ROMK L 4/RGU 11; Tetoiu, MC n = 6–9; Kuruksai, cranium PIN 3120-no n° (long-muzzle); Sesklo, cranial fragment LGPUT SES (Σ) 2003; Dafnero, MC and MT; Kuruksai, crania PIN 3120–319, 320, 360 (short-muzzled)

Acknowledgments First of all I (V.E.) wish to mention Claude Guérin, who was one of my oldest colleagues and friends. Without him, Martine Faure and Eric Delson, the whole project on Senèze would not have come to fruition. I thank them most sincerely for that. Of course I am indebted to all the curators of Lyon and Basel collections without whose help I could not have studied the fossils of Senèze. We thank Athanassios Athanassiou, George Koufos and an anonymous reviewer for comments which improved an earlier version.

Appendix

Table 11.A1 Cranial measurements of equids (in mm)

Origin or Breed	Locality	Species	Specimen number	Prosthion-Hormion	P2 to Hormion	Vomer length	Vomer-Basion	Muzzle length	N-i notch length	Cheek length
			Variable number	2	2–5	3	4	5	31	32
USA	Hagerman	*P. shoshonensis*	USNM 16991	280	139	145	112			
USA	Hagerman	*P. shoshonensis*	USNM 13841	275	149	130	105			
USA	Hagerman	*P. shoshonensis*	USNM 16982	288	146	149	107			
USA	Hagerman	*P. shoshonensis*	USNM 13835	300	153	158	100			
USA	Hagerman	*P. shoshonensis*	USNM 12538	280	135	142	115			
USA	Hagerman	*P. shoshonensis*	USNM 12528	295	147	145	112			
USA	Hagerman	*P. shoshonensis*	USNM 12576	275	137	141	112			
USA	Hagerman	*P. shoshonensis*	USNM 11989	275	135	156	100			
USA	Hagerman	*P. shoshonensis*	USNM 11988	290	145	160	100			
USA	Hagerman	*P. shoshonensis*	USNM 14560	290	145	145	92			
USA	Hagerman	*P. shoshonensis*	USNM 12155	300	146	145	103			
USA	Hagerman	*P. shoshonensis*	USNM 12501	290	142	142	117			
USA	Hagerman	*P. shoshonensis*	USNM 12535	280	152	140	95			
USA	Hagerman	*P. shoshonensis*	USNM 32555	287	140	148	109			
USA	Hagerman	*P. shoshonensis*	USNM 32553	290	145	147	111			
USA	Hagerman	*P. shoshonensis*	USNM 12543	288	143	155	107			
USA	Crawfish	*P. simplicidens*	AMNH-P 20077	290			104			
China	Bajiazui	*P. qingyangensis*	IVPP B 61249	275	132.3	136.8	97.6			
China	Longdan	*P.-A.. eisenmannae*	HPM 0978		185	180				
China	Longdan	*P.-A.. eisenmannae*	IVPP 13552	[376	199]	[135]	119			
China	Longdan	*P.-A.. eisenmannae*	HPM C 0055	345	175.5	156	118			
China	Longdan	*P.-A.. eisenmannae*	HPM C 0052	340	169	147	119			
China	Longdan	*P.-A.. eisenmannae*	HPM D 0014	340	173	151	102			
China	Longdan	*P.-A.. eisenmannae*	HPM EXPO 1	335	160	146	118			
China	Loc 32	*A. yunnanensis*	PMU M 1324–25 ?	292	146.7	126.6	104.5			
China	Madahai	*A.? yunnanensis*	IVPP 4250	272	140	124.5	106			
China	Nihowan	*A. sanmeniensis*	MNHN-F NIH 002	305	160	152	126	155		
China	Fan Tsun	*A.* sp.	FAM 60-B 719					151		
China	Loc. D	*A.* sp.	PMU M 1418					145		
Tajikistan	Kuruksai	*A. bactrianus*	n = 3					127.7		
Tajikistan	Kuruksai	*A. bactrianus*	GIN Kur 3120/320	295	155	118	106	134		
Tajikistan	Kuruksai	*A.* sp.	GIN no nb					170		
Russia	Liventsovka	*A. livenzovensis*	ZIN 31078		165	139		146		
Italy	Olivola	*A. stenonis stenonis*	IGF 11023		149	152		156		
Italy	Valdarno	*A. stehlini*	n = 4					114.4		
Italy	Valdarno	*A. stehlini*	IGF 563		118	114.5		113		
Italy	Valdarno	*A. stehlini*	IGF 581		135.5	127		113		
Italy	Valdarno	*A. stehlini*	IGF 582		126	114		114		
France	Saint-Vallier	*A. stenonis vireti*	MHNL QSV 222	300	147	137	128	153		
France	Saint-Vallier	*A. stenonis vireti*	n = 3					146.8		
Spain	La Puebla de Valverde	*A. senezensis guthi*	MNHN-P PUE 3280	298	155	122	125	137		
France	Ceyssaguet	*A.* sp.	9142					175.2		
France	Senèze	*A. senezensis senezensis*	n = 7					134.4		
France	Senèze	*A. senezensis senezensis*	FSL 210993 ex 96132	307			119	145		
France	Senèze	*A. senezensis senezensis*	Sen 5233	300			122	141		
France	Senèze	*A. senezensis senezensis*	FSL 210857	280			112	125		
France	Senèze	*A. senezensis senezensis*	NMB Se 336	297	164	135	110	140		

(continued)

Table 11.A1 (continued)

Origin or Breed	Locality	Species	Specimen number	Prosthion-Hormion	P2 to Hormion	Vomer length	Vomer-Basion	Muzzle length	N-i notch length	Cheek length
Greece	Gerakarou	*A. senezensis mygddoniensis*	n = 3	276.4			104.5	130.7		
Greece	Gerakarou	*A. senezensis mygddoniensis*	LGPUT-GER 8		141	116		130		
Greece	Gerakarou	*A. senezensis mygddoniensis*	LGPUT-GER 9					135		
Greece	Gerakarou	*A. senezensis mygddoniensis*	LGPUT-GER 31		148	134				
Greece	Gerakarou	*A. senezensis mygddoniensis*	LGPUT-GER 122		149	132		127		
Kenya	Koobi Fora	*A. koobiforensis*	KNM-ER 1484					150		
Russia	Mongolia	*E. nalaikhaensis*	GIN 3747/500	275			128			
Russia	NE Siberia	*E. cf. scotti*	SI 160–455 (BET 55)	325			145			
Algeria	Tighennif	*E. mauritanicus*	MNHN-F TER 1542	270			121			
Algeria	Tighennif	*E. mauritanicus*	MNHN-F TER 1543	260			122			
S. Africa	Elandsfontein	*E. capensis*	SAM E 21025	298			142			
Russia	Bug	*E. khomenkoi*	ZIN 1283–1	247			126			
Russia	N Yakutia	Fossil horse	ZIN 32300	258			118			
Russia	Liakhov	Fossil horse	ZIN 3965	264			131			
Russia	Lena	Fossil horse	IA 33	277			122.5			
Russia	N Yakutia	Fossil horse	IA 5059	265			126			
Russia	N Yakutia	*E. coliemensis*	IA 1741	282			123			
Russia	Kotelny	Fossil horse	PIN 301–539	250			119.5			
Russia	Kolyma	Fossil horse	MS 3752–25	268			126			
Russia	North Siberia	Fossil horse	Sher PIN no n°	268			127			
Russia	Toungouze	*E. chosricus* type	PIN 113–165	271			130			
Russia	Senguilei	Fossil horse	PIN 113–166	269			144			
Russia	Missy	*E. missi*	PIN 113–167	243			127			
Russia	Missy	*E. missi*	PIN 113–168	250			123			
Russia	Missy	*E. missi*	PIN 113–169	251			124			
Russia	Missy	*E. missi*	PIN 113–170	262			130			
Russia	Taburishche	Fossil horse	PIN 113–171	270			125			
Russia	Ukraine	Fossil horse	PIN 113–172	275			127			
Russia	North Siberia	*E. alaskae*	PIN 113–173	260			112.5			
Russia	North Siberia	*E. alaskae*	PIN 113–174	255			118			
Russia	Kotelny	Fossil horse	PIN 113–175	267			121			
France	Siréjol	*E. gallicus*	PIN 113–176	260			127			
France	Siréjol	*E. gallicus*	PIN 113–177	270			127			
Italy	ValdiChiana	Fossil horse	PIN 113–178	280			131			
Italy	ValdiChiana	Fossil horse	PIN 113–179	255			131			
Yukon		*E. lambei*	UNSM 8426	245			117			
Alaska		*E. alaskae*	UNSM 7700	265			122			
USA	Hay Springs	*E. niobrarensis*	UNSM 4999	285			122			
USA	Dawson	Fossil horse	NMC 9924–12	270			119			
USA	Gold Run	Fossil horse	NMC 13485	244			118			
USA	Gold Run	Fossil horse	NMC 17254	260			121			
USA	Gold Run	Fossil horse	NMC 34803 A	260			120			
USA	Dawson	Fossil horse	NMC 17905	265			129			
USA	Fairbanks	Fossil horse	AMNH-P 60026	265			117			
USA	Fairbanks	Fossil horse	AMNH-P 30702	270			116			
USA	Gilliland	*E.* cf. *scotti*	AA 46899	300			138			
USA	Rock Creek	*E. scotti*	NMC 2381	330			139			
USA	Rock Creek	*E. scotti*	AMNH-P 10612	297			138			
USA	Hay Springs	*E.* cf. *occidentaliss*	UNSM 5978	277			127			
USA	Hay Springs	Large caballine	UNSM 1346	308			153			
USA	Hay Springs	*E. calobatus*	AMNH-P "13"	260			117			
USA	Cedar Meadow	*E. fraternus*	AMNH-P FM 116143 + 3770	295			151			
USA	Channing	*E. semiplicatus*	AMNH-P FM 18–399	230			110			
USA	Lissie Fm	*E. (Amerhippus) francisci*	TAMU 2518	215			111			
USA	Rancho La Brea	*E. (Amerhippus) occidentalis*	AMNH-P 14396	264			122			
USA	Rancho La Brea	*E. (Amerhippus) occidentalis*	LACM 3500–14	270			129			
USA	Rancho La Brea	*E. (Amerhippus) occidentalis*	LACM 3500–26	283			124			
USA	Rancho La Brea	*E. (Amerhippus) occidentalis*	LACM 3500–5	286			125			

(continued)

Table 11.A1 (continued)

Origin or Breed	Locality	Species	Specimen number	Prosthion-Hormion	P2 to Hormion	Vomer length	Vomer-Basion	Muzzle length	N-i notch length	Cheek length
USA	Rancho La Brea	*E. (Amerhippus) occidentalis*	LACM 3500–21	273			120			
USA	Rancho La Brea	*E. (Amerhippus) occidentalis*	LACM 3500–1	260			125			
USA	Rancho La Brea	*E. (Amerhippus) occidentalis*	UCMP no n°	270			125.5			
USA	Rancho La Brea	*E. (Amerhippus) occidentalis*	UCMP 2051–12269	280			134			
USA	Rancho La Brea	*E. (Amerhippus) occidentalis*	UCMP 2051–21001	280			128			
Ecuador		*E. (Amerhippus) andium*	AMNH-P "14'	230			106.5			
Turkey		*E. asinus*	KI 3244	175			82			
Turkey		*E. asinus*	KI 3245	183			94			
?		*E. asinus*	KI 33	195			90			
?		*E. asinus*	KI 26192	180			82.7			
?		*E. asinus*	KI 4221	167			76			
Socotra		*E. asinus*	HL Eaw2	188			88			
Socotra		*E. asinus*	HL Eaw1	185			86			
Socotra		*E. asinus*	HL Eaw4	203			89			
?		*E. asinus*	HL Ea2	205			98			
?		*E. asinus*	HL Ea11	211			100			
?		*E. asinus*	HL E13	166			68			
?		*E. asinus*	HA no n°	207			95			
Abyssinia		*E. asinus*	HL Ea abs						135	140
		E. asinus	MCZ 14539						121	132
		E. asinus	MCZ 8272						118	135
		E. asinus	MS 3008						106	117
		E. asinus	MS 74781						130	138
		E. asinus	MS 74776						120	140
		E. asinus	MS 1747						115	122
		E. asinus	MS 102074						127	128
Kitengela		*E. burchelli granti*	KNM 2360	235			114			
Kitengela		*E. burchelli granti*	KNM 2383	213			116			
Kitengela		*E. burchelli granti*	KNM 2397	225			109			
Kitengela		*E. burchelli granti*	KNM 2399	235			97			
Kitengela		*E. burchelli granti*	KNM 2401	238			114			
Kitengela		*E. burchelli granti*	KNM 2402	228			104			
Kitengela		*E. burchelli granti*	KNM 2403	225			102			
Kitengela		*E. burchelli granti*	KNM 2407	237			107			
Kitengela		*E. burchelli granti*	KNM 2408	233			109			
Kitengela		*E. burchelli granti*	KNM 2409	230			106			
Kitengela		*E. burchelli granti*	KNM 2412	220			107			
Kitengela		*E. burchelli granti*	KNM 2413	235			105			
Kitengela		*E. burchelli granti*	KNM 2415	225			106			
Kitengela		*E. burchelli granti*	KNM 2418	225			114			
Kitengela		*E. burchelli granti*	KNM 2419	222			115			
Kitengela		*E. burchelli granti*	KNM 2421	240			101.5			
Kitengela		*E. burchelli granti*	KNM 2422	230			100			
Kitengela		*E. burchelli granti*	KNM 2423	220			115			
Kitengela		*E. burchelli granti*	KNM 2426	230			94.5			
Kitengela		*E. burchelli granti*	KNM 2428	225			95.5			
Kitengela		*E. burchelli granti*	KNM 2431	230			109			
Kitengela		*E. burchelli granti*	KNM 2432	227			107			
Kitengela		*E. burchelli granti*	KNM 2435	227			112			
Kitengela		*E. burchelli granti*	KNM 2436	228			100			
Kitengela		*E. burchelli granti*	KNM 2438	225			114			
Kitengela		*E. burchelli granti*	KNM 2439	245			116			
Kitengela		E. burchelli granti	KNM 2440	230			115			
Kitengela		*E. burchelli granti*	KNM 2441	222			108			
Kitengela		*E. burchelli granti*	KNM 2448	232			108			
Kitengela		*E. burchelli granti*	KNM 2449	220			109			
Kitengela		*E. burchelli granti*	KNM 2450	210			109			
Kitengela		*E. burchelli granti*	KNM 2451	227			110			
S. Africa		*E. burchelli burchelli*	NMBl 420						147	169
S. Africa		*E. burchelli burchelli*	NMBl 421						153	176
S. Africa		*E. burchelli burchelli*	NMBl 422						151	160
S. Africa		*E. burchelli burchelli*	NMBl 423						144	160

