# Chapter 19
# Summary and Conclusions of the Senèze Research Project

Eric Delson, Claude Guérin, Martine Faure, Luca Aprile, Alain Argant, Jacqueline Argant, Jean-Jacques Bahain, Federica Candelato, Evelyne Crégut-Bonnoure, Evelyne Debard, Véra Eisenmann, Christophe Falguères, Yolanda Fernández-Jalvo, Jean Gaudant, María Dolores Marín-Monfort, Bernard Ménouret, Angélique Monguillon, Cécile Mourer-Chauviré, Luca Natali, Sébastien Nomade, Fabio Parenti, Jean-François Pastre, María Dolores Pesquero-Fernández, Vittorio Rioda, Sevket Sen, Qingfeng Shao, and Andrea M. F. Valli

**Abstract** The new fieldwork at Senèze ran from 2000 to 2006, with the goals of clarifying the age, stratigraphy and taphonomy of Senèze, as well as finding additional remains, especially of the less well-known taxa. Here we summarize the findings of each chapter and discuss their broader implications. Four geological chapters consider field methods, stratigraphy, volcanology and tephra mineralogy and dating. Following a chapter on palynology, two chapters discuss non-mammalian paleontology: ichthyology and ornithology. Eight chapters cover work on the fossil mammals. The chapter on biochronology places Senèze among other sites at the start of MNQ 18. Based on that work and the mammal chapters, it is possible to review the relative frequency of mammalian families in the total Senèze assemblage. Of some 2200 specimens, over half are cervids, with bovids, rhinocerotids and equids far behind. According to data from palynology and the habitat preferences of the more common mammals, the paleoenvironment around the Senèze maar would have included forest, woodland and grassland, perhaps in a warmer and moister climate than

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Claude Guérin—Deceased 2016.
Jean Gaudant—Deceased 2015.

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E. Delson (✉)
Department of Vertebrate Paleontology, American Museum of Natural History, New York, NY, USA
e-mail: eric.delson@lehman.cuny.edu

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, Universitat Autònoma de Barcelona, Cerdanyola del Vallès, Barcelona, Spain

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

M. Faure
Université Lumière-Lyon 2, Lyon, France

M. Faure · E. Debard · C. Mourer-Chauviré
Université de Lyon, UCBL, ENSL, CNRS, LGL-TPE, Villeurbanne, France

L. Aprile
Associazione Aditus in Rupe, Floridia, SR, Italy

A. Argant · J. Argant
LAMPEA, UMR 7269 CNRS, MMSH, Université Aix-Marseille, Aix-en-Provence, France

J.-J. Bahain · C. Falguères
Département Homme et Environnement, UMR 7194 HNHP (MNHN-CNRS-UPVD), Muséum National d'Histoire Naturelle, Paris, France

F. Candelato
3A soc. coop, via Campofiore 33, 37129 Verona, Italy

E. Crégut-Bonnoure
Muséum Requien, Avignon, France

TRACES, UMR 5608 (CNRS—Université Toulouse 2 Jean-Jaurès), Toulouse, France

E. Debard
25 rue Paul Chevrel, 69370 Saint-Didier-au-Mont-d'Or, France

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

Y. Fernández-Jalvo · M.D. Marín-Monfort · M.D. Pesquero-Fernández
Museo Nacional de Ciencias Naturales (CSIC), Madrid, Spain

J. Gaudant
Université Paris 7, Paris, France

B. Ménouret
3 rue de l'Amouroy, 13680 Lançon-de-Provence, France

A. Monguillon
Réserve Naturelle Régionale du site géologique de Limay, Limay, France

L. Natali · F. Parenti · V. Rioda · Andrea M. F.Valli
Istituto Italiano di Paleontologia Umana, Anagni, FR, Italy

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today. Taphonomic studies revealed that bones often rested a long time under water, lacked any indication of carnivore attack and often displayed pathologies in their joints. Combining these results and those from stratigraphy, it is proposed that most associated skeletons were preserved after large mammals fell into the lake and drowned without being disturbed.

