Chapter 17
Biochronology of the Senèze Faunal Assemblage

Evelyne Crégut-Bonnoure, Claude Guérin, Alain Argant, Jacqueline Argant, Evelyne Debard, Eric Delson, Véra Eisenmann, Martine Faure, Bernard Ménouret, Cécile Mourer-Chauviré, and Andrea M. F. Valli

Abstract Our fieldwork at Senèze from 2000–2006 was designed to place the fauna from this important site in a precise stratigraphic and geochronologic framework, as well as to seek new elements of known taxa and possibly additional taxa. The analyses reported in this volume led to the recognition of six new taxa: *Dinofelis* sp., *Canis* sp., cf. *Hemitragus*, two indeterminate bovids and an indeterminate hyaenid; *Ovis claudiusguerini* n. sp. was newly named for a specimen previously indicated as *Ovis* sp. *Hystrix refossa* and Hyaenidae indet. (both recovered in our excavations) are new taxa for the site, as is *Bison* (*Eobison*) sp., a specimen of which was collected by A. Consigny on the surface and presented to the team. Senèze is the type-locality for 13 mammalian taxa: three genera, seven species and three subspecies. Fifty-eight vertebrates have now been recorded for the site: 39 mammals (one lagomorph, four rodents, 12 carnivores, two primates, 16 cetartiodactyls, three perissodactyls and one proboscidean), 17 birds and two fishes; three additional rare equids, if accepted, would raise the number of vertebrates to 61 and of mammals to 42. The major mammalian and avian taxa in the assemblage are reviewed, especially in terms of their chronological implications. The faunal list is compared to those from other sites in the Massif Central and the nearby Saint-Vallier, resulting in Senèze being distinguished from all others as representing the MNQ 18 biochronological unit, for which it is considered to be a reference locality. The definition of that unit is discussed and clarified. Further comparison was made with selected MNQ 17–18 localities from Spain, Italy, the Netherlands and Germany. The Senèze fauna (other than *Bison* and perhaps some rare equids) is relatively homogeneous, with no

Claude Guérin—Deceased 2016.

E. Crégut-Bonnoure (✉)
Muséum Requien, Avignon, France
e-mail: evelyne.cregut1313@orange.fr

E. Crégut-Bonnoure
TRACES, UMR 5608 (CNRS-Université Toulouse 2 Jean-Jaurès), Toulouse, France

C. Guérin
Université Claude Bernard – Lyon 1, Villeurbanne, France

A. Argant · J. Argant
Aix Marseille Université, CNRS, Minist. Culture, Lampea, UMR 7269, Aix-en-Provence, France

E. Debard
Université de Lyon, UCBL, ENSL, CNRS, LGL-TPE, Villeurbanne, France

Saint-Didier-au-Mont-d'Or, France

E. Delson
Department of Vertebrate Paleontology, American Museum of Natural History, New York, NY, USA

Department of Anthropology, Lehman College of the City University of New York, Bronx, NY, USA

Ph.D. Program in Anthropology, The Graduate Center of the City University of New York, New York, NY, USA

New York Consortium in Evolutionary Primatology, New York, NY, USA

Institut Català de Paleontologia Miquel Crusafont, Barcelona, Spain

V. Eisenmann
CR2P (Paléontologie), Muséum National d'Histoire Naturelle, Paris, France

M. Faure
Université Lumière Lyon 2, Lyon, France

Université de Lyon, UCBL, ENSL, CNRS, LGL-TPE, Villeurbanne, France

B. Ménouret
Lançon-de-Provence, France

C. Mourer-Chauviré
Université de Lyon, UCBL, ENSL, CNRS, LGL-TPE, Villeurbanne, France

A.M.F. Valli
Société Scientifique du Bourbonnais, Moulins (Allier), France

Istituto Italiano di Paleontologia Umana, Anagni, Italy

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evidence for a second assemblage as suggested by some previous authors. Its base age of ca. 2.20 Ma suggests this date for the beginning of MNQ 18, but the age of the end of this unit is still under discussion.

Résumé Nos travaux de fouille sur le site de Senèze, de 2000 à 2006, avaient pour objectif de situer la faune de ce gisement important dans un cadre stratigraphique et géochronologique précis, ainsi que de retrouver de nouveaux restes d'espèces connues, et éventuellement de nouvelles espèces. Nos recherches ont conduit à la reconnaissance de six nouveaux taxons: *Dinofelis* sp., *Canis* sp., cf. *Hemitragus*, deux bovidés indéterminés et un hyaenidé indéterminé; *Ovis claudiusguerini* n. sp. a été nouvellement nommé à partir d'un spécimen précédemment indiqué comme *Ovis* sp. *Hystrix refossa* et Hyaenidae indet. (trouvés dans nos fouilles) sont de nouveaux taxons pour le site, comme le *Bison* (*Eobison*) sp., dont un fossile a été découvert par A. Consigny en surface et donné à l'équipe. Senèze est la localité type de 13 taxons de mammifères: trois genres, sept espèces et trois sous-espèces. Cinquante-huit vertébrés sont désormais recensés sur le site: 39 mammifères (un lagomorphe, quatre rongeurs, 12 carnivores, deux primates, 16 cetartiodactyles, trois périssodactyles et un proboscidien), 17 oiseaux et deux poissons; l'existence de trois autres espèces rares d'Equidae reste incertaine, mais augmenterait le nombre total des vertébrés à 61 et celui des mammifères à 42. Les principales espèces de mammifères et d'oiseaux de l'assemblage sont passées en revue, notamment pour leurs indications biochronologiques. La liste faunique est comparée à celles d'autres sites paléontologiques du Massif Central, et du gisement proche de Saint-Vallier (Drôme). Depuis plus de 40 ans Senèze est le site de référence pour l'unité biochronologique MNQ 18. La définition de cette unité est discutée et clarifiée. Une comparaison plus approfondie a été effectuée avec des sites paléontologiques attribués aux unités biochronologiques MNQ 17–18 en Espagne, en Italie, aux Pays-Bas et en Allemagne. La faune de Senèze (en dehors du bison et peut-être de quelques rares équidés) est relativement homogène, sans aucune preuve d'un deuxième assemblage comme ont pu le suggérer par le passé certains auteurs. Son âge de base est d'env. 2,20 Ma, correspondant au début de MNQ 18, mais l'âge de la fin de cette unité est encore en discussion.

Keywords MNQ 17 • MNQ 18 • Late Villafranchian • Middle Villafranchian • Mammals • Birds • Faunal lists

Mots-clés MNQ 17 • MNQ 18 • Villafranchien supérieur • Villafranchien moyen • Mammifères • Oiseaux • Listes fauniques

Introduction

The Massif Central and its margins are home to a remarkable concentration of late Pliocene and early Quaternary paleontological deposits, of which Senèze is an important reference in Plio-Pleistocene paleontology. Before the Second World War, thanks to Pierre Philis, the site yielded a series of fossil mammals of remarkable quality and diversity (see Faure et al. 2024). However, most of this material suffers from a lack of spatial and, above all, stratigraphic localization, due to the field methods of his time. As a result, the age and the homogeneity of the Senèze fauna have been debated at length. The chronostratigraphic setting of Senèze is therefore of great importance. With this in mind, the excavations of 2001–2006[1] were aimed, among other things, at finding additional fossil remains and locating them as precisely as possible in the stratigraphy, in order to propose a reliable dating.

Geological Context

The Senèze site is located in a maar, on the edge of the lake that once occupied its bottom. Here the surrounding fauna, particularly herbivores and their predators, regularly came to drink, probably over a very long period of time. The exceptional wealth of vertebrate fossils is therefore entirely logical and explainable. This maar corresponds to a highly volcanic zone, which is not without consequences for the stratigraphy of the deposit. The analysis of sedimentology and stratigraphy (Debard 2024) shows how difficult it is to establish stratigraphic correlations between the various excavation sites and suggests the sliding of slope deposits into the lake, or even of lake sediment flowing into the water. As a result, it is difficult, if not impossible, to correlate stratigraphically the various faunal elements from the Philis collections and those from the new excavations, and also to establish relative dates. In the southeast sector (Trenches 5–7), fossils are associated with coarse deposits. These are the result of the reworking of slope formations that slid into the lake during cold periods when water levels dropped. In this sector, numerous faults affect both slope deposits and lake sediments, accentuating their plunge towards the center of the maar. In contrast, in the western sector (Trenches 1 and 2, zone H8), fossils are found in clayey or loamy deposits corresponding to lacustrine sediments, marking a high lake level. These different sedimentary dynamics from one side of the maar to the other should be taken into consideration to

[1]The 2000 season was dedicated to survey and prospecting, without any excavation or collecting of fossils.

explain the presence of the oldest tephras in the southeastern sector, whereas they are more recent in the western sector, despite an altitudinal shift of a few meters.