(continued)

Table 11.A1 (continued)

Origin or Breed	Locality	Species	Specimen number	Prosthion-Hormion	P2 to Hormion	Vomer length	Vomer-Basion	Muzzle length	N-i notch length	Cheek length
S. Africa		*E. burchelli burchelli*	NMBl 424						146	177
S. Africa		*E. burchelli burchelli*	NMBl 425						150	162
S. Africa		*E. burchelli burchelli*	NMBl 426						143	161
S. Africa		*E. burchelli burchelli*	NMBl 427						151	154
S. Africa		*E. burchelli burchelli*	NMBl 428						147	155
S. Africa		*E. burchelli burchelli*	NMBl 429						147	183
S. Africa		*E. burchelli burchelli*	NMBl 430						138	165
S. Africa		*E. burchelli burchelli*	NMBl 431						150	168
S. Africa		*E. burchelli burchelli*	NMBl 432						144	172
S. Africa		*E. burchelli burchelli*	NMBl 433						145	174
S. Africa		*E. burchelli burchelli*	NMBl 434						149	178
S. Africa		*E. burchelli burchelli*	NMBl 435						135	157
S. Africa		*E. burchelli burchelli*	NMBl 436						148	175
S. Africa		*E. burchelli burchelli*	NMBl 437						140	176
S. Africa		*E. burchelli burchelli*	NMBl 438						145	169
S. Africa		*E. burchelli burchelli*	NMBl 439						154	165
S. Africa		*E. burchelli burchelli*	NMBl 440						149	163
S. Africa		*E. burchelli burchelli*	NMBl 441						141	164
S. Africa		*E. burchelli burchelli*	NMBl 442						136	165
S. Africa		*E. burchelli burchelli*	NMBl 443						140	165
S. Africa		*E. burchelli burchelli*	NMBl 444						159	171
S. Africa		*E. burchelli burchelli*	NMBl 445						148	162
S. Africa		*E. burchelli burchelli*	NMBl 446						149	159
S. Africa		*E. burchelli burchelli*	NMBl 447						138	170
S. Africa		*E. burchelli burchelli*	NMBl 448						148	172
Turkmenistan		*E. hemionus kulan*	ZIN 19046	230			109			
Badkhyz		*E. hemionus kulan*	MS 49096	228			104			
Badkhyz		*E. hemionus kulan*	MS 49098	211			104			
Badkhyz		*E. hemionus kulan*	MS 74785	235			108			
Badkhyz		*E. hemionus kulan*	MS 74787	215			103			
Badkhyz		*E. hemionus kulan*	MS 74788	223			116			
Badkhyz		*E. hemionus kulan*	MS 74790	228			102			
Badkhyz		*E. hemionus kulan*	MS 74791	222			96			
Badkhyz		*E. hemionus kulan*	MS 74802	217			106			
Badkhyz		*E. hemionus kulan*	MS 74792	230			100			
Badkhyz		*E. hemionus kulan*	MS 74793	222			106			
Badkhyz		*E. hemionus kulan*	MS 74794	232			104			
Badkhyz		*E. hemionus kulan*	MS 74799	210			99			
Badkhyz		*E. hemionus kulan*	ZIN 32047	220			102			
Badkhyz		*E. hemionus kulan*	ZIN 32113	212			110			
Badkhyz		*E. hemionus kulan*	ZIN 2277	232			104			
Badkhyz		*E. hemionus kulan*	ZIN 32279	212			96			
Badkhyz		*E. hemionus kulan*	ZIN “49”	217			105			
Badkhyz		*E. hemionus kulan*	ZIN “47”	207			99			
Badkhyz		*E. hemionus kulan*	ZIN “50”	220			100			
?		*E. hemionus kulan*	HA 7682	225			96.5			
Zoo		*E. zebra*	ZIN 111	224			110		147	144
S Africa		*E. zebra*	NHMUK-ZD 1846.3.23.10	240			110			
S Africa		*E. zebra*	NHMUK-ZD 1847.1.27.2	240			105			
Zoo		*E. zebra*	MB-Z 8558	250			115			
Zoo		*E. zebra*	MB-Z 13415	245			104			
Kapland		*E. zebra*	MB-Z 47489	243			111			
Kapland		*E. zebra*	MU 542	220			110.5			
S Afrika		*E. zebra*	HA 1396	238			101			
Cape Prov		*E. zebra*	AMNH-M 83602	232			117.5		155	171
S Africa		*E. zebra*	AMNH-M 81775	227			109		148	160
?		*E. zebra*	AMNH-M 99700						156	170
?		*E. zebra*	AMNH-M 42753						155	171
Zoo		*E. zebra*	AMNH-M 90240	230			124		156	161
S Africa		*E. zebra*	NMBl 10918						155	166
S Africa		*E. zebra*	NMBl 7444	246			110		158	166
S Africa		*E. zebra*	NMBl 8702	232			114		158	173
S Africa		*E. zebra*	NMBl no n°	240			130		158	170
S Africa		*E. zebra*	NMBl 6026	230			110		148	164
S Africa		*E. zebra*	SAM 33855						169	171.8

(continued)

Table 11.A1 (continued)

Origin or Breed	Locality	Species	Specimen number	Prosthion-Hormion	P2 to Hormion	Vomer length	Vomer-Basion	Muzzle length	N-i notch length	Cheek length
S Africa		*E. zebra*	SAM 38645						163.5	175.5
S Africa		*E. zebra*	SAM 38646						164	166.4
S Africa		*E. zebra*	TMP no n°						167.5	178
Namibia		*E. zebra*	Windhoek CM 285						150	155
Namibia		*E. zebra*	Windhoek CM 361						170	156
Namibia		*E. zebra*	Windhoek C 459						166	173
Namibia		*E. zebra*	Windhoek XV 101						151	167
Namibia		*E. zebra*	Windhoek XV 102						160	165
Namibia		*E. zebra*	Windhoek XV 99–97						155	174
Namibia		*E. zebra*	Windhoek XIV 1082						168	161
Namibia		*E. zebra*	Windhoek XIV 88						167	169
Namibia		*E. zebra*	Windhoek XIV 80						175	161
Namibia		*E. zebra*	Windhoek XIV 86						164	169
Namibia		*E. zebra*	Windhoek XII 68						162	165
Namibia		*E. zebra*	Windhoek XII 60						165	162
Namibia		*E. zebra*	Windhoek XIV 81						161	175
Namibia		*E. zebra*	Windhoek XIV 92						172	180
Namibia		*E. zebra*	Windhoek XIV 83						159	172.5
Namibia		*E. zebra*	Windhoek XIV 78						158	167
Namibia		*E. zebra*	Windhoek XIV 87						175	165
Namibia		*E. zebra*	Windhoek XIV 82						162	169
Namibia		*E. zebra*	Windhoek XIII 74						153	175
Namibia		*E. zebra*	Windhoek XVI 108						160	170
Zoo		*E. przewalskii*	MNHN.Z-AC 1941.322	261			121			
Chaffanjon 1896–3		*E. przewalskii*	MNHN.Z-MO 1964–106	261			113			
Chaffanjon 1896–4		*E. przewalskii*	MNHN.Z-MO 1964–107	256			117			
"Kiang, Tibet"		*E. przewalskii*	MNHN.Z-AC 1986.269	257			120.3			
Zoo		*E. przewalskii*	MNHN.Z-AC 1973.109	250			115			
Gobi, Bedford		*E. przewalskii*	NHMUK-ZD 1907.5.15.1	255			118			
Zoo, Bedford		*E. przewalskii*	NHMUK-ZD 1945.6.11.1	275			119			
Mongolia	Bijsk	*E. przewalskii*	RNH-L 359	248			109			
Hagenbeck 1926		*E. przewalskii*	RNH-L 1534	267			113			
Zoo 1969		*E. przewalskii*	AM 11–913	253			119			
Gooilust 1938		*E. przewalskii*	AM 981	272			115			
?		*E. przewalskii*	MB-Z 60363	248			117			
Münich 1949		*E. przewalskii*	SMF 35389	260			122			
Bessie		*E. przewalskii*	ZSM 1951.173	255			109			
Neville		*E. przewalskii*	ZSM 1953.147	268			130			
Zoo melioïdose		*E. przewalskii*	MNHN.Z-MO 1977.55	270			122			
Bedford, Chubb 209		*E. przewalskii*	AMNH-M 32686	267			118			
Chubb 136		*E. przewalskii*	AMNH-M 16234	264			124			
?		*E. przewalskii*	AMNH-M 21523	255			113			
Zoo		*E. przewalskii*	AMNH-M 80062	251			117			
Sidor		*E. przewalskii*	NMB 10881	262			114			
?		*E. przewalskii*	MCZ 51058	261			112			
Roborovski and Kozlov		*E. przewalskii*	ZIN 5213	262			119			
Roborovski and Kozlov		*E. przewalskii*	ZIN 5214	263			116			
Roborovski and Kozlov		*E. przewalskii*	ZIN 5216	267			113			
Roborovski and Kozlov		*E. przewalskii*	ZIN 5218	265			119			
Zoo 1933		*E. przewalskii*	ZIN 17591	287			122			
Askania Nova		*E. przewalskii*	ZIN 27031	274			117			
Askania 1903–1909		*E. przewalskii*	ZIN 27089	255			119			
Zoo Tallin 1983		*E. przewalskii*	ZIN 31877	270			122			
Zoo 1987		*E. przewalskii*	ZIN 32578	255			116			
Zoo 1983		*E. przewalskii*	ZIN 32050	255			111			
Zoo London 1973		*E. przewalskii*	MS 95921	247			113			
Zoo London 1974		*E. przewalskii*	MS 133806	266			120			

(continued)

Table 11.A1 (continued)

Origin or Breed	Locality	Species	Specimen number	Prosthion-Hormion	P2 to Hormion	Vomer length	Vomer-Basion	Muzzle length	N-i notch length	Cheek length
Zoo London 1975		*E. przewalskii*	MS 1772	245			114			
Zoo London 1976		*E. przewalskii*	MS 110476	250			113			
?		*E. przewalskii*	HL wld 1	263			121			
Mongolia	Bijsk	*E. przewalskii*	HL wld 2	250			124			
?		*E. przewalskii*	HL wld 4	258			122			
Zoo Köln		*E. przewalskii*	BO 92324	254			117			
Vassienievitch 1892, Mongolia		*E. przewalskii*	ZIN 5230	255			112			
Prague 1976		*E. przewalskii*	NMP 47161	258			113			
Artemis		*E. przewalskii*	NMP 46585	262			118			
Uran		*E. przewalskii*	NMP 24688	255			122			
Hera		*E. przewalskii*	NMP 47160	257			112			
?		*E. przewalskii*	NMP 22772	250			120			
?		*E. przewalskii*	NMP 47165	260			118			
?		*E. przewalskii*	NMP 47167	260			115			
Nepal		*E. caballus*	NMUK-ZD 1858.6.24.119	243			113			
Nepal		*E. caballus*	NMUK-ZD 1858.6.24.150	232			118			
Norway		*E. caballus*	MNHN.Z-ACA 541	270			128			
France	Quercy	*E. caballus*	MNHN.Z-AC 1973.14	290			139			
Percheron		*E. caballus*	MNHN. Z-MO1977.84	315			152			
France		*E. caballus*	EV no n°	305			138			
France		*E. caballus*	MNHN.Z-AC 1880.744?	280			128			
France		*E. caballus*	MNHN.Z-AC 1926.301	280			133			
Tonkin		*E. caballus*	MNHN.Z-AC 1911.145	245			118			
Tonkin		*E. caballus*	MNHN.Z-AC 1900.108	243			114			
France		*E. caballus*	MNHN.Z-AC 1937–51	190			98			
Norway		*E. caballus*	MNHN.Z-AC 1925.78	265			124			
Flamand		*E. caballus*	MNHN.Z-AC 1930.28	307			153			
Boulonnais		*E. caballus*	MNHN.Z-AC 1930.32	310			139			
Russia	Irkoutsk	*E. caballus*	MNHN.Z-AC 1902.822	270			126			
France		*E. caballus*	MNHN.Z-AC 1930.31	275			142			
France		*E. caballus*	MNHN.Z-AC 1940.399	288			144			
France		*E. caballus*	MNHN.Z-AC 1930.30	255			131			
Scotland		*E. caballus*	MNHN.Z-AC 2319	230			124			
France		*E. caballus*	MNHN.Z-AC 1926.125	275			138			
France		*E. caballus*	MNHN.Z-AC 1950–8	180			87			
France		*E. caballus*	MNHN.Z-AC 1880.232.1	290			139			
France		*E. caballus*	MNHN.Z-AC 1930.27	275			136			
France		*E. caballus*	MNHN.Z-AC 1964–197	225			107			
Flamand		*E. caballus*	MNHN.Z-AC 1930.29	295			143			
France		*E. caballus*	MNHN.Z-AC 69	296			138			
Tarpan		*E. caballus*	ZIN 521	252			121			
France		*E. caballus*	MNHN.Z-MO 1977.72	270			132			
France		*E. caballus*	MNHN.Z-MO 1977.88	265			122			
Iceland		*E. caballus*	MNHN.Z-AC 1873–385	212			106			
Shetland		*E. caballus*	AMNH-M 204044	215			100			
'Jumper'		*E. caballus*	AMNH-M 204127	285			135			

(continued)

Table 11.A1 (continued)