**Résumé** Les nouveaux travaux de recherche à Senèze se sont déroulés de 2000 à 2006, avec pour objectifs de clarifier la stratigraphie, l'âge et la taphonomie du gisement, ainsi que de mettre au jour de nouveaux fossiles, plus particulièrement ceux des espèces les moins bien représentées. Nous résumons ici les conclusions de chaque chapitre et discutons de leurs implications plus larges. Quatre chapitres présentent tour à tour nos méthodes de fouille et de relevés topographiques, la stratigraphie, la volcanologie et la minéralogie des téphras, et les datations. Un chapitre traite ensuite de palynologie, deux autres de paléo-ichtyologie et paléo-ornithologie. Huit chapitres concernent les mammifères fossiles. L'étude biochronologique nous conduit à placer le gisement de Senèze, parmi d'autres sites, au début de MNQ 18. À partir de ce travail et des études des mammifères, il est possible de revoir la fréquence relative des différentes familles de mammifères dans l'assemblage faunique total du gisement. Sur quelques 2200 spécimens, plus de la moitié sont des Cervidés suivis, loin derrière, par les Bovidés, les Rhinocérotidés et les Equidés. Selon les données palynologiques et les préférences d'habitat des mammifères les plus communs, le paléoenvironnement autour du maar aurait été un paysage en mosaïque avec des zones boisées et de prairies, peut-être dans un climat plus chaud et plus humide que celui d'aujourd'hui. L'étude taphonomique a révélé que les os sont restés souvent assez longtemps dans l'eau, que certains présentaient des stigmates de pathologies articulaires, et qu'ils ne portaient aucune trace de carnivore. En combinant ces données et ceux de la stratigraphie, nous en déduisons que la plupart des squelettes retrouvés en connexion anatomique sont ceux d'animaux noyés dans le lac, qui ont été conservés grâce à l'absence de perturbations post-mortem.

**Keywords** Dating • Faunal composition • Mammal paleontology • Stratigraphy • Site formation • Taphonomy

**Mots-clés** Datation • Composition faunique • Paléontologie des mammifères • Stratigraphie • Formation du gisement • Taphonomie

## Background

The Early Pleistocene fossil mammal site of Senèze (Haute-Loire, France) was first discovered in 1892, when scholars from the region heard about a chance find and contacted Marcellin Boule of the Muséum national d'Histoire naturelle, in Paris. Boule (1892) reported the excavation of a proboscidean skeleton and other mammalian fossils. A young peasant from Senèze, Pierre Philis, was drawn by this find to a search for mammal fossils on his land and over the next half-century recovered many fossils including numerous partial skeletons which he sold to curators in Paris, Lyon and Basel. The details of Philis' life were presented by Faure et al. (2022) and are summarized in Chap. 1 of this book (Faure et al. 2024). After Philis' death in 1942, only a few short field campaigns were undertaken at Senèze in the twentieth century, although many fossils from the site were described and analyzed.

In 1999, Martine Faure, Claude Guérin and Eric Delson met at a field conference on Lesvos (Greece; see the preface) and agreed to collaborate on new field and laboratory research in hopes of clarifying the age, stratigraphy and taphonomy of Senèze, as well as finding additional remains, especially of the less well-known taxa. A short exploratory season of survey and introduction in 2000 was followed by six seasons of intensive excavation, stratigraphic analysis and sampling for dating, paleomagnetic records, palynology and taphonomy (details in Faure et al. 2024). Chapters 2–18 report the results of this work, and we summarize the major findings and implications here.

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S. Nomade
Laboratoire des Sciences du Climat et de l'Environnement, CEA Saclay, LSCE/IPSL, UMR CEA-CNRS-UVSQ, 8212 Gif sur Yvette, France

F. Parenti
Universidade Federal do Paraná, Curitiba, PN, Brazil

J.-F. Pastre
23, rue de l'Eglise, 93370 Montfermeil, France

Laboratoire de Géographie Physique, Environnements quaternaires et actuels, UMR 8591, CNRS, Thiais, France