Delson et al. (2024) interpreted $^{40}Ar/^{39}Ar$ ages (recalculated following Schaen et al. 2021) and linked paleomagnetic "columns" to date the finds from these two sectors. Fossils from the western sector ranged in age between 2.10 and 2.08 Ma, while those from the southeastern sector dated between ca. 2.20–2.18 Ma. It is likely that the fossils recovered by Philis dated within the broader 2.20–2.08 Ma interval as well, but no closer estimate can be provided.

Paleoflora

During the latest excavations, all sediment types directly related to the fauna discovered were sampled for pollen analysis, to which we must add 11 hyaenid coprolites. Out of 208 samples, only 24 preserved pollens, often in insufficient quantity for statistical analysis, so these results are essentially qualitative. Nevertheless, they provide important palynological information, as they are directly related to the fauna, without the classic risks of disturbance of lake sediments at the bottom of a maar. Palynological analysis of the paleontological sediments and hyaenid coprolites demonstrates the non-contemporaneity of these sediments with those of the Elhaï core (see J. Argant 2024).

Mammalian and Avian Fauna

Fauna from our excavations provide the essential data for precise spatial location of remains in a reliable chronostratigraphic context. However, the fauna from Pierre Philis's earlier discoveries is much more extensive and must be included in any analysis of the site's relative age. The analyses in this volume have revised several mammal groups, leading to the discovery of six new (but not fully identified) taxa (*Dinofelis* sp., *Canis* sp., cf. *Hemitragus*, two indeterminate bovids and an indeterminate hyaenid), and the better characterization of several others, including a new species dedicated to the late Claude Guérin (*Ovis claudius-guerini*). A total of 58 vertebrates has been recorded for the combined collection: 39 mammals (one lagomorph, four rodents, 12 carnivores, two primates, 16 cetartiodactyls, three perissodactyls and one proboscidean), 17 birds and two fishes (Table 17.1). Three additional equids represented only by one or two speciens each have also been tentatively recognized (Eisenmann & Delson 2024); if they are included, the totals would rise to 61 vertebrates and 42 mammals. The fauna discovered during our excavations includes 16 species: two rodents, two carnivores, 7 cetartiodactyls, three perissodactyls, one proboscidean and one fish. Three of these are new to Senèze (*Hystrix refossa*, Hyaenidae indet. and *Bison* (*Eobison*) sp.).

Table 17.1 Faunal list with indications of sources of the fauna from Senèze

Taxon	FGD[1] 2001–2006	Previous finds
Mammalia		
Lagomorpha		
Leporidae		
Oryctolagus cf. *lacosti*		x
Rodentia		
Sciuridae		
Sciuridae indet. aff. *Eutamias*		x
Arvicolidae		
Mimomys pliocaenicus–M. ostramosensis group		x
Mimomys pitymyoides (group)	x	x
Hystricidae		
Hystrix refossa	x	
Carnivora		
Felidae		
Dinofelis sp.		x
Acinonyx pardinensis	x	x
Homotherium crenatidens		x
Megantereon cultridens		x
Hyaenidae		
Chasmaporthetes lunensis		x
Pachycrocuta perrieri		x
Hyaenidae indet.	x	
Canidae		
Vulpes alopecoides		x
Nyctereutes megamastoides		x
Canis arnensis		x
Canis sp. cf. *C. etruscus*		x
Ursidae		
Ursus etruscus		x
Primates		
Cercopithecidae		
Paradolichopithecus arvernensis		x
cf. *Macaca sylvanus* (cf. *M. s. florentina*)		x
Cetartiodactyla		
Suidae		
Sus strozzii		x
Cervidae		
Metacervoceros rhenanus philisi	x	x
Croizetoceros ramosus minor		x
Eucladoceros ctenoides senezensis	x	x
Cervalces gallicus		x
Bovidae		
Antilopinae		
Gazellospira torticornis		x
Caprinae		

(continued)

Table 17.1 (continued)

Taxon	FGD[1] 2001–2006	Previous finds
Procamptoceras brivatense		x
Ovis claudiusguerini		x
cf. *Hemitragus* sp		x
Megalovis latifrons	x[2]	x
Pliotragus ardeus	x	x
Gallogoral meneghinii	x	x
Bovinae		
Leptobos furtivus	cf	x
Leptobos etruscus		x
Bison (*Eobison*) sp	x[3]	
Bovidae indet.		x
Perissodactyla		
Equidae		
Allohippus senezensis senezensis	x	x
Allohippus major	x[3]	x
Possible additional equids known from phalanges and/or metapodials:		
(1) larger than the average for *Allohippus stenonis vireti*		x
(2) cf. Valdarno *Allohippus stehlini*		x
(3) cf. small ?*Allohippus* of Pyrgos		x
Rhinocerotidae		
Dicerorhinus etruscus etruscus[4]	x	x
Proboscidea		
Elephantidae		
Mammuthus meridionalis meridionalis	x	x
Aves		
Ciconiiformes		
Ciconiidae		
Ciconia nigra		x
Anseriformes		
Anatidae		
Tadorna cf. *ferruginea*		x
Anas clypeata		x
Aythya sp.		x
Mergus cf. *merganser*		x
Mergellus sp. size of *M. albellus*		x
Anatidae indet.		x
Accipitriformes		
Accipitridae		
Haliaeetus albicilla		x
Buteo sp., size of *Buteo buteo* or *Buteo lagopus*		x
Galliformes		
Tetraonidae		
Tetrao cf. *partium*		x
Phasianidae		
Pavo bravardi		x
Alectoris cf. *graeca*		x
Gruiformes		
Otididae		
Otis sp. size of *Otis tarda*		x
Strigiformes		
Strigidae		
Bubo sp.		x
Surnia robusta		x
Passeriformes		
Turdidae		
Cf. Turdidae, size of *Turdus merula*		x
Corvidae		
Corvus corax antecorax		x
Osteichthyes		
Cypriniformes		
Cyprinidae		
Tinca sp.		x
Perciformes		
Percidae		
Perca fluviatilis	x	

[1] FGD: the Faure/Guérin/Delson fieldwork of 2001–2006

[2] One specimen of *Megalovis latifrons* was presented to our team in 2002 by A. Consigny, who recovered the fossil in parcel 263, whose stratigraphic position is unknown

[3] One specimen each of *Allohippus major* and *Bison* (*Eobison*) sp. were presented to our team in 2002 by A. Consigny, who recovered the fossils on the surface in parcel 164, from a horizon whose stratigraphic position is unknown. The latter taxon usually occurs in much younger sites

[4] Since 1993, most authors include this species in the genus *Stephanorhinus*, but we retain Guérin's allocation to *Dicerorhinus* as discussed in Chap. 10

This fauna is considered to belong to the MNQ 18 unit. Extending the biozonation of the Mediterranean Neogene based on mammals by Mein (1975, 1989), the foundations of Villafranchian biochronology, defined by Guérin (1980, 2007), are based on the analysis and comparison of mammalian faunal assemblages whose composition and evolution in different European deposits allow us to characterize several such units (MNQ = Mammal Neogene/Quaternary).

There has been significant disagreement over the distinctiveness and content of the MNQ 18 unit. We argue that there is sufficient faunal turnover between Saint-Vallier and Senèze to recognize a full MNQ unit here. Senèze is universally accepted as a reference locality for this unit.