Origin or Breed	Locality	Species	Specimen number	Prosthion-Hormion	P2 to Hormion	Vomer length	Vomer-Basion	Muzzle length	N-i notch length	Cheek length
Draft		*E. caballus*	AMNH-M 16274	361			166			
Arab?		*E. caballus*	YPM 1636	268			131			
Draft		*E. caballus*	AMNH-M 99	300			142			
Boulonnais		*E. caballus*	MNHN.Z-AC 1891.107	321			153			
Chubb 70		*E. caballus*	AMNH-M Chubb 70	258			125			
Shetland		*E. caballus*	FMNH 46019	185			89			
France		*E. caballus*	MNHN.Z-AC 1937–59	177			87			
Iceland		*E. caballus*	MNHN.Z-AC 1975.98	258			119			
Shetland		*E. caballus*	MNHN.Z-AC 1945–27	205			99			
Iceland		*E. caballus*	MNHN.Z-AC 1880.233	245			115			
Iceland		*E. caballus*	MNHN.Z-AC 1891–44	218			91			
France		*E. caballus*	EV no n°	232			103			
Arab		*E. caballus*	AMNH-M 204200	260			128			
Arab		*E. caballus*	AMNH-M 204191	260			137			
Arab		*E. caballus*	AMNH-M 204184	270			125			
Arab		*E. caballus*	AMNH-M 204176	270			146			
Arab		*E. caballus*	AMNH-M 204210	260			136			
Norway		*E. caballus*	AMNH-M 204174	270			130			
Norway		*E. caballus*	AMNH-M 204135	257			117			
Norway		*E. caballus*	AMNH-M204147	255			131			
Mongolia	Gobi	*E. caballus*	AMNH-M 204192	254			111			
Russia	Iakutsk	*E. caballus*	IA 1955	258			123			
Russia	Iakutsk	*E. caballus*	IA 1957	260			119			
Russia	Iakutsk	*E. caballus*	IA 1959	260			113			
Russia	Iana	*E. caballus*	IA 1944	261			117			
France		*E. caballus*	AA sans n°	319			146			
France		*E. caballus*	AMNH-M 1218	274			146			
Draft		*E. caballus*	AMNH-M 8178 A	315			147			
?		*E. caballus*	MCZ 16890	195			91			
Konik		*E. caballus*	PIN 657	230			105			
Israel		*E. caballus*	HUJ-ESE no n°	258			140			
France		*E. caballus*	MNHN.Z-AC 1971.325	248			115			
France		*E. caballus*	MNHN.Z-AC 1880.232.6	288			140			
France		*E. caballus*	MNHN.Z-AC 1880.232.7	277			143			
France		*E. caballus*	MNHN.Z-AC 1880.747	292			131			
France		*E. caballus*	MNHN.Z-AC 1880–232-5	315			144			
France	Gournay	*E. caballus*	CRA Gournay	290			140			
Welsh		*E. caballus*	MCZ 52978	212			97			
Tarpan		*E. caballus*	MS 94535	257			127			
Pushcha 1		*E. caballus*	MS 96873	255			124			
Pushcha 2		*E. caballus*	MS 96872	270			128			
Mongolia		*E. caballus*	MS 110478	240			119			
?		*E. caballus*	MS 106944	195			86			
?		*E. caballus*	MS 106942	230			105			
Shetland		*E. caballus*	KI 16449	197			88			
Shetland		*E. caballus*	KI 20253	208			91			
Shetland		*E. caballus*	KI 20214	199			86			
Shetland		*E. caballus*	KI 1661	204			102			
Iceland		*E. caballus*	Ki 16719	240			108			
Iceland		*E. caballus*	KI 18146	227			116			
Iceland		*E. caballus*	KI 2217	198			115			
Hannover		*E. caballus*	KI 1760	305			143			
Konik		*E. caballus*	HL CA 2	255			135			
?		*E. caballus*	HL Pol 1	199			86			
Iceland		*E. caballus*	HL 4	230			115			
Welsh		*E. caballus*	HL Epon2	203			108			
Welsh		*E. caballus*	HL mgl 2	234			118			
Iceland		*E. caballus*	HL mgl 1	258			118			

(continued)

Table 11.A1 (continued)

Origin or Breed	Locality	Species	Specimen number	Prosthion-Hormion	P2 to Hormion	Vomer length	Vomer-Basion	Muzzle length	N-i notch length	Cheek length
Iceland		*E. caballus*	HL mgl 3	238			115			
Arab		*E. caballus*	BO 1939	269			133			
Arab		*E. caballus*	BO 79629	272			131			
Arab		*E. caballus*	TMB no n°	253			124			
?		*E. caballus*	ZIN 518	238			113			
Mongolia		*E. caballus*	ZIN 18036	253			117			
Mongolia		*E. caballus*	ZIN 24504	258			125			
Mongolia		*E. caballus*	MS 102019	247			113			
'Przewalski'		*E. caballus*	NMP 14/60	267			123			
'Tarpan'		*E. caballus*	KI 1661	273			130			
Arab		*E. caballus*	Ki 16719	271			130			
Arab		*E. caballus*	KI 18146	260			126			
Kighize		*E. caballus*	KI 2217	265			141			
Russia	Carelia	*E. caballus*	KI 1760	313			149			
?		*E. caballus*	HL CA 2	273			135			
?		*E. caballus*	HL Pol 1	328			143			
?		*E. caballus*	NMP 2485.9884	282			143			
Turkmenistan		*E. caballus*	ZIN 18039	270			129			
Turkmenistan		*E. caballus*	ZIN 18046	273			123			
Turkmenistan		*E. caballus*	ZIN 18047	282			128			
Turkmenistan		*E. caballus*	ZIN 18052	280			129			
Berelekh		*E. caballus*	ZIN 31168	273			130			
Kighize		*E. caballus*	ZIN 18038	272			129			
Mongolie		*E. caballus*	ZIN 18055	255			119			
Turkmenistan		*E. caballus*	ZIN 18040	263			125			
Turkmenistan		*E. caballus*	ZIN 18041	260			129			
Turkmenistan		*E. caballus*	ZIN 18042	261			126.5			
Turkmenistan		*E. caballus*	ZIN 18043	262			118			
Turkmenistan		*E. caballus*	ZIN 18045	265			121			
Turkmenistan		*E. caballus*	ZIN 18048	255			120			
Turkmenistan		*E. caballus*	ZIN 18049	261			129			
Mongolia		*E. caballus*	ZIN 18056	250			113			
Russia	Selenga	*E. caballus*	ZIN 20135a	246			111			
Russia	Arctic	*E. caballus*	ZIN 29697	260			130			
Mongolia		*E. caballus*	ZIN 18057	245			114			
Mongolia		*E. caballus*	ZIN 18058	252			111			
Mongolia		*E. caballus*	ZIN 18059	238			106.5			
Kighiz		*E. caballus*	ZIN 18034	257			114			
Russia	Tobol	*E. caballus*	ZIN 4050	250			124			
Russia	Adycha	*E. caballus*	ZIN 4051	260			115			
Russia	Kolyma	*E. caballus*	ZIN 5233	237			114			
Russia	Kazakstan	*E. caballus*	ZIN 11485	257			127			
Russia	Iakoutsk	*E. caballus*	ZIN 12614	262			119			
Russia	Iakoutsk	*E. caballus*	ZIN 12615	252			112			
Russia	Iakoutsk	*E. caballus*	ZIN 12616	255			128			
Togo		*E. caballus*	NMP 47158	235			110			
Togo		*E. caballus*	NMP 47159	230			115			
?		*E. caballus*	NMP 4.1.1977	256			127			
?		*E. caballus*	NMP 1975	263			121			
Nesvera		*E. caballus*	NMP no n°	230			99			
Zoo		*E. grevyi*	MNHN.Z-AC 1913–58	276			126			
Expo coloniale		*E. grevyi*	MNHN.Z-AC 1931–392	265			134			
Zoo Vincennes		*E. grevyi*	MNHN.Z-AC 1932–123	273			122			
Zoo Vincennes		*E. grevyi*	MNHN.Z-AC 1939–75	278			125			
Zoo		*E. grevyi*	MNHN.Z-MO 1977–66	280			125		183	185
Somali		*E. grevyi*	ZIN 5237	278			125			
Ost Afr		*E. grevyi*	RNH-L 885	265			132			
?		*E. grevyi*	AM 980	288			144			
?		*E. grevyi*	AM 1923	275			137			
?		*E. grevyi*	AM 1963	265			142			
Kenya	Awash	*E. grevyi*	NMB 5463	270			136			
Kenya	Field	*E. grevyi*	Kenya field A	275			129			
Kenya	Field	*E. grevyi*	Kenya field B	278			144			

(continued)

Table 11.A1 (continued)

Origin or Breed	Locality	Species	Specimen number	Prosthion-Hormion	P2 to Hormion	Vomer length	Vomer-Basion	Muzzle length	N-i notch length	Cheek length
Kenya		*E. grevyi*	KNM 3965	255			127			
Kenya		*E. grevyi*	KNM 3967	270			119			
Kenya		*E. grevyi*	KNM 3968	272			123			
Kenya		*E. grevyi*	KNM 2488	268			135.5			
Kenya		*E. grevyi*	KNM 2489	290			131			
Somali		*E. grevyi*	NMUK-ZD 1893.12.1.2	280			127			
Juba		*E. grevyi*	NMUK-ZD 1923.10.20.16	268			134			
Kenya		*E. grevyi*	NMUK-ZD 1962.8.174	270			131			
Zoo		*E. grevyi*	SMLS 17490	272			132.5			
Ethiopia	Lake Stephanie	*E. grevyi*	NME ss n°	280			143			
Zoo		*E. grevyi*	NMB 10876	275			125			
Zoo		*E. grevyi*	NMB 10873	268			123			
Kenya		*E. grevyi*	BE 1923–177	270			129.5			
Ethiopia		*E. grevyi*	ZU 19018	270			127.5			
Zoo		*E. grevyi*	ZU 16656	270			125			
Kenya	Wamba	*E. grevyi*	HA 6879	278			132			
Kenya	Wamba	*E. grevyi*	HA 7196	275			132			
Kenya	Wamba	*E. grevyi*	HA 7197	270			134			
Kenya	Wamba	*E. grevyi*	HA 7198	268			136			
Kenya	Wamba	*E. grevyi*	HA 7201	262			135			
Kenya	Wamba	*E. grevyi*	HA 7202	282			134			
Kenya	Wamba	*E. grevyi*	HA 7203	273			125			
Kenya	Wamba	*E. grevyi*	HA 7204	272			126			
Kenya	Wamba	*E. grevyi*	HA 7205	265			127			
Kenya	Wamba	*E. grevyi*	HA 7206	268			138			
Kenya	Wamba	*E. grevyi*	HA 7207	263			134			
Kenya	Wamba	*E. grevyi*	HA 7209	275			138			
Kenya	Wamba	*E. grevyi*	HA 7210	272			131			
Kenya	Wamba	*E. grevyi*	HA 7211	262			128			
Kenya	Wamba	*E. grevyi*	HA 7212	280			130			
Kenya	Wamba	*E. grevyi*	HA 7213	280			136			
Kenya		*E. grevyi*	HA 6747	275			125			
Zoo		*E. grevyi*	HA 7111	268			123			
Kenya	Arussi	*E. grevyi*	SMF 657	278			146			
Zoo		*E. grevyi*	ZSM 1953–96	278			137			
Zoo		*E. grevyi*	ZMS 1965–113	275			126			
?		*E. grevyi*	AMNH-M 54247	285			137		188	206
?		*E. grevyi*	AMNH-M 82038	273			133		184	190
?		*E. grevyi*	NMBl 10899						192	183
?		*E. grevyi*	ZIN 32049						184	187
?		*E. grevyi*	HA 10.07.95						183	196
?		*E. grevyi*	NMP 6293						180	181
?		*E. grevyi*	NMP 46430						187	202
?		*E. grevyi*	NMP 46431						188	187
?		*E. grevyi*	SAM 39802						188	192
?		*E. grevyi*	FMNH 26987						184	199

[11.1] *A.* = *Allohippus*; *E.* = *Equus*; *P.* = *Plesippus*; *"P.-A."* = *Plesippus* or *Allohippus*

Table 11.A2 Cranial measurements (in mm) of Senèze equids

	FSL 210993	MHNL Sen 5233	NMB Se 336	FSL SEN 05–0081	FSL 210887	NMB Se 551	NMB Se 553	NMB Se 554	NMB Se 803
Sex	M	M	M	F	F	F	?	M	?
Age	adult	adult	old	adult	ca. 5 years	old	ca. 2 years	old	old
1	540	540	535	505	495				
2	307	300	297	282	280		270		
2–5	155	[159]	164	147	[155]		[150]		144
3		127	135	125	126				
4		122	110	101	112				
5	145	141	140	[135]	125	124	134	131	
6	112	110	97	99	95	94		104	
7	103	96	104	94	99	91	104	91.5	92
7bis	81	80	83	78	78	81		74	81
8	184	178	187	173	177	170	[188]	164	178
9	[60]	short	short		long		[70]		short
10	46		50				[45]		
10bis	38		42.5						
11	160	158	166		130	144	144		[164]
12	392	400	400		350				[393]
13	[220]	220	236		206	202	196		210
14		192	229		192	[200]			193
15	112	[100]	108		104	108			
16	[73]	70.5	69	[51]	65	64			
17	71	69	71	65–70	60	58		60	[62]
17bis	[51]	[53]	44				[40.5]	43	
18	[580]	605	600	580		560			
19	15	[11.5]	18	12	12.5	12	16	11	12
20	16.5			13	14				
21	65	[81]	67	58	62	58			63
22	62	[60]	60	54	55	56			57
23	450	440	438	410	415	400	415		
24	[205]	205	232	215	202	200			
25	[128]	121	[124]			105	[116]	112	
26	136	132	128		120	110	136	122	136
27	140	152	144		120	110			148
28	104	110	110		90				[103]
29	87	88	93	75	86.5	84	75	81	79
30	40	38	39	33	39		38	35.5	34
31	228	188	228	198–204		190	200	195	
32	165	166	165	154.5		140	146		140