Q. Shao
College of Geography Science, Nanjing Normal University, Nanjing, China

Andrea M. F.Valli
Société scientifique du Bourbonnais, Moulins (Allier), France

## Physical (Abiotic) Geology

In Chap. 2, Parenti et al. (2024) discuss the approach to survey and excavation techniques employed during our fieldwork. Recent widespread adoption of digital surveying and data recording techniques in paleontological and archaeological sites has transformed not only the daily routine of fieldwork but also the relationship among excavation, observation and interpretation. In the Senèze campaigns the field team included some specialists who already had worked on the middle Villafranchian site of Saint-Vallier between 1995 and 1999 (Faure & Guérin 2004), with some technical improvements, such as automatic recording of polar coordinates by total station and GIS elaboration in the field by digital camera. The Senèze maar was documented with good topographic and cadastral maps, but they were not adequately detailed for microrelief, vegetation cover, rural paths and local power lines. Stratigraphy and taphonomy require a very careful description of each sedimentary body, with a centimetric tolerance. Therefore, each targeted parcel (hereditary land unit) was surveyed at a 1:500 scale, drawing it at a 1:1,000 scale. For altimetric reference, they chose the 606 m a.s.l. point close to the village of Senèze; for planimetry a polygonal net was established with a Topcon GTS 229 total station and for topographic description a Breithaupt transit alidade with plane table was utilized, allowing manual drawing in the field. Digitization of contour lines was performed with *Topografia & Strade* software from Software Tecnico Scientifico. The positions of fossils and samples were plotted by total station and transferred to *ArcGIS* mapping software (ESRI). Detailed topographic recording of each fossil accumulation or remarkable isolated pieces was performed by direct drawing at a 1:10 scale and vertical digital photographs rectified by a GIS georeferencing module. Hand excavation and macrovertebrate collecting by "natural layers" followed removal of the topsoil with a backhoe, creating trenches. Students and other volunteer excavators were trained to draw the stratigraphy of these trenches to scale by using a grid placed against the exposed trench surface and drawing the visible contents of each grid square. Because of the good preservation of fossils, short or massive bones were recovered without any additional treatment. Fragile specimens were removed in plaster jackets. Based on the Senèze experience, Parenti et al. evaluated pros and cons of multiple techniques for recording the precise position of any piece of evidence, no matter its size, for the future understanding of its natural history. Two main methodological conclusions are: (1) optical and digital devices (levels, theodolites, tacheometers and total stations) are very precise and sophisticated but insufficient for the description of the landscape. (2) The growing availability of computer-assisted drawing (designed for engineering) is rapidly blurring any residual capacity of observation and understanding via the manual reproduction of forms and dimensions. As a synthesis, they present an evaluation of data recording techniques and sampling strategies in different kinds of unlithified fossil deposits.

Geological study (Chap. 3, Debard 2024) focused on the excavated trenches, enabling a detailed stratigraphic study of the layers exposed at Senèze, which clarified the nature and geometry of the deposits. Work was concentrated on two sectors of the maar, a western area excavated in the first years of study and a southeastern zone emphasized in the last three years. The trenches were numbered T1 to T9, and the layers distinguished were named alphabetically by trench (with numeric subdivisions in some cases), e.g., T2h, [T2] hi2; groups of such layers were combined into numbered "sets" with common origin. Some trenches were excavated in two sections, an upper ("sup") and lower ("inf"), but those indications did not necessarily agree with relative stratigraphic position, given local dip and faulting. Additional work was carried out on naturally exposed sections, some named (such as the "Philis ravine" where P. Philis recovered numerous fossils) and others identified by letter (e.g., section A). Detailed scaled drawings are presented for each trench or section studied, including positions of samples taken for palynology, magnetostratigraphy and tephra mineralogy (including dating).

After the emplacement of phreatomagmatic products linked to the formation of the maar, slope deposits, incorporating elements of the basement and products ejected by the maar, are organized in prograding lenses towards the center of the crater, following a slope of 15–20°. They form sedimentary bevels characteristic of maar lake margins. In the western sector, the first lacustrine deposits appear at elevation 625 m, in T2, where they thicken rapidly (set 2 = T2h) and have been recognized down to elevation 620 m, the lower limit of this trench. Trench T1 shows mainly slope deposits; lacustrine levels appear at around 621 m, with a thickness less than that of T2 (less than one meter); they only become more widespread towards the 616 m mark. In the south-east sector, slope formations predominate in T4, T8, T9 and T5 sup, at the same height as the lacustrine levels in trench T2. The highest lacustrine level was observed in T7 sup at 619.50 m, i.e., practically at the same altitude as the base of T2. Lake sedimentation becomes continuous at around 617.50 m, i.e., at about the same height as in trench T1. Trenches T6 and T7 inf show only lacustrine sediments, as they were dug below this elevation, marking the generalization of lacustrine levels.

From one sector to the next, and even from one trench to the next, there is great variability in the organization and nature of the deposits. Several hypotheses can be proposed to explain these rapid facies changes.