Senèze is the type-locality for 13 mammalian taxa, three genera, seven species and three subspecies (underlined in the list that follows): *Gallogoral* Guérin, 1965; *Procamptoceras brivatense* Schaub, 1923; *Megalovis latifrons* Schaub, 1923; *Paradolichopithecus arvernensis* (Depéret, 1928); *Cervalces gallicus* (Azzaroli, 1952); *Allohippus senezensis* Prat, 1964; *Leptobos furtivus* Duvernois, 1990; *Ovis claudiusguerini* Crégut-Bonnoure, 2024; *Eucladoceros ctenoides senezensis* (Depéret, 1912 in Depéret & Mayet, 1912); *Metacervoceros rhenanus philisi* (Schaub, 1941); and *Croizetoceros ramosus minor* Heintz, 1970. *Pliotragus* Kretzoï, 1941 was named to replace *Deperetia* Schaub, 1923 (preoccupied), which was in turn named for a species (*Antilope ardea* Depéret, 1883) typified at Les Etouaires. Schaub (1923) discussed a specimen from Senèze (NMB Se 1636) which he termed the "Typus der neuen Genus" (p. 288) or "Genustypus" (p. 289), but of course no such term exists in formal nomenclature. This genus is not among those for which Senèze is the type locality.

Azzaroli et al. (1988) proposed that the Senèze maar had yielded two associations of different ages, on the basis of an

analysis of Schaub's (1943) faunal list plus original studies. These authors, however, did not cite and may not have been aware of the revision by Heintz et al. (1974). Of the taxa listed in Table 17.1, Azzaroli et al. (1988, p. 82) considered that *Cervalces* (= *Libralces*) *gallicus, Megalovis* and *Allohippus major* (= *Equus bressanus* for them) were indicative of a younger age than the "main" fauna. They also included in that category *Canis senezensis* (included by them in *C. arnensis*) and "a small equid which may possibly be *Equus stehlini*." Azzaroli et al. (1988) suggested that the larger and more speciose assemblage might date to their middle Villafranchian, while the less extensive faunule might be placed near the end of the Villafranchian as they conceived of it.

According to sites in France and across Europe (modified after Guérin 2007), MNQ 18 is characterized by:

(a) Four associations: *Gallogoral* + *Metacervoceros rhenanus philisi*; *Acinonyx* + *Megalovis latifrons*; *Pliotragus* + *Canis arnensis*; *Cervalces gallicus* + *Sus strozzii*.

(b) The presence of six well-defined evolutionary stages in diverse mammalian lineages: *Mimomys pliocaenicus*, *Allohippus senezensis senezensis, Metacervoceros rhenanus philisi, Eucladoceros ctenoides senezensis*, *Croizetoceros ramosus minor* and *Dicerorhinus etruscus etruscus* (stage II).

(c) The first appearance of seven new taxa: *Canis arnensis; Cervalces gallicus; Leptobos etruscus; Procamptoceras brivatense; Megalovis latifrons; Pliotragus ardeus;* and *Ovis claudiusguerini*. *Dinofelis* sp. and cf. *Hemitragus* sp. are also new but not well defined. Contrary to Guérin (2007), *Mimomys pliocaenicus* is common in MNQ 17, while *Felis lunensis* (= *Felis sylvestris lunensis* for some authors) only appears later in MNQ 18. The European jaguar, *Panthera gombaszogensis*, is first known in Eurasia at Slivnitsa (Bulgaria), a site which Spassov (e.g., 1998, 2000, 2023) considered equivalent in age to Senèze; this taxon's next occurrences are at Dmanisi (Georgia) dated at 1.80–1.76 Ma and Olivola (Italy, estimated to date ca. 1.9 to 2.0 Ma). It is also present at Pirro Nord (Italy, probably dating between 1.6 and 1.3 Ma, following Napoleone et al. 2003, but see below on this date). It is not known at Senèze.

Following Mein (1975), the associations are pairings of taxa characteristic of the MN(Q) unit, combining a first appearance with a last appearance. The importance of this approach has changed over time, and some researchers (e.g., Delson) think it may actually be better just to consider a group of taxa typical of the unit (combining the "associations" and the lineage stages). The new paleontological analyses confirm Senèze's attribution to MNQ 18 and provide new information for the definition of this biochron.

Review of Senèze Taxa

The carnivore fauna, very limited in the fossils from the 2001–2006 excavations, is remarkable for the presence of the complete skeletons of *Homotherium crenatidens* and *Megantereon cultridens* from earlier collections. A new taxon, *Dinofelis* sp., is added to the list (A. Argant 2024); it is present in several European Villafranchian deposits but cannot provide biochronological information due to its extreme rarity. *Acinonyx pardinensis*, already reported from the older material, is confirmed by our recent excavation. Among Hyaenidae, the giant hyena *Pachycrocuta brevirostris* is not represented at Senèze despite the presence of three different species (*Chasmaporthetes lunensis*, *Pachycrocuta perrieri*, Hyaenidae indet.). It only appeared later, after 2 Ma. *Megantereon cultridens* from Senèze was later replaced in Europe by the African *Megantereon whitei* around 1.8 Ma. *Homotherium crenatidens* from Senèze is a middle to late Villafranchian form (Sotnikova et al. 2002). It differs from the Ceyssaguet *Homotherium* (ca. 1.2 Ma) but it is little different from that at Olivola (Olivola faunal unit ca. 2.0–1.8 Ma). As for *Canis arnensis*, its arrival in Italy was around 1.9 Ma (Bartolini-Lucenti & Rook 2016). A second species of *Canis* is less well-represented at Senèze but might indicate the presence of *C. etruscus*. Compared with the Saint-Vallier assemblage, the carnivore fauna at Senèze shows some similarities. It is, however, more recent, as attested by the presence of *Nyctereutes megamastoides* instead of *Nyctereutes vulpinus* in Saint-Vallier and by levels of evolution of *Ursus etruscus* and *Homotherium crenatidens*, more recent at Senèze than at Saint-Vallier.

Senèze has yielded two primate fossils, cf. *Macaca sylvanus* and *Paradolichopithecus arvernensis*, neither from the current field work (Delson 2024). These two primates provide only slight information about the local environment or age of the site. *Macaca sylvanus* is known across much of Europe in small numbers throughout the Pliocene and Pleistocene. It may be that Senèze *Paradolichopithecus* is younger than the form at Grăunceanu (Romania, whose precise age is still unknown: MNQ 17 or MNQ 18). The macaque and *Paradolichopithecus* are moderately to highly terrestrial, respectively, and they suggest a woodland to more open environment. Senèze may be one of the youngest known occurrences of *Paradolichopithecus arvernensis*.

Only two species of Cervidae were found during our excavations: *Metacervoceros rhenanus philisi* and *Eucladoceros ctenoides senezensis* (Valli 2024). With *Croizetoceros ramosus minor*, they are characteristic of the MNQ 18 unit, and this is even truer if we limit ourselves only to cervids from deposits in the Massif Central as well as those from Saint-Vallier, which have been assigned to MNQ 17 and are at different evolutionary stages. *Cervalces*

gallicus and the elks in general make their appearance in MNQ 18; it is perhaps one of the few taxa that is only present from this time onwards. In France, it is known only from MNQ 18, but it seems to persist up to MNQ 19 in the Balkans and Caucasus.

Seven incomplete remains of Bovidae have been found during the new fieldwork, representing four species: *Pliotragus ardeus*, *Gallogoral meneghinii*, *Megalovis latifrons* and *Leptobos furtivus*. All of them are already known from Senèze, but their fragmentary state makes it impossible to compare them with material from previous collections (Crégut-Bonnoure 2024). The review of Senèze's bovid assemblage highlights the morphological variability of the samples of *Pliotragus, Gallogoral* and *Megalovis*, which suggests an evolutionary change in these species over time and more than one fossil level. However, these possible distinct levels would not be very distant in time (the whole sequence seems to extend over about 100 kyr or less), and it is not possible to distinguish successive bovid assemblages. *Bison* (*Eobison*), known from a single specimen donated to the team by A. Consigny, is younger than the other species. It was discovered on the surface and must date from the end of the Early Pleistocene.

Only one species of suid, *Sus strozzii*, is known from Senèze, and it has little biochronological impact given its long temporal range (Faure & Guérin 2024).