M: male; F: female. Approximate measurements between brackets. Measurements as in Eisenmann, 1986 and http://www.vera-eisenmann.com: 1: basilar length; 2: overall palatal length; 2–5: palatal length (without the muzzle); 3: distance from palate to hormion; 4: distance from hormion to basion; 5: muzzle length; 6: diastema length; 7: occlusal length of P2-P4; 7bis: occlusal length of M1-M3; 8: length of P2-M3; 9: choanal length; 10: greatest choanal breadth; 10bis: choanal breadth between the pterygoid processes; 11: breadth between the foremost points of the facial crests; 12: distance between sesion and anterior ends of P2; 13: frontal breadth: 14: bizygomatic breadth; 15: greatest cranial breadth; 16: breadth of the supra-occipital crest; 17: muzzle breadth at the posterior border of the I3; 17bis: least muzzle breadth between the interalveolar borders; 18: vertex length; 19: infra-orbital height; 20: height of the external auditory meatus; 21: antero-posterior diameter of the orbit; 22: dorso-ventral diameter of the orbit; 23: anterior ocular line; 24: posterior ocular line; 25: facial height in front of P2; 26: facial height between P4 and M1; 27: facial height behind M3; 28: cranial height behind the orbits; 29: breadth of the occipital condyles; 30: breadth of the foramen magnum; 31: length of the naso-incisival notch (from prosthion to the back of the narial opening); 32: cheek length (from the back of the narial opening to the most anterior point of the orbit)

Table 11.A3 (a) Measurements (in mm) of third metacarpals of the reference *E. hemionus onager* and various *Allohippus* and a Shetland Pony. (b) Measurements (in mm) of third metacarpals of various equids (c) Measurements (in mm) of third metacarpals of *Allohippus senezensis senezensis* (d) Measurements (in mm) of some *?Allohippus* third metacarpals (e) Measurements (in mm) of *?Allohippus* third metacarpals from Sainzelles

	E. hemionus onager	Valdarno	*A. stenonis vireti*	A. *senezensis senezensis*	A. *senezensis mygdoniensis*	Shetland Pony
(a) Measurements (in mm) of third metacarpals of the reference *E. hemionus onager* and various *Allohippus* and a Shetland Pony.						
	n=29	n=6-11	n=36-50	n=12-18	n=10-12	FMNH 46019
Greatest length	210.2	241	229.6	220.4	233	187
Minimal breadth	26.5	37.2	37.4	33.5	31.9	30
Depth at same level	21.3	28.1	28.0	26.7	26.1	22
Proximal articular breadth	42.5	54.8	54.8	50.8	46.8	41
Proximal articular depth	26.8	36.1	35.2	33	30.4	25
Distal supra-articular breadth	38.8	50.3	51.0	45.7	43.5	41
Distal articular breadth	38.5	37.6	37.2	34.9	32.8	43
Depth of sagittal crest	29.6	29.7	29.4	27.4	26.6	29
Smallest depth of medial condyle	24.1	31.9	31	29.3	28.7	22.5
Greatest depth of medial condyle	25.8	50.3	51	45.7	43.5	25
(b) Measurements (in mm) of third metacarpals of various equids						
	Equus (S.) suesssenbornensis Süssenborn	*E. (S.) cf suesssenbornensis* Akhalkalaki	*E. (S.) verae* NE Siberia	*Allohippus stenonis stenonis*	*A. stenonis guthi*	*A. stehlini*
	n=3-5	n=20-27	n=10	n=15-31	n=31-56	n=9-15
Greatest length	273.2	268.8	265.2	242.4	233.2	208.5
Minimal breadth	41.3	42.7	43.4	37.2	35.2	31.7
Depth at same level	31.3	31.9	31.6	27.7	26.9	23.5
Proximal articular breadth	61.5	63.8	64.1	54.9	52.7	45.2
Proximal articular depth	38.3	39.6	40.2	35.8	33.6	30.5
Distal supra-articular breadth	58.5	60.5	61.6	51.5	48.2	42.3
Distal articular breadth	58.5	60	61.2	50.1	48.1	42.7
Depth of sagittal crest	41.8	42.6	43.2	37.2	35.1	32.2
Smallest depth of medial condyle	34.6	343	34.7	29.4	27.9	26.0
Greatest depth of medial condyle	36.2	367	37.5	31.4	29.7	27.9

(continued)

Table 11.A3 (continued)

	Würzburg Schalksberg	Gannat	Senèze	Oasele	Overstrand	Liventsovka			
	78-500	no nb	FSL 211079	IS 5400	NHMUK -P 19242	RGU 372	RGU 1341	RGU 326	ROMK L 39
Greatest length	285	301		283		265	270	300	259
Minimal breadth	44	47	42	42		38	42.5	42	35
Depth at same level	34	36	31	31.5		30	32.5	33.8	29
Proximal articular breadth	66.4	68		61.5		58.5	62	62	49.5
Proximal articular depth	40.9	43		39.5		39	38	38	32.7
Distal supra-articular breadth	65	64	57.0	60	67	54	57	60	50
Distal articular breadth	63	62	55.5	56	67.5	55		59.5	48.5
Depth of sagittal crest	44.5	45.5		41	49	39		42.5	35
Smallest depth of medial condyle	36	38.0	30		39	32		35	28.5
Greatest depth of medial condyle	40	42	35	35.5	42	34		38.5	30.1

(c) Measurements (in mm) of third metacarpals of *Allohippus senezensis senezensis*

	FSL 210884	FSL 210885	FSL 210886	FSL 210887	FSL 210888	FSL 210889j	FSL 210890	FSL 210891
Greatest length	222	220	211.5	212.5	224	216	221	224.5
Lateral length	215	213	205	204.5		209	213	217
Minimal breadth	33	36	32.5	30.5	33	28.5	35.5	34
Depth at same level	27	28	26	23	27.5		27	27.5
Proximal articular breadth	49	52	50	46.5			51	49.5
Proximal articular depth	31.5	32	33	31.5			34.5	34.5
Facet for Carpale 3	40.5	40	39	39			41	41
Anterior facet for Carpale 4	16.5	16.5	15	13.5			15.5	15
Posterior facet for Carpale 4	10	9	9	9			8	9.5
Facet for Carpale 2	0	0	[6]				0	0
Distal supra-articular breadth	46.5	51	44	42.5		41	47.5	45.5
Distal articular breadth	45.5	46	44.5	42.5	46	40	47	44.5
Depth of sagittal crest	34	36	34	32.5	37		35.5	33.5
Smallest depth of medial condyle	27.5	28	26.5	25	29		29	26.5
Greatest depth of medial condyle	29	30	28	27	31		30	28.5

(continued)

Table 11.A3 (continued)

	FSL 210993	FSL 211053	FSL 211079	FSL SEN 04-0132	FSL SEN 04-0062j	FSL SEN 06-0137	NMB Se 141j	NMB Se 180
Greatest length	[217]	223				225	223	[214]
Lateral length	210	216				220	217	
Minimal breadth	33	35	41.5	33.5	26	34	32.5	33
Depth at same level	25	28.5	31.2	27.4	17	28	25	
Proximal articular breadth	49	51			44.5	52	48	
Proximal articular depth	28	33.5			30	33	31.5	
Facet for Magnum (Carpale 3)	[40]	41			36	42	39	42
Anterior facet for Unciform (Carpale 4)	14.5	16			13.2	17.1	17	
Posterior facet Unciform (Carpale 4)	7	10.5			7	8.1		
Facet for Trapezoid (Carpale 2)		4				0	0	
Distal supra-articular breadth	45	47.5	57	49		48.5	46	
Distal articular breadth	46.5		55.5	46.9		47.5	45	
Depth of sagittal crest	34		40	36.8		35	33	
Smallest depth of medial condyle			31	27.9		28	26.5	
Greatest depth of medial condyle	27.5		35.2	30.9		30	29	
Greatest depth of lateral condyle						26.1		
	NMB Se 551	NMB Se 552j	NMB Se 553	NMB Se 554	NMB Se 829	NMB Se 830	NMB Se 831	
Greatest length	216	216	223	218		234	215	
Minimal breadth	33	31	32	35	33	35.1	33	
Depth at same level	28	25	26	27	25	26.5	26	
Proximal articular breadth	55	46.5	51	53		52.5		
Proximal articular depth		32	33	33		35	33	
Facet for Magnum (Carpale 3)		38	41	40.5		43	39	
Anterior facet for Unciform (Carpale 4)		15.5	16	17		17		
Posterior facet Unciform (Carpale 4)		7.5	7	11		7	9.5	
Facet for Trapezoid (Carpale 2)		3	3.5	0		0		
Distal supra-articular breadth	47	44.5	48.5	48	46	48.5	45	
Distal articular breadth	44	45	45	48	44.5	49	45	
Depth of sagittal crest		33	34	36	35	38	33	
Smallest depth of medial condyle		28	27.5	28	27	29	25.5	
Greatest depth of medial condyle	28	29	29	31.5	28	31	28.3	

(continued)

Table 11.A3 (continued)

(d) Measurements (in mm) of some ?*Allohippus* third metacarpals

	Montopoli IGF 11282	Sarikol Tepe MTA-M n=1-3	Loubières de Pardines MNHN-F LP 128	Vatera NHCV PO 121	Huelago MNCS-CSI 16079	Tegelen Pg 1958
Greatest length		253	254.5	253	268	281
Minimal breadth		39	40.5	36.1	35	40.3
Depth at same level		30	30	28.5	28	31.9
Proximal articular breadth		58		55.9	54	59
Proximal articular depth		37.5		35.2		40
Distal supra-articular breadth	57.7	54.5	58	52	49	56
Distal articular breadth	57.5	55	58	50.7	48	56
Depth of sagittal crest	41.5	37.9	41.5	38.7		42
Smallest depth of medial condyle	31.1	29.2	32.5	38.7		35
Greatest depth of medial condyle	34.4	31.6	35			37.1

	Morskaya MGRI 301-34	Khapry MGRI 300-27	Ceyssaguet *Allohippus* sp. n=41-47	Ceyssaguet *Allohippus* sp. minimum	Ceyssaguet *Allohippus* sp. maximum
Greatest length	278		257.9	246	270
Minimal breadth	40		39.4	36	43.4
Depth at same level	30		31.4	29	33.7
Proximal articular breadth	61		58.1	53.5	62
Proximal articular depth	39		39.1	37	43
Distal supra-articular breadth	55	55	54.7	51.3	57.3
Distal articular breadth	55	55	54.2	50.6	58
Depth of sagittal crest	40		40.5	38.2	43
Smallest depth of medial condyle	33	33.5	[33.1]	[31]	[35]
Greatest depth of medial condyle	35	36.5	34.9	32	38

(e) Measurements (in mm) of ?*Allohippus* third metacarpals from Sainzelles

	Sainzelles *?Allohippus* sp. n=4-6	Sainzelles *?Allohippus* sp. minimum	Sainzelles *?Allohippus* sp. maximum
Greatest length	246.9	241	255
Minimal breadth	35.5	34.5	37
Depth at same level	27.9	27	30.1
Proximal articular breadth	51	50	53
Proximal articular depth	34	33	35
Distal supra-articular breadth	48.2	46.5	50
Distal articular breadth	48.3	47	50
Depth of sagittal crest	35.1	33	36
Smallest depth of medial condyle	28.2	27	29
Greatest depth of medial condyle	30.1	28.5	31.1

j = juvenile

Table 11.A4 Means of measurements (in mm) of limb bones lengths and of maximal plantar breadths of anterior Ph3 of (a) various *Allohippus*. (b) equids from Senèze

	E. hemionus onager	Senèze maximum	Senèze minimum	Saint-Vallier maximum	Saint-Vallier minimum	Gerakarou	Matassino		
(a) various *Allohippus*									
	n=8-10								
Humerus	241.3	290	277	305	299	268			
Femur	329.7	388	352	410	405				
Radius	293.5	344	308	355	328.5	317	344.5		
Tbia	313.0	360	333	385	359		362.5		
MC	214.1	234	211.5	242	215	232.7	241.6		
MT	250.8	268	240	278	251	265.9	277.5		
Ph1 A	76.3	80	71	91	78	78	89.5		
Ph1 P	71.2	80.5	68	86.5	80	74.5	89.5		
Ph3 A breadth	54	67.3	63	83.0	72		70		
	Humerus	Femur	Radius	Tbia	MC	MT	Ph1 A	Ph1 P	Ph3 A breadth
(b) equids from Senèze									
* FSL 211095, 211077, 211074, 211075, 211078			427			335	110	105	ca. 100
** FSL 211055, 211082, 210899							91	85.5	ca. 70
FSL SEN 05-0081+	282	378	315	333		250			
FSL SEN 06-0137+			330	360	225	263	76.9	76	
NMB Se 551	280	380	ca. 316	ca. 340	ca. 216	249	ca. 71	ca. 68	67.3
NMB Se 553	286	388	326	349.0	223	253	76	73	64
NMB Se 554		388		343.0	218	247	80.2	76.5	66
FSL 210993	ca. 277		ca. 325		ca. 217				
NMB Se 141 juv	ca. 258.6	351	319	336.0	223	256	77.5	77	ca. 50
NMB Se 552 juv	260.5	363	316		216	253	78	76	ca. 60
** FSL 210887, 210868, MNHL Sen 1669					212.5	242		69	

* The measurements in this row were taken from separate unassociated bones (Radius FSL 211095, MT FSL 211077, etc.). ** The measurements in these rows were taken from separate but probably associated bones. juv: juvenile

Table 11.A5 Taxonomy and partial distribution (for fossil taxa) of Plio-Pleistocene equine species