The morphological context has clearly led to an evolution in sedimentation around the crater rim. Coastal bevels were built in the less steep areas. Slightly marked thalwegs have channelled colluvium, as in the case of Trench 4.

The formations outcropping around the crater also influenced the nature of the deposits below. Those in the western sector were largely fed by a slag cone in the form of stones, gravel and red grains, present in all layers. The phreatomagmatic tuffs produced much of the fine material, but also boulders, such as the one visible in the western part of section A. On the southeastern side, on the other hand, the sediments were largely fed by erosion of the gneissic basement.

Syn- and post-sedimentary reworking resulted in several types of modifications. Load, stretch and boudinage patterns are visible on many sections, revealing subaqueous landslides. In some cases, such as in Trenches 2 and 5, movements, perhaps linked to sediment desiccation, have induced settlement faults, resulting in a panel-like lowering of the deposits towards the center of the maar. Other, larger-scale subsidence is also apparent. Thus, the deposits in the area of section A appear to have been affected by mass detachment, revealed by the lack of deformation of the sediments beneath the tuff block. Slippage also affected the upper sections of trench T5, causing them to fold. Observations of present-day maars still holding water, such as Lac d'Issarlès and Lac Pavin, show that such gravity-driven reworking is a frequent occurrence. Several hypotheses can be put forward to explain these sublacustrine collapses: disruption of the equilibrium of sediments deposited in great thickness on the flats, seismic tremors, fluctuations in lake level, rapid drops in lake level induced by the incision of the outlet. At Senèze, this may have started at the very beginning of the formation of the fossiliferous deposits, perhaps in connection with the evolution from 2.5 to 2.0 Ma of the Sénouire river, into which the Senèze lake drained.

The interweaving of lacustrine deposits and slope formations indicates the emplacement of fossiliferous levels in the zone of water level variations in the paleolake, which may reflect climatic changes. Thus, the arrival of slope deposits may reflect reduced vegetation cover on the crater slopes, linked to periglacial conditions favoring solifluction flows and runoff during ground thaw. The slope deposits in Trenches 5–7 (the oldest layers) may represent a colder interval of lower lake level. Given the absolute dates, which place the bulk of the deposits between 2.19 and 2.07 Ma, this climatic deterioration could correspond to the marked cooling evident in the Tiglian or Pretiglian. Lake levels would have risen as a result of heavy precipitation, leading to a positive water balance. This change, linked to wetter climatic fluctuations, would initiate the transition to warmer conditions in the later Tiglian. These varied sedimentary dynamics show that the fossiliferous deposits developed in different physical and temporal contexts. It is therefore difficult to establish precise correlations between the two main excavated areas, although they are possible within each sector.

Building on the foregoing stratigraphic analysis and detailed mapping, Pastre (2024) was able to clarify the extent and succession of the products of the Senèze volcano and provide a more precise map of the entire area in Chap. 4. A first phreatomagmatic episode precedes the basanite flow which seems closely accompanied by the deposition of scoriae. In a later phase, the maar crater formed and the main phreatomagmatic tuffs were emitted. They are followed by a long lacustrine deposition phase in the maar crater.

The mineralogical study of several thin layers interbedded in the lacustrine and slope deposits containing the fauna on the shore of the maar lake led to the discovery of 10 tephra layers and 6 reworked tephric deposits coming from the Mont-Dore strato-volcano 60 km to the NW. These tephras were discovered in our paleontological excavations (mostly in trenches T2 and T5) and in two previously known sections (section A and the Philis Ravine). The sandy or silty-clayey texture of these beds results from weathering which has systematically destroyed the glass initially present. Because of the absence of ash, the tephra layers can only be characterized by their feldspars and heavy mineral content (ferromagnesians, oxides and accessory minerals) which are typical of each tephra.

Heavy mineral spectra are dominated either by brown amphiboles (kaersutite & pargasite), brown clinopyroxenes ($Al_2O_3$ and $TiO_2$ rich brown diopside), green clinopyroxenes (green diopside poor in $Al_2O_3$ and $TiO_2$, typical of the Mont-Dore) or by titanite. Among the accessory minerals, zircons and apatite are present in low percentages in most of the samples. Biotite and Fe–Ti oxides (magnetite, ilmenite) complete the assemblages. All these spectra are typical of the Mont-Dore pyroclastites, mostly from trachytic ones. Feldspars are more frequent minerals. Their compositions are typical of each sample. Several samples are dominated by alkali feldspars (anorthoclase, sodic sanidine) and less by plagioclases (oligoclase, andesine, labrador).