Two partial skeletons of equids 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, and are referred to *Allohippus senezensis senezensis* (Eisenmann & Delson 2024). Another specimen donated to the team by A. Consigny belongs to a large-bodied *Allohippus* termed *A. major*. The rich material of equids collected by Philis is not homogeneous. *Allohippus senezensis senezensis* is by far the most frequent, and in size and proportions it is intermediate between *Allohippus senezensis guthi* of La Puebla de Valverde (Spain; MNQ 17) and *Allohippus senezensis mygdoniensis* of Gerakarou (Greece; MNQ 18). *Allohippus major* is also represented in the older collection by a moderate number of postcranial elements and one tooth. There are moreover a few fossils which might represent up to three additional taxa: 2 specimens larger than the average of *A. stenonis vireti* of Saint-Vallier (MNQ 17), one similar to *Allohippus stenonis* from the Upper Valdarno and two others as small as ?*Allohippus* of Pyrgos (Greece; MNQ 19). It appears that some caballine specimens may also be 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; they are not included in our analysis.

The new excavations yielded many remains of rhinoceros. They belong to *Dicerorhinus etruscus etruscus* and are similar to the specimens coming from Philis' collections (Guérin 2024; following his view, this genus name is preferred to *Stephanorhinus*). Senèze is by far the richest locality for *Dicerorhinus etruscus.* Owing to its size and proportions, all the Senèze material is identified as belonging to evolutionary stage II of *Dicerorhinus etruscus etruscus*. Evolutionary stage I of this subspecies is known from the MN 16 locality of Les Étouaires and from Saint-Vallier (MNQ 17). Stage I thus corresponds to the early and middle Villafranchian (MN 16 and MNQ 17), while stage II corresponds to the late and final (or Epivillafranchian) Villafranchian (MNQ 18–20).

Only one proboscidean fossil, an incomplete tusk, was found during the new excavation. The revision of the material previously found at Senèze allowed the attribution of all the remains to *Mammuthus meridionalis* (Ménouret & Guérin 2024). The anatomical trends within this species distinguish several stages, recognized as subspecies. The evolutionary level of the molars and mandible from Senèze is comparable to the *Mammuthus meridionalis* from Upper Valdarno (Italy) and should accordingly be attributed to the nominotypical subspecies *Mammuthus meridionalis meridionalis*. However, the M3's collected by Boule (1892) are somewhat different. With a mixture of archaic and evolved characteristics, they are similar to the later Italian mammoth of Colle Mancino. It is not clear if this similarity implies a younger age for the Boule specimen. There is only one other M3 from Senèze, in a skull whose cranium is joined to the mandible, so the teeth are not easily seen.

Several taxa were not considered in detail in this volume. There are few rodents or other micromammals in the Senèze fauna, probably because Philis mainly searched by eye for larger specimens. As discussed briefly by Faure et al. (2024), Maul (2004) re-examined previous finds and identified the few arvicolid teeth as belonging to the *Mimomys pliocaenicus—M. ostramosensis* and *M. pitymyoides* groups. In the 2003 and 2004 field campaigns, Elvira Martín Suárez (Granada, Spain) processed quantities of sediment through a specialized screen-washing apparatus and recovered two teeth: a molar of *Mimomys pitymyoides* and an incisor of *Hystrix refossa* (which was reported by Mörs & Hugueney, 2017). Schaub (1943) also noted the presence of a sciurid (aff. *Eutamias*) and the leporid *Oryctolagus* cf. *lacosti*; there have been no recent studies of these specimens. The arvicolids indicate an Early Pleistocene age (effectively MNQ 18), following Maul and Markova (2007), although Minwer-Barakat et al. (2008) and Fejfar et al. (2011) discuss *M. pliocaenicus* in MNQ 17 (see also Tables 17.1 and 17.2).

One taxon which does not figure in our faunal list is *Hippopotamus*. Jung (1946) first suggested its presence at Senèze, but Faure and Guérin (1979) rejected that idea. They

reported that five specimens could represent this taxon (four teeth or fragments and a right IVth metacarpal), but that the preservation was unlike that of any Senèze specimen. Faure (1985) suggested that they in fact came from Chambezon, another site in Haute-Loire exploited by P. Philis in 1939 (Faure, 1982; Faure et al., 2022, p. 355). Unfortunately, the idea of a hippopotamid at Senèze continues to reappear. Mazza and Rustioni (1994) discussed a first phalanx (FSL 211082) which had previously been identified as *Equus*, but which they suggested to represent *Hippopotamus* cf. *antiquus*. Most recently, Iannucci et al. (2023) repeated that identification. However, two posterior first phalanges catalogued as FSL 211082 are discussed as *Allohippus senezensis* by Eisenmann and Delson (2024), which suggests that Mazza and Rustioni (1994) were incorrect in their allocation. In sum, there is no evidence of *Hippopotamus* in the Senèze assemblage.

As far as birds are concerned, it is not possible to consider only material from recent excavations, as these yielded only two remains, which were poorly preserved and could not be identified. The biochronological aspect can therefore only be based on material from earlier excavations (Mourer-Chauviré, 2024). The avifauna of Senèze is particularly close to that of Saint-Vallier, with several taxa in common, particularly *Pavo bravardi*. This species is also known from other, older deposits, and Senèze is the last time this large peacock was present in Europe. The avifauna at Senèze appears to be more recent than that at Saint-Vallier, with the presence of a tetraonid, *Tetrao* cf. *partium*. Tetraonidae are known in Central Europe as early as the Early Pliocene (MN 15), but in Western Europe they first appear at Senèze. They subsequently became very abundant in all Middle and Late Pleistocene deposits. Tyrberg (2022) provided additional records for birds from western and central European sites.

Comparison of Senèze with the Villafranchian Localities of the Massif Central and Saint-Vallier

Western Europe is rich in Villafranchian sites, most of which were excavated in the late nineteenth and early twentieth centuries, and their chronostratigraphic data is often imprecise. In addition, the faunas sometimes come from distinct levels that are not always identified. Some localities, such as Senèze, remain paleontological references. Analyses and syntheses based on geochronology (including paleomagnetic correlation and chronometric dating when such data are available) and biochronology provide a framework for positioning Villafranchian reference localities. We begin this analysis of relative Villafranchian biochronology at the local scale, comparing the Senèze faunal assemblage to those of the Massif Central and the nearby Saint-Vallier (Drôme) fauna. This avoids potential problems of diachronicity in the appearance and disappearance of species on a Eurasian scale.

Comparison of Senèze with these nearby Villafranchian localities (see Table 17.2) highlights the differences among the three oldest sites (from MN 16) due to the presence of taxa which are not represented in Senèze: *Mammut borsoni, Dicerorhinus jeanvireti, Procapreolus cusanus, Cervus perrieri* and *Leptobos bravardi* from Vialette (3.2–3.0 Ma; see notes to Table 17.2); *Procapreolus cusanus, Cervus perrieri, Tapirus arvernensis* from Les Étouaires (ca. 2.75 Ma, or broadly 3.1–2.6 Ma); and *Anancus arvernensis* from Rocca-Neyra (2.56 Ma). The association *Anancus arvernensis-Mammuthus meridionalis* can be seen in MNQ 17 at Saint-Vallier (approx. 2.4 Ma), Chilhac (2.28 Ma) and Le Coupet (2.27 Ma) but is not present at Senèze or in the younger sites of MNQ 19–20: Le Creux de Peyrolles (1.45 Ma), Sainzelles (1.3 Ma) and Ceyssaguet (1.2 Ma). At these, *M. meridionalis* is the only proboscidean present. Given the abundance of fossils at Senèze and the wide exploitation of the maar by Philis and our fieldwork, the absence of *Anancus* seems significant to us. As discussed above, *Pachycrocuta brevirostris* and *Panthera gombaszogensis* are absent from Senèze; the former only occurs in much later sites, while the latter occurs at Slivnitsa, close in age to Senèze but farther east. Despite some similarities, evolutionary stages of *Ursus etruscus*, *Homotherium crenatidens*, *Allohippus senezensis*, cervids and rhinoceros are different at Senèze in comparison to those of MNQ 17 localities. Furthermore five species disappear whereas nine new mammalian taxa appear: *Trogontherium cuvieri*, *Gazella borbonica*, *Anancus arvernensis*, *Tapirus arvernensis* and *Allohippus stenonis* (which appears again in MNQ 19-20) do not occur in MNQ 18, while *Dinofelis* sp., *Canis arnensis*, *Cervalces gallicus*, *Procamptoceras brivatense*, *Pliotragus ardeus*, cf. *Hemitragus* sp., *Megalovis latifrons*, *Ovis claudiusguerini* and *Leptobos etruscus* (plus *Tetrao* cf. *partium* among the birds) are new arrivals in MNQ 18 (at Senèze). These differences are significant enough to place Senèze in a MNQ unit different from MNQ 17, namely MNQ 18. The age range determined here for Senèze (ca. 2.20–2.08 Ma; Delson, 2024) suggests that the "boundary" between MNQ 17 and MNQ 18 is close to 2.2 Ma (see Fig. 17.1).