GENUS	Subgenus/Species group	SPECIES	SUBSPECIES	Localities	Countries
Plesippus Matthew, 1924		*simplicidens* Cope, 1892	*simplicidens*		
			shoshonensis Gidley, 1930		
Allohippus Kretzoi, 1938	*stenonis*	*stenonis* Cocchi, 1867	*stenonis*	Valdarno, Olivola, Matassino	Italy
			vireti Prat, 1964	Saint-Vallier, Ceyssaguet	France
			athanasiui Samson, 1975	Tetoiu	Romania
		livenzovensis Bajgusheva, 1978		Liventsovka	Russia
		sp. Kuruksai (GIN-KU no number)		Kuruksai	Tajikistan
		sanmeniensis Teilhard de Chardin and Piveteau, 1930		Nihowan	China
		sp. SE Shansi (AMNH 60-B 719)		Fan Tsun, Taigu	China
		koobiforensis Eisenmann, 1983		East Turkana	Kenya
	senezensis	*senezensis* Prat, 1964	*senezensis*	Senèze	France
			guthi Bœuf,1986	Chilhac	France
				La Puebla de Valverde	Spain
			mygdoniensis Koufos, 1992	Gerakarou	Greece
		stehlini Azzaroli,1965		Valdarno	Italy
		bactrianus Zhegallo, 1998*		Kuruksai	Tajikistan
		sp. China, locs A & D, M 1357, M 1418		Honan	China
Equus Linnaeus, 1758	(*Sussemionus*) Eisenmann, 2010	*suessenbornensis* Wüst, 1901	*suessenbornensis*	Süssenborn	Germany
			cf. *suessenbornensis*: Vekua, 1962	Akhalkalaki	Georgia
			verae Sher, 1971	NE Siberia	Russia
		hipparionoides Vekua, 1962		Akhalkalaki	Georgia
		coliemensis Lazarev, 1980		Kolyma	Russia
		granatensis Marin, 1987		Venta Micena	Spain
		wuesti Musil, 2001		Untermassfeld	Germany
		ovodovi Eisenmann and Vasiliev, 2011		Proskuriakova Cave	Russia
	(*Dolichohippus*) Heller, 1912	*grevyi* Oustalet, 1882			
	(*Quagga*) Shortridge, 1934	*quagga* Boddaert, 1785			
		burchelli Gray, 1824	numerous subspecies		
		mauritanicus Pomel, 1897			
		capensis Broom, 1909			
	(*Hippotigris*) Smith, 1841	*zebra* Linnaeus, 1758			
	(*Asinus*) Gray, 1824	*africanus* Heuglin and Fitzinger, 1866	and other species		
	(*Hemionus*) F. Cuvier, 1823	*hemionus* Pallas, 1775	numerous subspecies		
	(*Equus*) Linnaeus, 1758	*caballus* Linnaeus, 1758	and other species		

* in Vangengeim et al. 1998

Table 11.A6 (a) Measurements (in mm) of third metatarsals of various equids. (b) Measurements (in mm) of third metatarsals of various *Allohippus* and *E*quus (*Sussemionus*). (c) Measurements (in mm) of some *Allohippus major* third metatarsals (d) Measurements (in mm) of third metatarsals of Senèze equids

	Equus hemionus onager	Lunel Viel MNP-Bonifay	?*Allohippus* Pyrgos	?*Allohippus* Pyrgos	?*Allohippus* Pyrgos	?*Allohippus* Pyrgos	*A. senezensis senezensis*
(a) Measurements (in mm) of third metatarsals of various equids							
	n = 32	IV-6 10009	Pg II 55	Pg II 41	Pg I 15	Pg I 23	n = 9–15
Greatest length	246.9	280	260	251	255		252.7
Minimal breadth	25.6	40	30	28.8	31	28	33.7
Depth at same level	25.4	36	29	30.3	29.5	[26]	31
Proximal articular breadth	39.9	52	44	44	44.8		49
Proximal depth	34.6	43	38	35.6			42.2
Distal supra-articular breadth	38.4	52.5	41.1	42	41.5	41.7	47.4
Distal articular breadth	37.6	53	42	42.7	42.8	42	46.5
Depth of sagittal crest	30.2	39	33	32.2	33.2	32	35.6
Smallest depth of medial condyle	23.7	29	26	24.8	25.9	25	27
Greatest depth of medial condyle	26.1	32	28	26.6	27.5	27.7	29.6
	A. stenonis stenonis	*A. stenonis vireti*	*A. senezensis guthi*	*A. senezensis mygdoniensis*	*E. (S.) suesssen bornensis*	*E. (S.)* cf *suesssen bornensis*	*E. (S.) verae*
(b) Measurements (in mm) of third metatarsals of various *Allohippus* and *Equus (Suessemionus)*							
	n = 8–11	n = 64–80	n = 42–82	n = 7	n = 1–4	n = 13–22	n = 15–23
Greatest length	270.6	264.4	269.3	265.2	327	317.9	310.8
Minimal breadth	36.2	36.9	35	30.9	40.5	40.7	41.1
Depth at same level	329	33.8	32.1	28.7	38.3	38.5	36.5
Proximal articular breadth	52.2	53.5	51.4	46.1	57.5	59.9	58.8
Proximal depth	43.4	45.4	42.1	35.5	48	49.1	49
Distal supra-articular breadth	51 6	52.7	49.5	43.8	58.5	59.2	60.5
Distal articular breadth	49.9	51.1	47.7	42.9	60.5	59.2	59.5
Depth of sagittal crest	37.8	38.2	36.2	34.9	44.5	43.5	44.1
Smallest depth of medial condyle	29	28.6	27.1	26	34	33.3	34.1
Greatest depth of medial condyle	32.3	31.5	30.1	29.1	37.5	36.6	37.2

(continued)

Table 11.A6 (continued)

	A. major Würtsburg-Schalksberg no number	*A. major* Gannat no number	*A. major* Senèze FSL 211077	*A. major* Kislang no number	*A. major* Chagny no number	*A. major* Vatera NHCV PO 5	*A. major* Tataourova GIN 920	*A. major* Liventsovka ROMK L-778
(c) Measurements (in mm) of some *Allohippus major* third metatarsals								
Greatest length	342.7	345	335	330	321	315	334	329
Minimal breadth	44	46	46	45	42	42	43	41.5
Depth at same level	40.5	40	39.5	38	38	39	40	37.6
Proximal articular breadth	63	62	64.5	58	64	66	63.5	61
Proximal articular depth	52	51	50.5	46	49		51	51.6
Distal supra-articular breadth	64	63.5	64.5	60	58.5	57.7	59.5	60.7
Distal articular breadth	62	61	60	58	58	58	58	57.5
Depth of sagittal crest	45	47	46.5	44.5		44.1	43	45
Smallest depth of medial condyle	36	37.5	38	35	33.2	34	34	35
Greatest depth of medial condyle	39	43	41.5	39	38	37	38	39
	FSL SEN 02-0006 parcelle 164	FSL SEN 04–0132	FSL SEN 06–0270	FSL SEN 06–0249	FSL SEN 05–0127	FSL 210868	FSL 210868b	
(d) Measurements (in mm) of third metatarsals of Senèze equids								
Greatest length			263		244	257	242	
Lateral length			253		239	252	237.5	
Minimal breadth		32	33	33	31	33.5	29.5	
Depth at same level		[29]	31	32.5	30	32	28.5	
Proximal articular breadth			49.5	49	46	49	44.5	
Proximal depth			42	42.5	42	40	38.5	
Facet for Large Cuneiform (Tarsale 3)			45.5	45	44.7	42.5	41.5	
Facet for Cuboid (Tarsale 4)			[14]	10.5	10.7	12	11	
Facet for Small Cuneiform (Tarsale 2)			7.1	6	7.8	8	6.5	
Distal supra-articular breadth	61	48	48.1	50	45	46.5	43	
Distal articular breadth	[58]	47	48	48	44	46	42.8	
Depth of sagittal crest	[43]	37	35.1	36	35.1	34.5	33	
Smallest depth of medial condyle	33	28	27	26	26.2	26	24.5	
Greatest depth of medial condyle	35.7	31	30.5	30	30.1		28	
Greatest depth of lateral condyle	32	27	25.5		25.5			

(continued)

Table 11.A6 (continued)

	FSL 210882	FSL 210883	FSL 211077	MNHN.F (Sen) 69	NMB Se 141j	NMB Se 185j	NMB Se 378
Greatest length	247.5	258.5	335	240	256	241	245
Lateral length	244	252		237	251	237	240
Minimal breadth	32.5	32.5	46	33.2	30	30	33.1
Depth at same level	31.5	29.5	39.5	30.3	29	28	30
Proximal articular breadth	47.5	47	64.5	47.5	48.5	45	49
Proximal depth		42.5	> 50	40.2	40	40	42
Facet for Large Cuneiform (Tarsale 3)	42.5	43	58	43	44	42.5	44
Facet for Cuboid (Tarsale 4)	10	9	16	10	11	11	12
Facet for Small Cuneiform (Tarsale 2)	7	7.5		6	7	6.5	6.5
Distal supra-articular breadth	44	45	64.5	47	48	46	48
Distal articular breadth	44.5		60	45	46	44	46.2
Depth of sagittal crest	32.5	34.5	46.5	35	34	32	35
Smallest depth of medial condyle	26	27	38	27	25.5	24	26.5
Greatest depth of medial condyle	28	[31]	41.5	30.5	29	28	30
	NMB Se 551	NMB Se 552j	NMB Se 553j	NMB Se 554	NMB Se 811j?	NMB Se 819	NMB Se 820
Greatest length		253	253	247	242	252	268
Lateral length	245	245.5	248	242			261
Minimal breadth	32	29.5	31.5	35.3	32	35	35
Depth at same level	29	29.9	31	31	30	[30]	34.5
Proximal articular breadth	46.5	47	48.5	50.5			53
Proximal depth		40.8	40.5	42.5			45
Facet for Large Cuneiform (Tarsale 3)		43	44	44			49
Facet for Cuboid (Tarsale 4)		9.2	10	12			12
Facet for Small Cuneiform (Tarsale 2)		7.5	7.5	8			7
Distal supra-articular breadth	46	45.5	49	49	[45]		51
Distal articular breadth	45	45.5	45.5	48.6	44.2		50
Depth of sagittal crest		34.5	35	37.5	34		38.5
Smallest depth of medial condyle		26	27	27	26		28
Greatest depth of medial condyle	28.5	29.5	30.5	31.8	29		32

(continued)

Table 11.A6 (continued)

	NMB Se 821	NMB Se 822j?	NMB Se 1586	NMB Se 1728	NMB Se 1769
Greatest length	256			258	253
Lateral length	250			254	
Minimal breadth	38	32.5	33	35.5	34
Depth at same level	32.5	[32]	32	34	31
Proximal articular breadth	49	48.5		51.5	
Proximal depth	40.5	43.5		43	
Facet for Large Cuneiform (Tarsale 3)		43.5		44	
Facet for Cuboid (Tarsale 4)		11		9.5	
Facet for Small Cuneiform (Tarsale 2)	6	6		7.5	
Distal supra-articular breadth	48			50	[45]
Distal articular breadth	48			48	[44]
Depth of sagittal crest	35			36.5	
Smallest depth of medial condyle	26.5			27	27
Greatest depth of medial condyle	29.5			30	31

j = juvenile

Table 11.A7 (a) Upper cheek teeth measurements (in mm) of Senèze equids. (b) Isolated upper cheek teeth measurements (in mm) of Senèze equids

		MNHL Sen 5233	FSL 210887	FSL 210993	FSL SEN 05–0081	NMB Se 336	NMB Se 553	NMB Se 554	NMB Se 803
(a) Upper cheek teeth measurements (in mm) of Senèze equids									
Age		adult	ca. 5 years	adult	adult	old	ca. 2 years	old	old
P2	L	39	39	41.5	35.2	43			39
	Lp	7.5	8		6.5	7			
	W	25	26.5	28	25.2	28			28
P3	L	30	31	31	25.7	31		27	27
	Lp	9	11.5	8	7.7	7		7.5	
	W	27.5	28.5	30.7	27.4	29		27	28
P4	L	29.5	29	30	26.3	30		26	29
	Lp	11	10.5	9	9.1	7		7.5	
	W	27.5	26.5	29.5	27.1	29.5		27.5	30
M1	L	25.5	25.5	26	22.8	25	29	22	22
	Lp	9.5	9	7.8	8	10	10	9	
	W	25.5	27	27.8	26.2	26	26	25	27
M2	L	26	27	26	24.9	26	30	23.5	25
	Lp	11	10.1	10	9.4	10	13	10	10.2
	W	26	25.5	27.5	25.2	26	25.5	25	27
M3	L	27.5	24.5	28	26.7	30			34
	Lp	10	10	10	8	10.5			12
	W	22.5	20	24	22.4	23			25

(continued)

Table 11.A7 (continued)

		NMB Se 804	NMB Se 806	NMB Se 890	NMB Se 1855	NMB Se 1858
Age		adult	old	adult	adult	adult
P2	L	38	35		40	
	Lp	7	6.5		7.5	
	W	26.5	27		26	
	H		23			
P3	L	29	26.5		32	30
	Lp	8.5	7.5		9.5	8
	W	27.5	26.5		28	31
	H		28			49
P4	L	27	26		31	30.5
	Lp	10	8		9	7
	W	27	25		28	30
	H		29		ca. 60	50
M1	L	24	22.5	25.5	28	28
	Lp	10	9	8	9.5	10
	W	26.5	24.5	25	25.5	28
	H		27	57		44
M2	L	24	24	26	29	26.5
	Lp	10	9	8.5	10	8.5
	W	25	24	25	25.5	28
	H		36	55		40
M3	L	28	25	24	27	30.5
	Lp	10	8.5	9	12	12
	W	22	20	20	20	23
	H		27	44		36

(b) Isolated upper cheek teeth measurements (in mm) of Senèze equids

		L	Lp	W	H
P2	MNHN.F (Sen 41)	40.2	7	26	32
P2	MNHN.F-AC 1938–373	37	7	23.5	25
P3	NMB Se 338	34.1	10.7	32	27
P ?	MNHN.F-AC 1938–373	27	9	26	35
P ? young	MNHN.F-AC 1938–373	31.5	10	29	
P	MNHN.F (Sen 37)	30	9	29	32
P	MNHN.F (Sen 40)	29	9	[27]	34
P	MNHN.F (Sen 45)	28	8	25	29
P	MNHN.F (Sen 46)	29	[9]	[27]	25
P	MNHN.F (Sen 51)	31.3*	10.2*	29.5*	63
P	MNHN.F (Sen 70)	29*	8*	28*	77
M	MNHN.F (Sen 33)	27*	11*	26.5*	67
M	MNHN.F (Sen 34)	26*	9.2*	27.5*	62
M	MNHN.F (Sen 35)	28*	11*	28*	69
M	MNHN.F (Sen 36)	25	9.5	25.2	36
M	MNHN.F (Sen 39)	26	8	25.2	40
M	MNHN.F (Sen 49à	26*	10*	25*	
M ?	MNHN.F-AC 1938–373	24	10	27	18
M ? young	MNHN.F-AC 1938–373	29	10	25	
M ? young	MNHN.F-AC 1938–373	28	9	26	68
M3	MNHN.F (Sen 31)	27	10.1	21	63
M3	MNHN.F (Sen 38)	27	10	23	10