The different mineralogical compositions of the tephras indicate distinct ages for each deposit sequence (section) in which they occur. These sequences characterize several evolutionary stages of the lacustrine shore and of the crater slopes featured by the various stratigraphic sequences observed in the paleontological excavations. The frequency of the discovered tephra indicate the high pyroclastic activity of the Mont-Dore around 2.1–2.0 Ma. If no known pyroclastic unit of the strato-volcano can be directly correlated with a Senèze tephra bed, several in the Guéry area in its NE part may be contemporaneous: for example, the Guéry pumice flow dated at 2.09 ± 0.03 Ma.

The heavy mineral assemblages of sedimentary beds precise their origin. Brown clinopyroxenes and olivine which dominate several samples are basaltic minerals and can come from scoriae. The olivine, enstatite and chromian diopside which are common in many samples are mantellic minerals issued from lherzolite (peridotite) nodules. The basement minerals are dominated by garnets and sillimanite with some staurolite and andalousite. Like a part of the brown amphiboles, most of these minerals derive from the phreatomagmatic tuffs dominating the crater where they have been pulverized by phreatomagmatic explosions. The green automorphic diopside and/or titanite which are present in several samples, like other minerals of the Mont-Dore, show the reworking of tephras from the strato-volcano which fell on the crater rim.

In Chap. 5, Delson et al. (2024) analyze data from two complementary sources bearing on the age of the Senèze deposits and fauna. Nomade et al. (2014) published five $^{40}$Ar/$^{39}$Ar ages for Senèze tephra, but their stratigraphic positions were not completely known then. These ages were recalculated (based on the guidelines in Schaen et al. 2021) and placed in precise stratigraphic position following Debard (2024). Two ages were obtained on tephra from Trench 2, two from Trench 5 and one from section A (far from any fossils but on the stratigraphically highest horizon at Senèze).

In addition, S. Sen collected samples for paleomagnetic analysis from five sequences across the site. These came from Trenches 1, 2 and 5 (both upper and lower portions), zone H8 (near Trench 2) and a pit dug for sampling at the north end of parcel 233. Virtual geomagnetic polarity was calculated for each sample and the sequences examined for magnetostratigraphic zonation. Most of the polarity was reversed (Figs. 5.5 and 5.6), but there were normal zones at the top of Trench 2, in the lower half of the pit and in the upper part of Trench 5 inf (lower; in fact stratigraphically above T5 sup). The two T2 normal zones were correlated to the Huckleberry Ridge excursion (ca. 2.07 Ma) because they lie above the SEN 1 dated tephra (2.10 ± 0.03 Ma) located in a reversed zone (Fig. 5.7). The Trench 5 normal is most likely correlated to the Feni subchron (2.140–2.116 Ma), although there is a slight possibility it equates to the Huckleberry Ridge (Fig. 5.8). The section A dated tephra is the youngest of the five, and its age fits well with its inferred position near the top of the Senèze sequence (Fig. 5.9). Two other dates have also been published, one from an unknown level in section A (Paquette et al. 2021) and one on a normally magnetized tephra in a core drilled into the maar in 1989 (Roger et al. 2000). Both ages agree with their correlated position in the stratigraphy (Fig. 5.9). The fauna recovered during our fieldwork occurs in two relatively restricted intervals: 2.10–2.08 Ma in the western sector and roughly 2.20–2.18 Ma in the southeastern sector. It is not known if the fossils collected by Philis before 1942 also occurred in these intervals or throughout the 2.20–2.07 span of the Senèze sediments we studied, or even through a longer interval. The rare co-occurrence of argon-argon ages and geomagnetic polarity zones allows the Senèze sequence to be dated with great precision.

In a brief appendix, Bahain, Shao and Falguères report their attempt to obtain comparable dates using the ESR/U-series approach. The combination at Senèze of relatively early U-uptake history reconstructed from the analytical data and high dose rates linked to the volcano-sedimentary context yielded ages which were far too young by comparison to the dates discussed above.