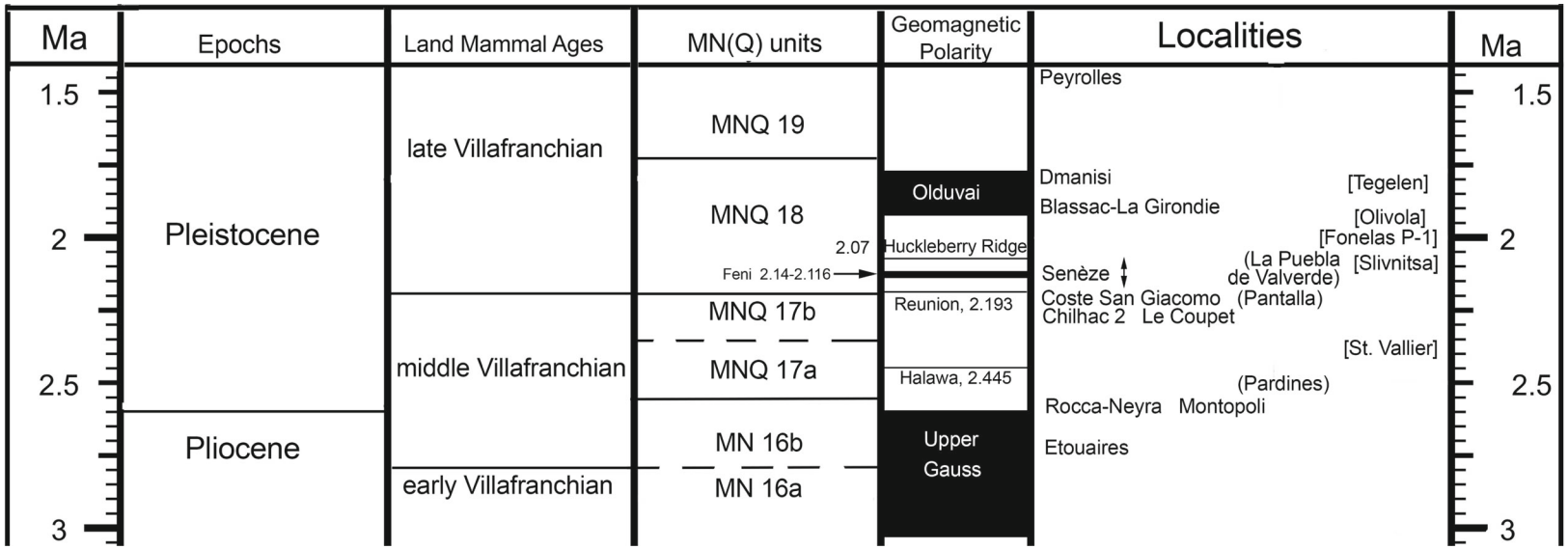

Fig. 17.1 Selected Villafranchian localities discussed in the text, placed on a magneto-biochronologic time scale. Sites indicated only by name and on the left side have chronometric dates; double-headed arrow indicates range of time represented at Senèze. Sites in parentheses and in the center are approximately or questionably dated; sites in square brackets and to the right side are placed in estimated position, as discussed in the text

Rook and Martínez-Navarro (2010, Figs. 2–3) have used the appearances and disappearances of the main lineages of large mammals to better characterize the early, middle and late Villafranchian intervals, particularly in Italy and France. In this context, they placed Senèze in the late Villafranchian, which agrees with Guérin (2007) as well. More recently, the Montopoli site has been the subject of a detailed study of large mammal biochronology in order to situate it among Pliocene and Early Pleistocene sites, using several variants of the GFRI (Genus-rank Faunal Resemblance Index) (Bartolini-Lucenti et al. 2022). The BCA (Bootstrapping Cluster Analysis) dendrogram of 58 Eurasian and African deposits shows, among other things, the close association of Saint-Vallier with Senèze and Le Coupet (Bartolini-Lucenti et al. 2022: Fig. 5, node 20). In this analysis Senèze was considered to belong in the middle Villafranchian whereas Le Coupet was considered as late Villafranchian. These decisions do not agree with our assessments above, but their work only considers genera, not species or evolutionary stages within them. Moreover, those a priori allocations do not affect the analysis. The BCA dendrogram also reveals an important geographical component among the European sites which in some cases outweighs the temporal sequencing.

In addition to providing zircon U–Pb dates for Chilhac and Le Coupet (see Table 17.2 notes), Paquette et al. (2021) published dates for the fossiliferous horizons of Blassac-La Girondie and Vazeilles. Blassac is usually considered to be an MNQ 19 site (although Kahlke et al. 2011 considered it to lie close to the MN 16/MNQ 17 boundary), with three cervids which separate it from Senèze: *Metacervoceros rhenanus* perolensis, *Eucladoceros tetraceros* (also at Vazeilles) and *Alces* cf. *carnutorum*. Paquette et al.'s (2021) date for Blassac was 1.946 ± 0.029 Ma, and on that basis they suggested the MNQ 18/MNQ 19 boundary was close to 2 Ma, much older than usually thought. Vazeilles was dated slightly younger, but its fauna is very limited and adds little to this analysis. Paquette et al. (2021) also suggested that the MNQ 17/MNQ 18 boundary could be located at 2.22 Ma, but they did not have the latest values for Senèze and only considered central French localities. It is interesting to take our analysis one step further and consider some of the most comparable localities of MNQ 17–19 age from Spain and Italy, as well as other western and central European sites.

Table 17.2 Comparison of Senèze taxa with those of Massif Central sites and Saint-Vallier

Site	Vialette	Les Etouaires	Rocca-Neyra	Pardines	Saint-Vallier	Chilhac	Le Coupet	La Rochelambert	Saint-Vidal	Senèze	Blassac-La Girondie	Peyrolles	Sainzelles	Ceyssaguet
MNQ unit	MN 16a	MN 16b	MN 16b	MNQ 17a	MNQ 17	MNQ 17b	MNQ 17b	MNQ 17	MNQ 17	MNQ 18	MNQ 18 or 19	MNQ 19	MNQ 19	MNQ 19 or 20
Age (chronometric or estimated)	ca. 3.2–3.0 Ma[1]	ca. 2.75 Ma[2]	ca. 2.56 Ma[2]	ca 2.5 Ma[3]	ca. 2.4 Ma[3]	2.285 Ma[4]	2,274 Ma[4]			2.20–2.08 Ma[5]	1.946 ± 0.029 Ma[4]	1.5–1.4 Ma[2]	1.3 Ma[6]	1.2 Ma[7]
Leporidae														
Lepus lacosti					+					cf				
Arvicolidae														
Mimomys pitymyoides										+				
Mimomys pliocaenicus					+					+				
Hystricidae														
Hystrix refossa					+	+				+				
Hystrix sp.		+												
Felidae														
Felis lunensis											sp.			
Lynx issiodorensis	+	+	+	+	+									
Lynx lynx														+
Acinonyx pardinensis					+					+				+
Homotherium crenatidens		+		+	+	+	+	+		+				+
Homotherium latidens													+	
Megantereon cultridens		+		+	+	+				+	+			+
Puma pardoides		+			+									
Dinofelis sp										+				
Panthera gombaszogensis														+
Hyaenidae														
Chasmaporthetes lunensis			+	+	+					+				
Pachycrocuta perrieri	+	+		?	+	+	+			+	+			
Pachycrocuta brevirostris													+	+
Hyaenidae indet										+				
Canidae														
Nyctereutes megamastoides		+	+	+		+				+				
Nyctereutes vulpinus					+									
Vulpes alopecoides					+	cf				+				+
Canis arnensis (=C. senezensis)										+				+
Canis sp.	+				+	+				cf. *etruscus*	*etruscus*		+	
Xenocyon lycanoides													+	