L: occlusal length; Lp: protocone length; W: occlusal width without cement; H: crown height

* measurements taken at mid-crown; approximate measurements between brackets

Table 11.A8 (a) *Allohippus vireti*: statistics of limb bone breadths (b) *Allohippus senezensis senezensis*: statistics of limb bone breadths (c) *Allohippus major*: statistics of limb bone breadths (d) *Allohippus* sp. of Ceyssaguet: statistics of limb bone breadths

	n	x	s	v
(a) *Allohippus vireti*: statistics of limb bone breadths				
Scapula, minimal breadth at the neck	7	64.2	5.99	9.33
Scapula, maximal breadth of articular process	5	100.7	4.02	3.99
Humerus, minimal breadth	27	39.2	1.44	3.66
Humerus, distal articular breadth	22	82.3	2.23	2.71
Femur, minimal breadth	19	43.9	2.56	5.84
Radius, proximal articular breadth	20	81.0	3.95	4.87
Radius, distal articular breadth	29	68.8	2.61	3.79
Third metacarpal, proximal articular breadth	44	54.8	1.82	3.33
Third metacarpal, distal articular breadth	42	51.0	1.56	3.06
Tibia, minimal breadth	20	48.2	1.44	2.99
Tibia, distal breadth	21	80.5	3.00	3.73
Talus, distal articular breadth	102	54.9	1.77	3.21
Calcaneum, proximal maximal breadth	20	36.7	1.91	5.20
Calcaneum, distal maximal breadth	25	56.2	1.88	3.34
Third metatarsal, proximal articular breadth	70	53.5	1.92	3.59
Third metatarsal, distal articular breadth	68	51.1	1.48	2.89
First phalanges, minimal breadth	74	35.8	1.24	3.46
Second phalanges, minimal breadth	54	47.4	2.21	4.67
Third phalanges, articular breadth	27	49.5	2.50	5.05
	n	*x*	*s*	*v*
(b) *Allohippus senezensis senezensis*: statistics of limb bone breadths				
Scapula, minimal breadth at the neck	16	55	7.18	13.06
Scapula, maximal breadth of articular process	15	89.2	4.11	4.61
Humerus, distal articular breadth	13	76.2	6.93	9.09
Femur, minimal breadth	7	38.6	2.07	5.38
Radius, proximal articular breadth	15	76.5	8.28	10.81
Radius, distal articular breadth	15	64.9	8.11	12.50
Third metacarpal, proximal articular breadth	15	50.3	2.66	5.29
Third metacarpal, distal articular breadth	18	46.3	2.79	6.03
Tibia, minimal breadth	15	44.5	3.02	6.79
Tibia, distal breadth	16	73	5.10	9.98
Talus, distal articular breadth	11	52.3	3.95	7.54
Calcaneum, proximal maximal breadth	8	34.1	3.13	9.20
Calcaneum, distal maximal breadth	8	51.9	1.90	3.65
Third metatarsal, proximal articular breadth	17	49.2	4.51	9.16
Third metatarsal, distal articular breadth	19	47.2	4.56	9.66
First phalanges, minimal breadth	27	33.2	3.70	11.16
Second phalanges, minimal breadth	29	42.6	5.81	13.64
Third phalanges, articular breadth	18	43.6	4.74	10.87
	n	*x*	*s*	*v*
(c) *Allohippus major*: statistics of limb bone breadths				
Humerus, distal articular breadth	1	49.00		
Humerus, distal maximum breadth	1	98.00		
Radius, proximal articular breadth	2	96.00	4.24	4.42
Radius, distal articular breadth	2	83.75	3.89	4.64
Third metacarpal, proximal articular breadth	2	62.20	5.94	9.55
Third metacarpal, distal supra-articular breadth	4	61.68	3.87	6.27
Third metacarpal, distal articular breadth	4	59.13	3.92	6.64
Tibia, minimal breadth	2	50.75	1.06	2.09
Tibia, distal breadth	2	81.55	2.19	2.69
Talus, distal articular breadth	2	62.50	1.41	2.26
Third metatarsal, proximal articular breadth	5	62.30	2.59	4.15
Third metatarsal, distal supra-articular breadth	5	62.10	2.68	4.31

(continued)

Table 11.A8 (continued)

	n	x	s	v
Third metatarsal, distal articular breadth	5	58.80	1.79	2.99
First phalanges, minimal breadth	3	45.17	2.08	4.61
Second phalanges, minimal breadth	3	57.17	3.69	6.45
Third phalanges, articular breadth	2	54.00	0.00	0.00
	n	*x*	*s*	*v*
(d) *Allohippus* sp. of Ceyssaguet: statistics of limb bone breadths				
Radius, proximal articular breadth	1	87		
Radius, distal articular breadth	2	77.5	2.12	2.74
Third metacarpal, proximal articular breadth	66	58.29	2.43	4.17
Third metacarpal, distal supra-articular breadth	69	54.89	2.16	3.93
Tibia, minimal breadth	2	55	1.41	2.57
Tibia, distal breadth	2	92.5	3.54	3.82
Talus, distal articular breadth	2	61.25	1.77	2.89
Third metatarsal, proximal articular breadth	5	59	2.87	4.87
Third metatarsal, distal articular breadth	77	55.8	2.75	4.93
First phalanges, minimal breadth	45	38.54	2.25	5.84

n: number of measurements, *x:* mean (in mm), *s:* standard deviation, *v:* coefficient of variation

Table 11.A9 (a) Cranial measurements (in mm) of *Allohippus senezensis senezensis* and *A. stehlini*. (b) Cranial measurements (in mm) of *Allohippus stenonis* species group (c) Cranial measurements (in mm) of *Allohippus senezensis* species group and the reference *Equus hemionus onager*

	FSL 210887	FSL 210993	MNHL Sen 5233	FSL SEN 05–0081	NMB Se 336	NMB Se 551	NMB Se 553	NMB Se 554
(a) Cranial measurements (in mm) of *Allohippus senezensis senezensis* and *A. stehlini*								
16	65		70.5	[51]	69	64		
23	415	450	440	410	438	400	415	
3	126			125	135			
4	112			101	110			
2–5	155	155	164	147	164		[150]	
5	125	145	141	135	140	124	134	131
17	60	71	69	65	71	58		60
17bis		[51]	[53]		44		[40.5]	43
13	206	220	220		236	202	196	
10		46			50			
25		[128]	121		[124]	105	[116]	112
28		104	110		110			
9		60			64			
20	14	16.5		13	16.5			
31		228	188	204	228	190	200	195
32		165	166	155	165	140	146	
	NMB Se 803	NMB Se 1767	*A. stehlini* n = 1–4					
16								
23			382.8					
3			119.7					
4								
2–5	144		125.3					
5			114.4					
17	[62]	63	64.3					
17bis		44	47.5					
13	210		195					
10			44.8					
25								
28	[103]							
9			76.5					
20								
31			167					
32	140		145					

(continued)

Table 11.A9 (continued)

	A. stenonis stenonis	*A. stenonis vireti*	*A. stenonis livenzovensis*	*A. stenonis* sp.	*A. sanmeniensis*	*A. stenonis* sp.	*A. stenonis* sp.	*A. koobiforensis*
(b) Cranial measurements (in mm) of *Allohippus stenonis* species group								
	Valdarno n = 1–3	Saint-Vallier n = 1–7	Liventsovka ROMK L 4, L 11	Kuruksai PIN 3120	Nihowan MNHN-F NIH 002	Fan Tsun AMNH-P 60-B 719	Ceyssaguet MNP-Bonifay 9142	East Turkana KNM- ER 1484
16			70					
23	435	449	452	490	480	425	489	472
3	152	135.3	144		152		152.3	
4		128	110		126		134.3	
2–5	152.3	151.2	152		160	145	157.7	
5	161.5	146.8	146	170	155	151	175.2	150
17	74.3	67.7	65.5		70	[60]	81	[64]
17bis	45.9	51.4	[39]		53	[40]	50.4	[46]
13	200	227	222			215		225
10		47.8	43			43		53
25		112			130			
28		103.3	112					
9	94	70	70		80	72		
20			16					
31	214	230	186.5	250	225	210		195
32	171	184.5		180	193	170		162
	E. hemionus onager	*A. senezensis senezensis*	*A. senezensis guthi*	*A. senezensis mygdoniensis*	*A. bactrianus*	*A.* sp.	*A. stehlini*	
(c) Cranial measurements (in mm) of *Allohippus senezensis* species group and the reference *Equus hemionus onager*								
	n = 30	Senèze n = 2–9	La Puebla de Valverde n = 1–2	Gerakarou n = 1–3	Kuruksai n = 1–3	China Loc A and D PMU 1357, 1418 n = 1–2	Valdarno n = 1–4	
16	56	67.1		55				
23	348.1	424	415	393	420	430	382.8	
3	116.9	128.7	123	127.3	110.5		119.7	
4	101	107.7	124	104.5	106			
2–5	115.6	154.8	155.5	145.8	163.7	168	125..3	
5	104.9	134.4	137	130.7	127.7	145	114.4	
17	55.9	65.2	69	68.3	69	70	64.3	
17bis	40.7	43.7	47	36.7	46.5		47.5	
13	196.8	212.9	220	203.8	245	262	195	
10	48.1	48	52	45.5	51	50	44.8	
25	102	112.7						
28	89.8	108	108	93				
9	63.3	62						
20	14.3	15						
31	143.3	203.9	205	193	217.5	230	167	
32	162.2	153.9	164	151.5	152	180	145	

Approximate measurements between brackets. Measurements as in Eisenmann (1986) and http://www.vera-eisenmann.com: 16: breadth of the supra-occipital crest; 23: anterior ocular line; 3: distance from palate to hormion; 4: distance from hormion to basion; 2–5: palatal length (without the muzzle); 5: muzzle length; 17: muzzle breadth at the posterior border of the I3; 17bis: least muzzle breadth between the interalveolar borders; 13: frontal breadth; 10: greatest choanal breadth; 25: facial height in front of P2; 28: cranial height behind the orbits; 9: choanal length; 20: height of the external auditory meatus; 31: length of the naso-incisival notch (from prosthion to the back of the narial opening); 32: cheek length (from the back of the narial opening to the most anterior point of the orbit)

Table 11.A10 (a) Means of measurements (in mm) of mandibles of *Allohippus* and extant *Equus*. (b) Measurements (in mm) of mandibles of Senèze equids

	variable:	1	2	3	6	7	9	12	13
(a) Means of measurements (in mm) of mandibles of *Allohippus* and extant *Equus*									
A. stenonis vireti n = 2–7	Saint-Vallier	505	133	116.5	97.9	57.6	73	141.5	38.3
A. senezensis guthi MNHN-F PUE 3283	La Puebla de Valverde			104	92	60		138	38
A. senezensis senezensis n = 4–15	Senèze	451.9	127	95.9	85.6	48.6	60.6	115.5	33.7
E. hemionus onager n = 4–22		384.5	115.1	71.7	74.4	50.5	51.8	94	38
E. przewalskii n = 20–30		422.5	119.9	84.4	82.1	60.3	54.7	106.4	41.1
E. africanus n = 8–28		*390.8*	113.2	75.8	75.7	46.8	52.9	99.5	34.9
E. grevyi n = 5–61		461.2	130.5	103.9	91.1	52	61.8	130.4	36
E. zebra n = 26–79		414.3	126.3	85.5	83.9	52.3	60.7	107.5	36.2
E. quagga n = 18–57		404.7	120.8	90.4	80.3	52.2	58.9	108.1	34.5
	MNHL Sen 5233	FSL 210845	FSL 210847	FSL 210849	FSL 210850	FSL 210851	FSL 210852	FSL 210859	
(b) Measurements (in mm) of mandibles of Senèze equids									
Sex	M				M	F	M	F	
Age	adult	adult		adult	adult	old	ca. 5 years	old	
1. Greatest length	460							480	
2. Mandibular angle radius	132							[135]	
3. Length of diastema	103		90	92	90			109	
4. Occlusal length of P2-P4	91	98	86	88				88	
4 bis. Occlusal length of M1-M3	87.5	84	80	82				85	
5. Occlusal length of P2-M3	179	180	164	168				174	
6. Length of symphysis	94		82	87	85 or 90	85	94	95	
7. Breadth at posterior borders of I3	56		54	51	52 or 55	48.5	66	[50]	
8. Height of ascending ramus								230	
9. Height in front of P2		62		62				55.5	
10. Height between P4 and M1								80	
11. Height behind M3									
12. Muzzle length				112	114			135	
13. Least symphysis breadth	[38]			34	39	29.1	34		

(continued)

Table 11.A10 (continued)

	FSL SEN 05–0081	NMB Se 551	NMB Se 553	NMB Se 554	NMB Se 804	NMB Se 805	NMB Se 1776	NMB Se 1855
(b) Measurements (in mm) of mandibles of Senèze equids								
Sex	F	F		M			F	F
Age	adult	old	ca. 3 years	old	adult	old		ca. 5 years
1. Greatest length	435	440	445	438			465	
2. Mandibular angule radius	126	120	130	119			129	
3. Length of diastema	91	90	90	96	84	102	116	97
4. Occlusal length of P2-P4	91	86	102	85.5	89	74	81	100
4 bis. Occlusal length of M1-M3	78	83		80	80	77	80	88
5. Occlusal length of P2-M3	170	170		163.5	170	151	162	187
6. Length of symphysis	[79]	72	87	92 or 121	80	79	90	84
7. Breadth at posterior borders of I3		51	52	51	[35]	[38]	53	53
8. Height of ascending ramus	210							
9. Height in front of P2	63							
10. Height between P4 and M1	79							
11. Height behind M3	107							
12. Muzzle length	101							
13. Least symphysis breadth				32				30

Variables listed by number at top of table and defined on left in section b. For NMB Se 374, Female, Length of symphysis = 83.5; breadth at posterior borders of I3 = 50

Table 11.A11 (a). Lower cheek teeth measurements (in mm) of Senèze equids. (b) Isolated lower cheek teeth measurements (in mm) of Senèze equids