## Palynology

J. Argant (2024) reviewed earlier palynology at Senèze and analyzed new samples taken during our fieldwork in Chap. 6. The first palynological analysis was carried out by Elhaï (1969), on a 175 m borehole drilled in 1965 into the lacustrine deposits at the center of the maar (altitude 590 m). The first five meters were sterile. The following 120 m yielded pollen and spores. Due to the size of the column, the analysis was carried out at a sampling interval of 40–60 cm. The top of this core is 30 m below the fauna from the nearby western sector. It was therefore necessary to carry out systematic sampling in conjunction with the new paleontological excavations in order to avoid the disadvantages associated with deep lake deposits, which may have suffered from sediment mixing over time.

Two hundred eight samples were taken between 2001 and 2006, to test all sediment types: coarse sands and gravels from slope deposits, fine sands and clays from lacustrine deposits collected in columns on the sections of trenches T1 to T6 or near the bones as they were cleared by the excavators. Eleven hyaenid coprolites, four of which were found in the vicinity of the *Dicerorhinus etruscus* skeleton, were also analyzed, along with the sediment on which they were found. This would avoid some of the drawbacks associated with deep lake deposits. Only 24 samples retained pollen grains, generally in excellent condition, but unfortunately often not very abundant. The other samples were sterile.

For the most part, therefore, the data remain qualitative. Forty-two taxa were identified: 18 trees, 22 herbaceous plants, one pteridophyte (monolete spore) and one moss (*Sphagnum*). Deciduous trees are constantly present: *Quercus*, *Corylus*, *Alnus* and, more sporadically, *Carpinus*, *Castanea*, *Fagus*, *Tilia*, *Betula*, *Fraxinus*, *Juglans*, *Ligustrum* and *Platanus*. *Hedera* is noted once. Conifers include *Pinus*, *Abies*, *Cedrus* and *Juniperus*. The presence of *Alnus*, *Fraxinus* and *Ligustrum* evokes the wettest substrates along the lake shore. Although the number of tree pollen grains is often higher than that of herbaceous plants, the role of grass should not be underestimated, as evidenced by the ever-present Poaceae, *Plantago*, *Rumex* and heliophilous trees such as *Betula*, *Juniperus*, *Alnus*, *Platanus* which take advantage of the openness of the landscape. Hygrophilous plants are rare. Only *Filipendula*, Cyperaceae and Typhaceae are regularly noted, but the lake shore seems to have been unfavorable to the establishment of an extensive megaphorbia. Climatic variations probably existed during the deposition of the layers containing the paleontological remains, but it is impossible to clearly identify and quantify them in a diagram.

Comparison with the Elhaï results remains problematic due to the sterility of the sediments in the upper five meters of the deep borehole. However, it appears that the pollen spectra of the fossiliferous sediments can only be more recent than those of the upper part of the Elhaï diagram. The climatic conditions encountered by the animals living in the vicinity of the Senèze maar were probably cool and temperate.

## Non-mammalian Paleontology

The few fishes found at Senèze were reported by Gaudant (2024) in Chap. 7. A partial skeleton of a tench (*Tinca*) was found in the 1965 core, 12 m below the top. Our fieldwork recovered two partial skulls and several other fragments of the modern perch, *Perca fluviatilis*.

Birds are more frequent among the fossils from Senèze, as discussed in Chap. 8 by Mourer-Chauviré (2024). Seventeen species are represented, all from the older collections. Most of these are extant taxa, known from one to three specimens. Four extinct taxa are recognized: *Pavo bravardi*, *Tetrao* cf. *partium*, *Surnia robusta* and *C. corax antecorax*. Of these, the first is known by two specimens, the others only by one each. *P. bravardi* is a peafowl, closely related to the modern southeast Asian species *Pavo muticus*, the Green Peafowl. It is known from seven Plio-Pleistocene localities in France, Bulgaria, Greece and Moldavia; Senèze appears to be the youngest of these. *Tetrao partium* may be the direct ancestor of *Tetrao tetrix*, the Black Grouse, although known elements differ in proportions. The modern species inhabits the northern Palearctic, but not in the tundra. *T. partium* has been recovered from many European localities of Late Pliocene to Middle Pleistocene age. *Surnia robusta* is a very large hawk-owl, probably not the ancestor of the modern *Surnia ulula*. The fossil species is known only from a few localities in Hungary (MN 16-MNQ 20) and Ahl al Oughlam in Morocco (age estimated at 2.5 Ma). *Corvus corax*, the Common Raven, is widely distributed across the Holarctic province (and in the northern Ethiopian province), in a great range of climatic zones. *C. c. antecorax* was originally described as a distinct species but is now usually recognized as a subspecies of the modern taxon, smaller than most extant subspecies. It is known from MNQ 17 at Saint-Vallier to the late Middle Pleistocene, mainly in warmer intervals. The overall avifauna from Senèze is most similar to that from Saint-Vallier. They share five taxa: *Ciconia nigra*, *Haliaeetus albicilla*, *Pavo bravardi*, *Otis* sp. (size of *O. tarda*) and *C. corax antecorax*. The paleoenvironmental implications of the Senèze birds will be discussed with that of the mammals, below.