(continued)

Table 17.2 (continued)

Site	Vialette	Les Etouaires	Rocca-Neyra	Pardines	Saint-Vallier	Chilhac	Le Coupet	La Rochelambert	Saint-Vidal	Senèze	Blassac-La Girondie	Peyrolles	Sainzelles	Ceyssaguet
Ursidae														
Agriotherium sp.	+													
Ursus etruscus	+	+		+	+	+				+	+			+
Cercopithecidae														
Paradolichopithecus arvernensis	+									+				
Macaca sylvanus					+					**cf**				
Suidae														
Sus arvernensis	+	+					+							
Sus strozzii					+					+				
Hippopotamidae														
Hippopotamus major													+	
Cervidae														
Procapreolus cusanus	+	+												
Croizetoceros ramosus	*ramosus*	*ramosus*		*medius*	*medius*	+	+	*medius*	*medius*	*minor*				+
Metacervoceros pardinensis	+	+												
Metacervoceros rhenanus				*valliensis*	*valliensis*	+	*valliensis*			*philisi*	*perolensis*	*perolensis*		+
"Cervus" perrieri	+	+												
Arvenoceros ardei	+	+												
Eucladoceros sp.	**?**										*tetraceros*	+		
Eucladoceros ctenoides			*vireti*	*vireti*	*vireti*	+	*senezensis*	+		*senezensis*				+
Praemegaceros obscurus													cf	+
Cervalces gallicus										+			+	
Alces cf. *carnutorum*											+			
Bovidae					+									
Gazellospira torticornis	+		+	+	+	+	+			+				
Gazella borbonica	+	+	+	+	+			+	+					
Procamptoceras brivatense										+				
cf. *Hemitragus*										+				
Pliotragus ardeus	**?**	+	+							+				
Gallogoral meneghinii				+	+	+	+			+				
Ovis claudiusguerini										+				
Megalovis latifrons										+				
Leptobos bravardi		+												
Leptobos elatus		*elatus*	*elatus*		*merlae*									
Leptobos furtivus							+			+				
Leptobos etruscus										+	+	+		
Equidae														
Hipparion crusafonti			+											
Allohippus sp.			+											
?*Allohippus* sp. 1				+										

(continued)

Table 17.2 (continued)

Site	Vialette	Les Etouaires	Rocca-Neyra	Pardines	Saint-Vallier	Chilhac	Le Coupet	La Rochelambert	Saint-Vidal	Senèze	Blassac-La Girondie	Peyrolles	Sainzelles	Ceyssaguet
Allohippus stenonis	cf. *vireti*				*vireti* (LD3)		*vireti*					cf. *vireti*	cf.	several subsp.
Allohippus senezensis						*guthi*				*senezensis*	+			
Allohippus other							+			1–3 Taxa				
Allohippus major and/or very large *Equus*										+	+			
Equus cf. *granatensis*							+							
Rhinocerotidae														
Dicerorhinus jeanvireti	+	+												
Dicerorhinus etruscus etruscus		stage I		+	stage I	+		+	+	stage II	+		+	
Tapiridae														
Tapirus arvernensis	*arvernensis*	*arvernensis*					+							
Mammutidae														
Mammut borsoni	+	+												
Gomphotheriidae														
Anancus arvernensis	+	+	+	+	*falconeri*	*chilhiacensis*	*falconeri*	+	+					
Elephantidae														
Mammuthus meridionalis					+	+	+		+	*meridionalis*	+		+	+
Aves														
Phalacrocoracidae														
Phalacrocorax carbo														+
Ciconiidae														
Ciconia nigra					+					+				
Anatidae														
Cygnus cf. *cygnus*					+									
Anser sp.						+								
Tadorna cf. *tadorna*						+								
Tadorna cf. *ferruginea*										+				
Anas clypeata										+				
Aythya sp.										+				
Bucephala cereti						+								
Mergus cf. *merganser*										+				
Mergellus sp. size of *M. albellus*										+				
Accipitridae														
Aquila claudeguerini														+
Accipiter gentilis														+
Haliaeetus albicilla					+					+				

(continued)

Table 17.2 (continued)

Site	Vialette	Les Etouaires	Rocca-Neyra	Pardines	Saint-Vallier	Chilhac	Le Coupet	La Rochelambert	Saint-Vidal	Senèze	Blassac-La Girondie	Peyrolles	Sainzelles	Ceyssaguet
Buteo sp.										+				
Tetraonidae														
Tetrao cf. *partium*										+				
Phasianidae														
Pavo bravardi					+					+				
Alectoris cf. *graeca*										+				
Otididae														
Otis sp					+					+				
Strigidae														
Bubo sp										+				
Surnia robusta										+				
cf. Turdidae, size of *Turdus merula*										+				
Corvidae														
Corvus pliocaenus														+
Corvus corax antecorax					+					+				

[1] Vialette is a complex maar with a possibly long interval represented (as at the nearby Senèze). Bandet et al. (1978) and Couthures (1979) provide a simplified stratigraphic overview. Savage and Curtis (1970) offered an early K–Ar date of 3.8 Ma for a lava said to overlie the fauna; this date was only given in a table with no further details. Bandet et al. (1978) dated a number of carefully selected samples from across the Vialette region. Five of these yielded a mean age of 3.3 ± 0.11 Ma for a basalt flow underlying the fauna. Two others from a flow overlying the mammals provided a mean date of 2.6 ± 0.2 Ma. Biquand et al. (1981) reported a normal geomagnetic polarity near the level with fossils, as well as a fission-track date of 3.14 ± 0.6 Ma from the fossiliferous horizon (note the large error range); they also dated an overlying basalt at 2.9 ± 0.05 Ma but noted a probable loss of potassium and suggested the date was not reliable. Fouris et al. (1991) dated a basanite flow underlying the fossils at 3.07 ± 0.08 Ma. These early K–Ar dates cannot readily be converted to modern standards (see Delson et al. 2024), and the ages must be considered approximations. Lacombat et al. (2008) updated the Vialette fauna and accepted the 3.3 Ma date as preceding the fauna while 3.14 Ma was thought to date it; no other dates were mentioned. Taken together, these data suggest an age for the Vialette fauna roughly between 3.3 and 3.0 Ma, with the normal interval perhaps the middle Gauss normal (C2An.2n), 3.21–3.12 Ma. Other evidence suggests that MN 16 begins after 3.2 Ma, which shortens the age range for Vialette

[2] The Les Étouaires fauna on the Perrier plateau is usually considered a reference fauna for the 16b unit. The stratigraphy and history of study of the Perrier region is discussed in detail by Pastre (2004). Savage and Curtis (1970) reported a K–Ar date of 3.4 Ma on an ash supposedly below the Les Etouaires fauna and a whole-rock date of 3.5 Ma said to be correlative with the fauna. Numerous other dates were published by various authors with conflicting links to the faunas. Biquand et al. (1990) summarized these to show the Les Etouaires fauna lay between dates of 2.4 and 2.5 Ma, just above a normal to reversed paleomagnetic transition (documented by only a few samples) correlated to the Gauss/Matuyama boundary. Pastre (2004) reviewed additional dates and suggested that the Les Etouaires fauna was in fact younger than 2 Ma. The Perrier sequence was re-dated by Nomade et al. (2014), who (in collaboration with Pastre) obtained a concordant series of dates (recalculated here following Schaen et al. 2021) including 2.74 ± 0.02 Ma underlying or equivalent to the Les Etouaires faunal level. Iannucci and Sardella (2023) have questioned this date, noting that the Les Etouaires fauna probably derived from several different horizons, not just the Côte d'Ardé dated by Nomade et al., and thus could only be bounded by an underlying date of 3.07 ± 0.05 Ma and the overlying date of 2.56 ± 0.02 Ma (both recalculated) for the Rocca-Neyra faunal assemblage. Pending further analysis of the provenance of the Les Etouaires fossils, the fauna can be dated between 3.1 and 2.6 Ma, perhaps close to 2.75 Ma. Few if any European sites with large mammals are solidly dated between 3.1 and 2.8 Ma, so no further comparisons are possible. The highest faunal level of the Perrier complex, le Creux de Peyrolles, was dated by Nomade et al., (2014, recalculated) at 1.45 ± 0.03 Ma