		MNHL Sen 5233	FSL 210834	FSL 210835	FSL 210841	FSL 210842	FSL 210843	FSL 210844	FSL 210845
(a) Lower cheek teeth measurements (in mm) of Senèze equids									
Age		adult	< 4 years	adult	old	old	adult	adult	adult
p2	L	34	37	30.4	34	32.5	32	31	[35.5]
	Lpf	14.5	14.7	11.5	15.3	13	12.5	15.6	15
	W	15.5	14.3	14.5	15	15.5	14	15	15.7
	H		60	[43]		32			
p3	L	30	32.3	27.5	29	27	28.5	28	30
	Lpf	15	13.8	11.4	10	9	14	15	14.5
	W	16	16.5	15.7	15	15.3	15	16	16
	H		70						
p4	L	29	31	26	27	25.2	27.5	28	29.5
	Lpf	12.5	12	10.5	8.7	7.5	13.5	13	13
	W	16	15.5	16.5	16.3	15.5	15.5	16	15.7
m1	L	26.5	29	25.2	24	21	25.5	25.5	26
	Lpf	12	9.8	7.5	0	0	8	8	9.5
	W	14	14.8	15	15.4	14.5	13.5	15	15.5
	H			[31]					
m2	L	27	30.5			24	26.5	26	26.5
	Lpf	11.5	9.7			4.5	8	7.8	9
	W	14	13.6			13.5	13	14.5	14.8
	H		68			[18]			
m3	L	32			37		30	30	29.5
	W	13			12.7		12.5	13	13
		FSL 210847	FSL 210849	FSL 210857	FSL 210877	FSL 210887	NMB Se 142	NMB Se 553	NMB Se 554
Age		adult	adult	adult	old	ca. 5 years	ca. 5 years	ca. 2 years	old
p2	L	33	34.5	32		36.5	36.5	[38]	30.5
	Lpf	14	15.5	14.5		16.5	14.5		12
	W	14.5	14.8	15.5		14	14		13.5
p3	L	28.5	29.5	27	26.5	32	30	[33]	27.5
	Lpf	13.5	13.5	9.5		15	15		10.3
	W	16	16.5	16.5	15	16	16		15
	H		52						
p4	L	27.5		27	26.5	30.5	28.5		27
	Lpf	12		10.5	7.5	13.5	13		10
	W	16		17.5	14	13	16		15.5
m1	L	24.5		23.5	22.5	29.5	25.5	30.5	23
	Lpf	6.5		0	0	11	11	13	5
	W	15.5		16	15	14	15	13	14
m2	L	24		25	25	28	25.5	34	24.5
	Lpf	7.5		0	4.5	11	11	12	6
	W	13.5		15	14	12	15	12.5	14
m3	L	31		31		29	30		31
	W	12		12.5		9.5	14		12

(continued)

Table 11.A11 (continued)

		NMB Se 694	NMB Se 804	NMB Se 806	NMB Se 918	NMB Se 1496	NMB Se 1855	NMB Se 1857	MNHN.F (Sen 68)
Age		4 years	adult	old	4 years	adult	ca. 5 years	adult	adult
p2	L	37.5	34	31	33	34	35.5		31
	Lpf	17.5	12	13.5	16	14.5	17		14.5
	W	15.5	16	14	15.5	16	15		15
p3	L	32	28.5	26.5	29	30	32	28	29
	Lpf	14	13	12.5	13.5	15	15	12	14
	W	16.5	16.5	15	15	17	16	16	16.5
	H								[40]
p4	L	31	27	27	31	29	31	28	
	Lpf	12.5	13	12	13	13	13	11	
	W	15	16	15.5	15	16.5	14.5	16.5	
m1	L	29	24.5	24.5	27.5	27	27.5	25	
	Lpf	9	7.5	7	10	10.5	10.5	8	
	W	15	15	14		15	14.5	[14]	
m2	L	31	25	24.5	29	27.5	28.5	25	
	Lpf	10.5	9	7	12	9.5	10	7.5	
	W	13	15	13.5	14	15	14	14	
m3	L	31	30	30	31.5	33	30.5	32	
	W	10	13	12.5	11	13.5	11.5	13	
		MNHN.F-AC 1938–373	FSL SEN 05–0081						
Age		adult	adult						
p2	L	32	32.3						
	Ldn		13.5						
	Lpf	13	15						
	W	13	14.4						
p3	L	28	28.9						
	Ldn		17.3						
	Lpf	13.2	13.4						
	W	14.5	15.1						
p4	L	27	26.8						
	Ldn		15.8						
	Lpf	12.5	12.1						
	W	15.1	16.1						
m1	L	24.5	24.2						
	Ldn		14						
	Lpf	8	7						
	W	14	14						
m2	L	26	23.9						
	Ldn		12.8						
	Lpf	8	7.4						
	W	13	13.7						
m3	L		30.1						
	Ldn		12.6						
	W		12.4						

(continued)

Table 11.A11 (continued)

		L	Lpf	W	H
(b) Isolated lower cheek teeth measurements (in mm) of Senèze					
P2 unworn	MNHN.F-AC no n°	[39]			[56]
P2	MNHN.F-AC no n°		15	15.5	[46]
P2	MNHN.F-AC no n°	34	14	15	39
P2	MNHN.F-AC no n°	[35]	15	15	38
P2	MNHN.F (Sen 16)	[30]	10.5	14	16
P2	MNHN.F (Sen 17)	32	15	[14.5]	27
P2	MNHN.F (Sen 18)	32	14.5		45
P	FSL 211060	30.5	13.5	17.2	36
P	MNHN.F-AC no n°	31.5	13	16	51
P	MNHN.F-AC no n°	32	15	17	54
P	MNHN.F-AC no n°	27	13	17	42
P	MNHN.F-AC no n°	29.5	13.5	16	34
P	MNHN.F (Sen 19)	30.5	15	15	46
P	MNHN.F (Sen 20)	29.5	15	17	64
P	MNHN.F (Sen 21)	30.5	13.5	16.5	49
P caballine	MNHL Sen 3982	28.5	12	17	66
P caballine	MHNL Sen 3982	28	12	17	52
P ?	MNHN.F (Sen 9)	27.5	9.5	15.5	23
P ?	MNHN.F (Sen 10)	27	11	15	24
M young	MNHN.F-AC no n°	[34]	12		> 60
M young	MNHN.F-AC no n°	[33]	10		72
M young	MNHN.F-AC no n°	[31]	10		> 63
M	MNHN.F-AC no n°	27	10	14	50
M	MNHN.F-AC no n°	26.3	8.2	12.5	39
M	MNHN.F-AC no n°	26.5	10	13.5	32
M	MNHN.F-AC no n°	26	10	13	31
M unworn	MNHN.F (Sen 1)	[35]			> 64
M young	MNHN.F (Sen 2)	29	11.5	12	> 63
M young	MNHN.F (Sen 3)	29.5	10.5	12	> 55
M young	MNHN.F (Sen 4)	[33]	11.5		> 61
M	MNHN.F (Sen 5)	27.5	9.5	13.5	60
M	MNHN.F (Sen 6)	26	8.5	14.5	30
M unworn	MNHN.F (Sen 7)	[35]			
M	MNHN.F (Sen 11)	30	10.5	[14]	68
M	MNHN.F (Sen 12)		7	12.5	
M young	MNHN.F-AC 1938–373	29	11.5	13.2	60
M3	MNHN.F-AC no n°	32	13	13	33
M3	MNHN.F (Sen 22)	33	13	13	32
M3	MNHN.F (Sen 23)	31.5	13.5	13.5	34

L: occlusal length; Ldn: double knot length; Lpf: postfossette length; W: occlusal width without cement; H: height. Approximate measurements between brackets

Table 11.A12 (a) Measurements (in mm) of first anterior phalanges of *Allohippus major*, Sussemiones, and *E. hemionus onager*. (b) Measurements (in mm) of first posterior phalanges of *Allohippus major* and Sussemiones (c) Measurements (in mm) of first anterior phalanges of Senèze equids (d) Measurements (in mm) of first posterior phalanges of Senèze equids

	Würtsburg Schalksberg no number *A. major*	Senèze FSL 211074 *A. major*	East-Runton NHMUK -P 6760 *A. major*	Süssenborn n = 2–5	Akhalkalaki n = 17–22	NE Siberia GIN 3722–17	*E. hemionus onager* n = 14–15
(a) Measurements (in mm) of first anterior phalanges of *Allohippus major*, Sussemiones, and *E. hemionus onager*							
Greatest length	104	110	107.5	99.4	98.8	103	76.5
Smallest breadth	45	44.5	47	39.9	42	41	24.6
Proximal breadth	70	67.5	70	60.8	65.9	65	41.1
Proximal depth	47	47.5	45	41	44.1	44.5	30.8
Supra-articular distal breadth	60	59.5	60	51.5	56.5	56.5	36.7
Greatest length of trigonum phalangis	72	71	75	70.6	66.9	65	48.1
Medial supratuberosital length	74.8	73.9	74	74.8	73.9	74	58.5
Medial infratuberosital length	14	16.5	19	13.9	15.3	18	10.3
Distal articular breadth	57	57.5	59	50.6	55.1	57	48.1

	Senèze FSL 211075 *A. major*	Chagny FSL no number *A. major*	Süssenborn n = 2	Akhalkalaki n = 18–19	NE Siberia Loc 37 PIN 3100–333-79
(b) Measurements (in mm) of first posterior phalanges of *Allohippus major* and Sussemiones					
Greatest length	105	100.2	100	96.5	95
Smallest breadth	43.5	47.5	42	41.4	45
Proximal breadth	69	69.5	67.7	68.2	70.9
Proximal depth	50	51	42	45.9	45
Supra-articular distal breadth	57	58.1	55	54.7	59
Greatest length of trigonum phalangis	64	61	67.5	62.3	56
Medial supratuberosital length	76	77	73	68	67
Medial infratuberosital length	20	23.5	18.5	18.7	20
Distal articular breadth	54.5		50.8	51.8	54

(continued)

Table 11.A12 (continued)

	FSL 210899	FSL 211055	FSL 211074	FSL SEN 06–0279	MNHN.F (Sen 61)	NMB Se 141j	NMB Se 179	NMB Se 180
(c) Measurements (in mm) of first anterior phalanges of Senèze equids								
Greatest length	80	91	110	76.9	80	77.5	77.5	86
Anterior length	70		101	70.1		70	70	
Smallest breadth	32	36.5	44.5	33.5	32	31.5	31	31.5
Proximal breadth	49	55	67.5		50	50	51.5	
Proximal depth	35.5	37	47.5		35	33.5	34	
Supra-articular breadth	41.5	49	59.5	46	44	41	44	41.3
Greatest length of trigonum phalangis	50		71	47.5	49	49	50	
Smallest length of trigonum phalangis	45		67	42	43	43	44	
Posterior length	70		99	67.5		67	68.5	
Medial supratuberosital length	58		82	58	58	55	57.5	
Lateral supratuberosital length			83	59	58	55	55.5	
Medial infratuberosital length	14		16.5	12.9	13	13	13	
Lateral infratuberosital length			15.5	11	14	13	13.5	
Distal articular breadth	40.5		57.5	44	43	41.5	41.5	[41]
	NMB Se 552j	NMB Se 553j	NMB Se 554	NMB Se 828	NMB Se 833	NMB Se 835	NMB Se 1689jjj	
Greatest length	78	76	80.2	83	80	76.3	71	
Anterior length	71	67	71.5		72	67.5	65	
Smallest breadth	30.5	32	34.5	34	31.5	31.5	26	
Proximal breadth	48.5	51.5	54.5	54	52	53	42	
Proximal depth	33.5	34	37	37.5	34.5	35	29	
Supra-articular breadth	[41.5]	43	48.5	47.5	42	42.5	36	
Greatest length of trigonum phalangis	48	47	53	51	50.5	46		
Smallest length of trigonum phalangis	41	42	48		45	40		
Posterior length	68	66	71		70	66	63	
Medial supratuberosital length	58	52	57	60	58	54		
Lateral supratuberosital length	58	52	57.5		57	54		
Medial infratuberosital length	12	14	13	14	14	13.5		
Lateral infratuberosital length	11	14	12.5			13		
Distal articular breadth	[42]	42	45	46	42.5	43.5	37	

(continued)

Table 11.A12 (continued)

	FSL 210898	FSL 210900	FSL 211075	FSL 211082	FSL 211082bis	FSL 211083j	FSL SEN 04–0133	FSL SEN 06–0267
(d) Measurements (in mm) of first posterior phalanges of Senèze equids								
Greatest length	77.5	80.5	105	85.5	80		77.5	76
Anterior length	68	71	97	78	71.5		69	68
Smallest breadth	33	35.5	43.5	33.5	32.5	28	31.5	34
Proximal breadth	50.5	55	69	54	53.5		51.2	53.7
Proximal depth	36.5	39.5	50	39	38		37	37.2
Supra-articular breadth	41.5	45	57	45	[43]	37.5	39.6	44.1
Greatest length of trigonum phalangis	46.5	46	64	51	48		42	45
Smallest length of trigonum phalangis	40	42	57	45	42		35.5	38
Posterior length	66.5	71	94	74	70.5		67	65
Medial supratuberosital length	51	54	76	61	53		52	52
Lateral supratuberosital length			76	61			53	52
Medial infratuberosital length	17	18	20	16	17	15.5	18	17
Lateral infratuberosital length			19	15			16	17
Distal articular breadth	39	43	54.5	42		37	40	42
	NMB Se 141j	NMB Se 551	NMB Se 552j	NMB Se 553j	NMB Se 554	NMB Se 811	NMB Se 1689jjj	
Greatest length	77		76	73	76.5	74.5	69	
Anterior length	69		70	65.5	68.8	67	63.5	
Smallest breadth	31	33.5	31.5	33.1	35.5	31	28	
Proximal breadth	51.2	51	50.5	53	54	51	43	
Proximal depth	35.5	37	35.5	36.5	40	37	31	
Supra-articular breadth	40	42.5	[40]	43	47.3	43	35	
Greatest length of trigonum phalangis	43		43.5	43	48.5	40	40	
Smallest length of trigonum phalangis	37		36.6	37	42	34.5	34	
Posterior length	66		65.5	63	66	65	61	
Medial supratuberosital length	53	[48]	54	48	52	51		
Lateral supratuberosital length	54		52	48	52.5	50		
Medial infratuberosital length	16	[15]	15.5	18	16	17		
Lateral infratuberosital length	15		15	16	15.5	17		
Distal articular breadth	40	39.5	39.5	40	45	40	35.5	

j = juvenile

Table 11.A13 Upper cheek teeth measurements (in mm) of *Allohippus stenonis stenonis* from Olivola and Matassino