## Mammalian Paleontology and Systematics

Drawing on the results from Chaps. 9–16 (see below), the Senèze mammalian fauna includes 39–42 species (one lagomorph, four rodents, 12 carnivores, two primates, 16 cetartiodactyls, 3–6 perissodactyls and one proboscidean). One of the cetartiodactyls, the bovid *Bison* (*Eobison*) sp., is known from a single donated specimen and must derive from a significantly younger horizon. Three of the equid perissodactyls are represented by only one or two specimens each and may not document distinct species or might derive from other sites. Less than half this number of mammalian species were recovered during our fieldwork: two rodents, two carnivores, seven cetartiodactyls (including *Bison*), three perissodactyls and one proboscidean; many taxa are known from only one to three specimens. We can examine the material of each order in more detail.

In Chap. 9, A. Argant (2024) revised the Senèze carnivores. The fossil carnivore remains unearthed during our excavations are extremely limited, in contrast to the material from the last century. The study of this recent material provided an opportunity to review all the carnivore remains at Senèze and to attempt to date the deposit using biochronology. Twelve species were identified: four Canidae (*Nyctereutes megamastoides*, *Vulpes alopecoides*, *Canis arnensis* and *Canis* sp. cf. *C. etruscus*); one Ursidae (*Ursus etruscus*); three Hyaenidae (*Pachycrocuta perrieri*, *Chasmaporthetes lunensis*, Hyaenidae indet.); and four Felidae (*Acinonyx pardinensis*, *Megantereon cultridens*, *Homotherium crenatidens* and *Dinofelis* sp.). Most of these were known from previous finds, including skeletons of *Homotherium crenatidens* and *Megantereon cultridens*. One tooth and a radius suggest a second canid, possibly referable to *C. etruscus*, while a single calcaneus indicates the presence of a *Dinofelis*. These are old finds but new taxa compared to the previous faunal list. Among the few specimens recovered recently is a small hyaenid fragmentary half mandible with p3. This specimen differs from the other two hyaenids known at Senèze and also from *Hyaena* and

*Parahyaena*; it must be identified for now simply as Hyaenidae indet., another new taxon for the site.

Our large-scale fieldwork has provided invaluable data on the fossiliferous levels in place, enabling their stratigraphy and paleoenvironments to be clarified. The Senèze carnivores probably span a long interval, but there is no evidence to suggest two distinct chronological periods. This assemblage of carnivores corresponds perfectly to the usual guild of Villafranchian predators. They regularly visited the banks of the Senèze maar to hunt the herbivores that came to the lake to drink. Carnivores put the Senèze deposit chronologically after that of Saint-Vallier and before those of Val d'Arno and Dmanisi, at around 2.2–2.1 Ma.

Guérin (2024) analyzed the remains of *Dicerorhinus etruscus etruscus* in Chap. 10. As documented here, over 530 fossils are known, representing at least 19 individuals (based on the number of mandibles recognized). Senèze is thus the richest locality for this species. Following a complete list of every Senèze specimen by element, each element is described, illustrated and measured, with comparisons to other species of the genus.