[3] The Perrier-Pardines fauna lies slightly above that of Rocca-Neyra, suggesting an age close to 2.5 Ma. In turn, Saint-Vallier is usually thought to be faunally younger than or close to Pardines but older than Chilhac (Guérin et al. 2004). Its age may be estimated close to 2.4 Ma

[4] Chilhac (localities 2 and 3) has been dated several times with improving results. Boivin et al. (2010) K–Ar dated an underlying lava at 2.47 ± 0.1 Ma and an overlying lava at 1.8 ± 0.2 Ma. Nomade et al. (2014) dated an overlying tephra at 2.344 ± 0.03 Ma (recalculated). Paquette et al. (2021) U–Pb dated zircons from the fossiliferous layer of Chilhac 2 at 2.285 ± 0.046 Ma. Le Coupet was first dated by Savage and Curtis (1970), who reported a K–Ar date of 1.9 Ma, presumably on an overlying horizon. Fouris et al. (1991) dated an underlying lava not directly linked to the fauna at 2.12 ± 0.09 Ma (this date cannot be recalculated due to lack of details provided. Paquette et al. (2021) dated zircons from the Le Coupet fossiliferous slope deposits at 2.274 ± 0.032

[5] As discussed by Delson et al. (2024), Senèze faunal elements recovered by the FGD team date between 2.2–2.08 Ma, with fossils known between 2.2–2.18 Ma and 2.1–2.08 Ma and probably inbetween

[6] Thouveny and Bonifay (1984) placed the Sainzelles fauna in a reversed interval between the top of the Olduvai subchron and a K/Ar date of 1.4–1.3 Ma. Bonifay and Brugal (1996) erroneously reported that as 1.4 Ma. Kahlke et al., (2011, Fig. 17.1) charted the site close to 1.3 Ma (just older than Ceyssaguet), but without any discussion in the text. Palombo (2016, Fig. 17.1), on the other hand, charted it possibly slightly younger than Ceyssaguet, ca. 1.1 Ma, but again without discussion

[7] Croitor and Bonifay (2001) stated that Ceyssaguet is located on the slopes of a volcano whose last eruption was K–Ar dated at 1.3 Ma and estimated that the overlying faunal level might date to 1.2 Ma. Later, Mourer-Chauviré and Bonifay (2018) reported an unpublished K–Ar age of 1.4 Ma for the underlying basalt and suggested that the maar infilling might have taken 200 kyr, resulting in an approximate date for the fauna of 1.2 Ma

Table 17.3 Comparison of Senèze taxa with those of similar age (MNQ 17–18) from Spain, Italy, Netherlands and Germany

Site	Coste San Giacomo	Pantalla	La Puebla de Valverde	Senèze	Huélago	Olivola	Fonelas P1	Tegelen	Erpfingen
MNQ unit	MNQ 17b	MNQ 17b	MNQ 17	MNQ 18	MNQ 18	MNQ 18	MNQ 18	MNQ 18	MNQ 18
Age (chronometric or estimated)	2.23 ± 0.03 Ma	2.23 ± 0.18 Ma	ca. 2.0 or 2.3	2.20–2.08 Ma		??2.0–1.8 Ma	ca. 2 Ma	ca. 1.8 Ma	
Arvicolidae									
Mimomys pitymyoides				+				+	
Mimomys pliocaenicus	+			+				+	+
Hystricidae									
Hystrix refossa	+			+					+
Felidae									
Felis lunensis						+			
Lynx issiodorensis		+	+			+			
Lynx pardinus spelaeus							+		
Acinonyx pardinensis		+	+	+		+	+		
Homotherium crenatidens				+			+		
Homotherium latidens	sp.		+			+			
Megantereon cultridens			+	+		+	+		
Puma pardoides			+						
Dinofelis sp				+					
Panthera gombaszogensis						+		+	+
Hyaenidae									
Chasmaporthetes lunensis			+	+		+			*lunensis*
Pachycrocuta perrieri	?		+	+				+	+
Pachycrocuta brevirostris						+	+		
Hyaenidae indet				+					
Hyaena (Parahyaena) brunnea							+		
Canidae									
Nyctereutes megamastoides			+	+					
Nyctereutes vulpinus			+						
Vulpes alopecoides	cf	sp.		+		+	+		
Canis arnensis (=C. senezensis)				+					
Canis sp.	sp.								
Canis etruscus	cf	+		cf		+	+		+
Canis accitanus							+		
Xenocyon falconeri			cf				+		
Ursidae									
Ursus etruscus	cf		+	+		+			
Cercopithecidae									
Paradolichopithecus arvernensis			cf	+					
Macaca sylvanus	+		+	cf				+	
Suidae									
Sus strozzii	+	+		+		+		+	
Potamochoerus magnus							+		
Hippopotamidae									
Hippopotamus sp.	sp								
Cervidae									
Croizetoceros ramosus	cf		*pueblensis*	*minor*	+				+
"Cervus" lyra	+								
Metacervoceros rhenanus			+	*philisi*			cf. *philisi*	+	cf. *philisi*
Eucladoceros sp.	+					+	+		
Eucladoceros ctenoides			*vireti*	*senezensis*	*senezensis*			*tegulenis*	*tegulenis*
Cervalces gallicus				+		+			+
Cervus nestii		+				+			+
Giraffidae									
Mitilanotherium sp.					+		+		
Bovidae									
Gazellospira torticornis	+		+	+	+		*hispanica*		+
Gazella borbonica	+		+		+				
Gazella							+		
Procamptoceras brivatense				+		+			

(continued)

Table 17.3 (continued)

Site	Coste San Giacomo	Pantalla	La Puebla de Valverde	Senèze	Huélago	Olivola	Fonelas P1	Tegelen	Erpfingen
cf. *Hemitragus*				+					
?Capra/Hemitragus							+		
Hesperidoceras merlae			+						
Pliotragus ardeus				+					
Gallogoral meneghinii	+		*pueblensis*	+		+			cf
Ovis claudiusguerini				+					
Megalovis latifrons				+					+
Praeovibos sp.							+		
Parabos soriae					+				
Leptobos elatus		*merlai*			+	*merlai*	*merlai* (or *furtivus*)	+	
Leptobos furtivus				+					
Leptobos etruscus	sp.			+			+		
Equidae									
Allohippus stenonis	+	+	*guthi*						
Allohippus senezensis				*senezensis*					
Allohippus other				1–3 Taxa					
Allohippus major and/or very large *Equus*				+			cf		+
Allohippus large and slender								+	
Onager-like equid					+				
Rhinocerotidae									
Dicerorhinus etruscus etruscus	sp.		+	Stage II			+	+	+
Gomphotheriidae									
Anancus arvernensis	+								
Elephantidae									
Mammuthus meridionalis	+	cf	+	*meridionalis*	+		+	+	+
Aves									
Ciconiidae									
Ciconia nigra				+					
Anatidae									
Tadorna cf. *ferruginea*				+					
Anas clypeata				+					
Aythya sp.				+					
Mergus cf. *merganser*				+					
Mergellus sp., size of *M. albellus*				+					
Accipitridae									
Aquila cf. *chrysaetos*			+						
Haliaeetus albicilla				+				+	
Buteo sp				+					
Tetraonidae									
Tetrao cf. *partium*				+					
Tetrao praeurogallus									+
Phasianidae									
Pavo bravardi				+					
Alectoris cf. *graeca*				+					
Gruiformes sp.							+		
Gruidae									
Grus cf. *grus*			+						
Otididae									
Otis sp				+					
Columbidae sp.							+		
Strigidae									
Bubo sp				+					
Surnia robusta				+					
cf. **Turdidae**, size of *Turdus merula*				+					
Corvidae									
Corvus corax antecorax				+					
Corvus cf. *corax*			+						

Comparison of Senèze with the Later Villafranchian Localities of Italy, Spain, the Netherlands and Germany

As indicated in Table 17.3, several of these sites have yielded chronometric age determinations. Coste San Giacomo (Italy) is clearly in MNQ 17, with *Anancus* and *Mammuthus* alongside *Axis (=?Cervus) lyra* and a range of mostly fragmentary remains of MNQ 17–18 taxa (Bellucci et al. 2014). Spassov (e.g., 2016, 2023) has proposed to include Coste San Giacomo in an early MNQ 18a subunit, along with Senèze and Slivnitsa, but the date and presence of *Anancus* keep Coste San Giacomo in MNQ 17. *Allohippus stenonis* might also suggest MNQ 17 but could just be a marker of an Italian site. Florindo et al. (2021) reported an argon-argon age of 2.233 ± 0.032 Ma, which is recalculated here to 2.228 ± 0.032 Ma, rounded to 2.23 ± 0.03 Ma. This seems to be the youngest date for any definitive MNQ 17 assemblage and fits well with the idea of beginning MNQ 18 at 2.2 Ma.