		IGF 11023	IGF 11025	IGF 1432	IGF 1431
Age		old	young adult	adult	adult
P3	L	30.2	33	30.5	32
	Lp	7.8	8.4	8.1	10
	W	30	30	31	30
P4	L	28.4	31.5	27.5	
	Lp	8.8	10.2	9	
	W	29.5	29.3	29	
M1	L	25.8	26.8	25	
	Lp	10.1	9.2	9	
	W	28.3	27.6	28	
M2	L	26.9	27.6	26	
	Lp	11.1	9.5	9	
	W	27.3	26.7	27.3	

L: occlusal length; Lp: protocone length; W: occlusal width without cement

Table 11.A14 Measurements (in mm) of scapula and pelvic acetabulum of Senèze equids

	Maximal length	Minimal breadth at the neck	Maximal breadth of articular process	Articular maximal breadth	Articular maximal depth	Pelvic acetabulum diameter
FSL 210993		64	92	54	43	[62]
MNHN.F-AC 1921–9		58	84	51	46.5	
MNHN.F (Sen 55)		60	90	56	49	
NMB Se 141j		50.5	87.5	55	46	
NMB Se 181		58	95	59	49	
NMB Se 551	345	58	91	56	47.5	58
NMB Se 552j	290	51.5	90	55	[47]	60
NMB Se 553j	[320]	59	91.5	56	51.5	62
NMB Se 570		51	85	53	45.5	
NMB Se 862		49.5	86	[53]	43	
NMB Se 863			91.5	58	42	
NMB Se 864				59.5	41.5	
NMB Se 864bis		< 58				
NMB Se 865		64			51	
NMB Se 866					50.5	
NMB Se 868		59.5	95.3	57	49	
NMB Se 869		40				
NMB Se 870		43		52	42.5	
NMB Se 923			90	55		
NMB Se 1471		60	89	54.5	43.5	
NMB Se 1471bis					48	
NMB Se 1511		47.5	80	51	43.5	
NMB Se 696						60
NMB Se 854						60
NMB Se 857						[64]
NMB Se 859						63

j = juvenile

Table 11.15 Measurements (in mm) of humeri of Senèze equids

	Greatest length	Posterior length	Smallest breadth	Proximal breadth	Proximal depth	Distal articular breadth	Distal medial depth	Trochlear smallest height
FSL 210864j	262	244	32.5		[80]	71	79	32
FSL 210869–70			35			73		34
FSL 210871			36			76	84	37
FSL 211091			[49]			98	107	43
FSL 210993	[277]	[263]	[33]	[99]	97	73	76	32
FSL SEN 05–0097	282	263	35	96	98	74	79	36
MNHN-F (sen 54)		260	34.5			71	80	36.5
NMB Se 141j		238	31.5		[90]	75	82	35
NMB Se 551	280	250	34	92	102	73	80	
NMB Se 552j	260.5	240	30.1			70	80	36.5
NMB Se 553j	286	261	34.5	92	103	76	82.5	36
NMB Se 554						78		37.2
NMB Se 824	290	268	38			78	87.5	39
NMB Se 825			34.5			74.5	82.5	34.5

Table 11.A16 Measurements (in mm) of radii of Senèze equids

	FSL 210860	FSL 210861	FSL 210862	FSL 210863	FSL 211093	FSL 211095	FSL 211101
Greatest length	398	315	344	308	[325]	427	
Lateral length	383.5	296		295	312	412	
Smallest breadth	58	39	44.5	40	38		
Proximal breadth	103.5	81		79	80.5	110	82.5
Proximal articular breadth	93	72.5		70	72	99	75
Proximal articular depth	49.5	38	39	33	[36]	46.5	38.5
Distal breadth	100	72	78	70	71.5	102	
Distal articular breadth	81	61	66	60	57	86.5	
Greatest distal articular depth	49	38	41	36.5	[35]	47	
Breadth of radial condyle	31	24.5	25.5	22.5	25	33	
Breadth of ulnar condyle	21	14.5	17	15	14.5	23	

(continued)

Table 11.A16 (continued)

	FSL SEN 05–0098	FSL SEN 06–0288	FSL SEN 06–0297	MNHN.F (Sen 66)	NMB Se 141j	NMB Se 551	NMB Se 552j
Greatest length	315	[330]		330	319		316
Lateral length	295			316.5	300	302	302
Smallest breadth	36.6	40	40	43.5	38	38	35.2
Proximal breadth	81	84		83.5	82	78	81
Proximal articular breadth	72.5	72.5		72.5	75	70	72
Proximal articular depth	37	40			38		35
Distal breadth	71		77	73	73	69.5	71
Distal articular breadth	59		62	61	64	60	59.5
Greatest distal articular depth	34		[42]	35	38		36.5
Breadth of radial condyle	23		27	26	26		26
Breadth of ulnar condyle	16.7		16	16.5	16		17
	NMB Se 553	NMB Se 554	NMB Se 827	NMB Se 828	NMB Se 1768		
Greatest length	326			327	340		
Lateral length	306			306	320		
Smallest breadth	40		44.5	43	43		
Proximal breadth	84	83		84	85.5		
Proximal articular breadth	76	75		75	78		
Proximal articular depth	38	39		37.5	40		
Distal breadth	76	76		74	79		
Distal articular breadth	63	63		64	66		
Greatest distal articular depth	37	38		38	41		
Breadth of radial condyle	26.5	26		27	28		
Breadth of ulnar condyle	17	18		16	17		

j = juvenile

Table 11.A17 Measurements (in mm) of femora of Senèze equids

	Greatest length	Medial length	Smallest breadth	Proximal breadth	Proximal depth	Depth of caput femoris	Distal breadth	Trochlear breadth	Distal medial depth
MNHN.F Sen 1223–4							[86]	[62]	118
NMB Se 551	380	340	38	117	81	51	89	60	114
NMB Se 554	388	347	39	123.5	88	58	93	64	115.5
NMB Se 552j	363	333	33.5	107	[76]	53	87	59	110.5
NMB Se 808		367	42			57	93	66	120
NMB Se 785	352	321	38	113	87	51	85.5	55.5	109
NMB Se 553j	388	349	39			56	92	63	116
NMB Se 141j	351	325	35	108	80	54	89		
FSL SEN 05–0148	378	340	39.1	112	86	53	89	65	112

j = juvenile

Table 11.A18 Measurements (in mm) of tibiae of Senèze equids

	FSL SEN 05–0151	FSL SEN 06–0274 right	FSL SEN 06–0278 left	MNHN.F (Sen56)	MNHN.F (Sen 57)	MNHN- AC 1938–373	NMB Se 107a	NMB Se 141j	
Greatest length	333	360					[335]	336	
Lateral length	300							321	
Smallest breadth	42	45	45	[46]		[43.5]	40	41	
Smallest depth	31	31	32	30		30	26	28	
Proximal breadth	[95]	[102]						[94]	
Proximal depth	[82]							80	
Distal breadth	69.5	76	80	67	76	70	65	71	
Distal depth	48		51	44	50	48		49	
Length of fossa digitalis	54							58	
Breadth of fossa digitalis	22							18	
Greatest length		349	343	338	355			348	
Lateral length	330	335	325	325	339			337	[290]
Smallest breadth	43	43.5	45	44	50	51.5	43	44.5	39
Smallest depth	31	30	32.5	31	35	33.5	30	31	27
Proximal breadth	94	98	100	[91]	104			96.5	
Proximal depth	80	83	89	80	87			84	
Distal breadth	70	75	74	69	80	83.1	[69]	74	[60]
Distal depth	47	47	47	46.5	50	56	47	47	
Length of fossa digitalis	58	60	54	54	64			54	
Breadth of fossa digitalis	19	19	18	[22]	20			19	

j = juvenile

Table 11.A19 Measurements (in mm) of tali of Senèze equids

	Gratest length	Length	Medial length of trochlea	Greatest breadth	Trochlear breadth	Distal articular breadth	Distal articular depth	Medial depth
FSL 210854–55	59.5		58.5	60	27	52	33.5	49.5
FSL 210856	63.5		64	61	27.5	53.5	36	51
FSL 211073	79		76.5	79	36	63.5	45.5	62.5
FSL 211082	61		60.5	61	29	51	36	52.5
FSL SEN 05–0137	57	55	56.2	59	27	49	33.1	50
FSL SEN 06–0278	63	61	62	62	28.5	52	35.1	
MNHN.F (Sen 58)	[63]		60	[63]	[30]	52.5	37.5	52.5
NMB Se 141j	64		62	61.5	26.5	50	36	52
NMB Se 181	64.5			63.5	27.5	[52]	34	
NMB Se 198			59.5		27			
NMB Se 551				59	27.5			
NMB Se 552j	61.5		59	55	27	49	35	49
NMB Se 553j	59		60	62	27	50	33	52
NMB Se 554	62		61.5	61	27	52	35	51
NMB Se 692	63		60	60		50	35.5	

j = juvenile

Table 11.A20 Measurements (in mm) of calcanei of Senèze equids

	Geatest length	Length of proximal part	Smallest breadth	Proximal breadth	Proximal depth	Distal breadth	Distal depth
FSL SEN 06–0255	114	77	22	36	50	52	55.1
FSL SEN 06–0261	114	75		35.5	50.5	55	54
MNHN.F (Sen 59)	113	76	20	31.5	47.5	53	52
NMB Se 141j	110	71.5	22.5	33	49	50	51
NMB Se 551	107	73	22	28	48		
NMB Se 552	104	68	20.5	32	47	49	50
NMB Se 553j	111	75	22	35.5	52	51	51
NMB Se 554	113	80	23	38	51	53	55
NMB Se 811	108		19			49	51
NMB Se 843	123	80	23	35	55		58
NMB Se 844j	118		20			52.5	45

j = juvenile

Table 11.A21 (a) Measurements (in mm) of second anterior phalanges of Senèze equids. (b) Measurements (in mm) of second posterior phalanges of Senèze equids

	Greatest length	Anterior length	Smallest breadth	Proximal breadth	Proximal depth	Distal articular breadth
(a)						
FSL 210899	45.5	33	40	47	32	43.5
FSL 210919	57.5	43.5	58.5	68.5	40.5	65.5
FSL 211067	48.5	36.5	42.5	51.5	32.5	48
FSL 211075	57.5	43	60	66	43	62.5
FSL SEN 06–0276 left	45	34	44	51	33	46.6
FSL SEN 06–0312 right	45.7	34	44	51.5	33	47
MNHN.F (Sen 62)	45	33	42.5	50.5	30.5	44.5
NMB Se 141j	44	33	41.5	47	31	44
NMB Se 180	47		42	49		47
NMB Se 551	39		43	47.1	31	45.5
NMB Se 552j	46	34	40	46.5	30.5	44.5
NMB Se 553j	46	33	42	50	32	45.2
NMB Se 554	47.5	34	46	53	33	50
	Greatest length	Anterior length	Smallest breadth	Proximal breadth	Proximal depth	Distal articular breadth
(b)						
FSL 210898	46.5	36	37	45	32.5	39.5
FSL 210900	46	35.5	37.5	45.5	32	40
FSL 211064		34	38			40
FSL 211075	59	43.5	48.5	58	38.5	52.5
FSL 211078	59	46	53	63	42.5	56
FSL 211083	45	34.5	37	43.5	30	38.5
FSL SEN 04–0134	47.2	35	38.7	46.2	32	41
FSL SEN 06–0264	47	35	41.5	50	33	43
MNHN.F (Sen 60)	47	37	41	50	32.5	42
NMB 141j	47	33.5	40	45	32.5	40.5
NMB Se 377	43	31	37	44	29	39
NMB Se 551	45		40	47	33	42
NMB Se 552j	47	37	39	46	32	41.5
NMB Se 553j	46.5	34.5	40	48.5	32	42
NMB Se 554	49	37	43	52	35	46.5
NMB Se 838	47	[33]	39	46	32	40.5
NMB Se 839	47	35	38	47	32	39.5
NMB Se 845	46.5	33	40	47.2	32	39.5

j = juvenile

Table 11.A22 (a) Measurements (in mm) of third anterior phalanges of Senèze equids. (b) Measurements (in mm) of third posterior phalanges of Senèze equids

	Anterior length	Greatest antero-posterior diameter	Height	Greatest breadth	Articular breadth	Articular antero-posterior diameter	Distal "circumference"
(a)							
FSL 210899	52.5	62	[42]	[70]		26	[170]
FSL 210901	[62]	80.5		[100]			[210]
FSL 211082	66	73	[44]	[98]	[54]	32	[200]
NMB Se 115, ant.?			39		[48]	29	
NMB Se 141j	44	46	40	[50]	44	25	120
NMB Se 551	52	67	41.5	67.3	44	25	160
NMB Se 552j	[45]	[53]	37	[60]	44	[24]	[130]
NMB Se 553j	47	60	42	64	[44]	25	145
NMB Se 554, ant.?	52	62	40.5	66	46	29	[150]
NMB Se 917jjj	42		28.5			24	
NMB Se 1861, ant.?	52	65	39	63	46	25	155
	Anterior length	Greatest antero-posterior diameter	Height	Greatest breadth	Articular breadth	Articular antero-posterior diameter	Distal "circumference"
(b)							
FSL 210898	51.5	59		[62]	[40]	25	[150]
FSL 210900	51	58.5	40	60	39	25.5	145
FSL 211078, post.?	66	78	[44.5]	[90]	54	31	
FSL 211083	40.5	43	33.5	43	38	24	[110]
FSL SEN 04–0135	51	[54]	40	58	44	28	> 136
FSL SEN 05–0130	50	59	40	57.2	41	27	147
NMB Se 141j	49	50	40	51.5	41	26	120
NMB Se 375	48	57.5	39	57.5	37	25	140
NMB Se 551	51	63	42	62.5	42	27	150
NMB Se 552j	46	50.5	34	54	40	24	125
NMB Se 553j	49.5	53	40	[59]	41	24	130
NMB Se 811	[50]	54	35.5	59	42	25	[143]
NMB Se 917jjj	43	39	35.5	42	40	26	103

j = juvenile

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