Pantalla (Italy) has an even more limited fauna, including a number of "Italian" taxa in common with Olivola and other cosmopolitan species. Cherin et al. (2023) placed the assemblage close to the middle-late Villafranchian "boundary" but included it as well as Senèze in MNQ 17b. It seems most likely an MNQ 17 locality as interpreted in this chapter. It was ESR/U-series dated to 2.227 ± 0.177 Ma by Cherin et al. (2023), with the possibility of a slightly older age from another sample. This date corresponds closely to Coste San Giacomo.

Olivola (Italy) has yielded a more extensive fauna but not a clear date. The assemblage is broadly similar to that from Senèze and lacks definitive MNQ 17 taxa such as *Anancus*. Following detailed paleomagnetic calibration of the Upper Valdarno faunal sequence (e.g., Napoleone et al. 2003), Olivola was considered to predate the oldest Valdarno assemblage, from Matassino (within the Olduvai subchron) and estimated to date roughly between 2 and 1.8 Ma. It would thus fall later in MNQ 18. It is worth noting that Bartolini-Lucenti et al. (2022) erroneously included *Anancus* at Olivola in their supplementary table of genera at sites in their analysis. Recently, however, Mattei et al. (2023) have suggested that the Matassino and other Upper Valdarno mammal paleofaunas might be less definitively dated by paleomagnetic correlation, due to problems with the mineral carrying the magnetic signal. Their arguments appear solid, but further analysis is required: for the moment, precise ages of the later Upper Valdarno faunal units must be reconsidered, although they probably span 2.0–1.3 Ma.

La Puebla de Valverde (Spain) has long been considered an MNQ 17 locality with a fauna similar to that of Saint-Vallier and Chilhac (Sinusía et al, 2004). In an analysis of their paleomagnetic results, Sinusía et al. (2004) suggested that the fossil mammals occurred above a short normal interval correlated to what is now the Feni subchron, dated ca. 2.140–2.116 Ma and below the base of the (not seen) Olduvai at 1.935 Ma. This would be younger than Senèze and far too young if the fauna were equivalent to Chilhac. One possibility is that some of the Spanish taxa persisted longer than in southern France and Italy , such as *Eucladoceros ctenoides vireti*, *Allohippus stenonis guthi*, *Metacervoceros rhenanus ?valliensis* and *Croizetoceros ramosus pueblensis* (a form close to that from Saint-Vallier). Alternatively, the short normal could be correlated to the Halawa (= X) excursion at ca. 2.445 Ma (see Ogg 2020), in which case the fauna would fall between that and the Feni, around 2.3 Ma, well within MNQ 17.

Still younger sites usually included in MNQ 18 (Huélago and Fonelas P-1, Spain) yield species not found at Senèze or other localities, such as *Pachycrocuta brevirostris*, *Hyaena brunnea*, *Potamochoerus magnus*, *Gazella* spp. and *Praeovibos* sp. Fonelas P-1 was suggested to date ca. 2 Ma (Arribas et al. 2009), thus close to Olivola. The age of Tegelen (Netherlands) has been contentious, perhaps implying several different assemblages among the collections under this name, but some of the taxa are surely MNQ 18, as is also true of the comparably-aged Erpfingen (Germany). They are often suggested to date close to 1.8 Ma, but that would contradict Paquette et al.'s (2021) contention that MNQ 19 began close to 2.0 Ma. An alternative interpretation could place Blassac-La-Girondie later in MNQ 18 than Senèze, but not in MNQ 19; its three "late" cervids are unique to this site and are not found in younger MNQ 19 assemblages. The youngest locality often included in MNQ 18 may be Dmanisi (Georgia). Despite some analogies of the fauna (Kahlke et al. 2011), it is now dated firmly at 1.80–1.76 Ma (Ferring et al. 2022), which would suggest MNQ 19 might begin between 1.75–1.70 Ma. In Bulgaria, Slivnitsa is an important site of the Balkans which is close to Senèze in terms of fauna, perhaps the most similar of any known site (Spassov 1997, 2003, 2016; Spassov & Crégut-Bonnoure 1999). The two localities belong to the same biozone, but the evolutionary differences/stages of the bovids indicate a small biochronological difference or a geographical difference (Crégut-Bonnoure 2024). Spassov (2003, 2016) proposed the creation of subzone MNQ 18a including these two localities, but we do not recognize this distimction here. Further analyses of a wider range of sites than examined here (and additional dates) are required to resolve these questions.

Conclusions

The systematic study of the Senèze fauna collected by Pierre Philis led to the discovery of seven new species: *Canis* sp., *Dinofelis* sp., an indeterminate hyaenid, cf. *Hemitragus* sp., *Ovis claudiusguerini* (previously *Ovis* sp.) and two indeterminate bovids. The mammalian fossils recovered during our excavations, although few in number, mostly represent taxa known from the earlier collections: *Mimomys pitymyoides*, *Acinonyx pardinensis*, *Allohippus senezensis senezensis*, *Metacervoceros rhenanus philisi*, *Eucladoceros ctenoides senezensis*, *Pliotragus ardeus*, *Gallogoral meneghinii*, *Megalovis latifrons*, *Leptobos furtivus*, *Dicerorhinus etruscus* and *Mammuthus meridionalis*. Three new taxa for Senèze come from our fieldwork: *Hystrix refossa,* Hyaenidae indet. (distinct from the *Chasmaporthetes* and *Pachycrocuta* lineages) and *Bison* (*Eobison*) sp. (the last is a surface find presented to the team by A. Consigny and probably representing a younger horizon than the rest of the fauna).

Despite similarities with MNQ 17 faunas from the Massif Central and Saint-Vallier, there are some major differences at Senèze (as detailed above): disappearance of five mammalian species and appearance of nine new ones (plus one bird). In addition, the "evolutionary stages" (mainly subspecies) of five cervid and perissodactyl species confirm the attribution of the Senèze fauna to MNQ 18, at the beginning of this unit.

The bulk of the fauna is relatively homogeneous, with no evidence for more than one assemblage (contrary to the proposal of Azzaroli et al. 1988). Tentative evidence suggests some intraspecific evolutionary change in *Pliotragus*, *Gallogoral* and *Megalovis*. The site saw several episodes of sedimentation between ca. 2.20 and 2.08 Ma, resulting in a pattern of isolated bones on the slopes of the maar or clusters of elements on the lakeshore. The western sector preserves a lakeshore with terrestrial elements, hyena coprolites and fish remains in the excavated Trenches 1 and 2. The southeastern sector (Trenches 5–7) represents slope deposits from a colder interval of low lake level. In both areas, animals likely slipped into the lake and drowned when unable to climb out (Debard 2024; Fernández-Jalvo et al. 2024). The result was a 100+ kyr interval as a natural trap for the mammals and birds living around the lake, characterized by rapid sedimentation allowing quick fossilization and good preservation of this remarkable fauna, which corresponds to the beginning of MNQ 18 (and the late Villafranchian) about 2.2 Ma in the Early Pleistocene around the Feni subchron.

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