*D. etruscus* ranged from the second half of MN 16 (MN 16b: Les Etouaires, Montopoli) to about 0.5 Ma or later. Two subspecies are recognized: *D. etruscus etruscus* (MN 16b to MNQ 19) and the larger *D. etruscus brachycephalus* from the Epivillafranchian (e.g., Le Vallonnet) to the later Middle Pleistocene (e.g., Lunel-Viel and Mosbach). In turn *D. etruscus etruscus* is divided into two informal stages: stage I (MN 16b-MNQ 17 [Saint-Vallier]) and stage II (MNQ 18–19: Senèze, Upper Valdarno, Cueva Victoria). These two stages are distinguished by a series of morphological trends in the cranium (receding of the orbit and widening of the posterior part); mandible (thinning and shallowing of the corpus); dentition (reduction in width of the upper cheek-teeth, slight increase of hypsodonty); and post-cranium (e.g., slight reduction of the length of the long bones and the metapodials, slight changes in the proportions of the carpal and tarsal bones). *D. etruscus* was more cursorial than extant species of rhinoceros and probably ate soft foods like leaves, buds, young bark and twigs.

The Senèze equids are described, illustrated, documented with measurements and interpreted in Chap. 11 by Eisenmann and Delson (2024). First, they distinguish three genera of monodactyl equines by cranial proportions: *Equus*, *Plesippus* and *Allohippus*. The Senèze sample comprises over 170 fossils (from complete skeletons to isolated teeth) found by Philis, as well as two partial skeletons and some possibly associated hindlimb elements recovered during our excavations from stratigraphically low horizons in the southeastern sector. The great majority of them belong to *Allohippus senezensis senezensis*, which is intermediate in size and proportions between *A. senezensis guthi* from La Puebla de Valverde and *A. senezensis mygdoniensis* of Gerakarou.

Despite suggestions of similarity, it does not seem that *A. senezensis* and *A. stehlini* are closely related, even if one MC III does resemble *A. stehlini* from the Upper Valdarno. The geographic and possible temporal occurrences of these taxa and other forms of *Allohippus* are shown in a chart; *A. senezensis* ranges from MNQ 17b through MNQ 18.

One tooth and 16 postcranial elements (including one donated to the team in 2002 by A. Consigny) are identified as the much larger *A. major*, although the lack of information on its cranial proportions renders the generic attribution uncertain. This taxon is rare but has been recognized from early MNQ 17 through MNQ 19 and perhaps in the Epivillafranchian. It is broadly similar in size to but morphologically distinct from *Equus (Sussemionus)* sp.

In addition, the Senèze equid collection includes two first phalanges larger than the average for *A. stenonis vireti* of Saint-Vallier; one MT III and one first phalanx resembling the small ?*Allohippus* sp. of Pyrgos; the *A. stehlini*-like MC III from the Upper Valdarno (both the latter sites are significantly younger than Senèze) and some caballine teeth and metapodials. The caballine material is presumably from a potential younger horizon at Senèze such as that which yielded the specimen of *Bison* (*Eobison*) or are wrongly labeled as to the locality of origin. The five distinctive *Allohippus* specimens might also derive from other localities or represent extremely rare Senèze taxa.

In Chap. 12, Faure and Guérin (2024) discuss the rare fossils of *Sus strozzii* from Senèze. No material was recovered during our fieldwork, but the nearly complete skeleton of a young male was found in 1937 and is exhibited in the Naturhistorisches Museum Basel (which also has a partial scapula of an adult). The skeleton was studied and illustrated by Azzaroli (1954), and this chapter provides measurements and scatter-plots with comparison to congeneric species. *Sus strozzii* is large and morphologically more similar to the modern southeast Asian long-snouted *S. verrucosus* and *S. barbatus* than to the extant Eurasian *S. scrofa*. The cheek teeth of *S. strozzii* are wider and lower, its molars less complicated and covered with thicker enamel than those of *S. scrofa*, and its limb bones are stockier and relatively short [which Azzaroli (1954) suggested could be an adaptation to soft and marshy soils]. The Senèze specimen retains I3, which has been lost in the younger sample from the Upper Valdarno, suggesting a possible temporal trend. *S. strozzii* is known across Europe and in the Middle East from MNQ 16 up to the early Middle Pleistocene.

As reviewed by Valli (2024) in Chap. 13, four species of deer are known from Senèze: *Eucladoceros ctenoides senezensis*, *Metacervoceros rhenanus philisi*, *Croizetoceros ramosus minor* and *Libralces gallicus*. All four taxa have Senèze as their type locality. The remains of the last two are quite rare, while those of the other two are by far the most common mammals of the locality; they were also the only cervids recovered during our fieldwork. Valli discusses the morphology and morphometrics of these remains, as well as their taxonomy.

*M. rhenanus philisi* is a cervid slightly larger than a European fallow deer, but its antlers have only three points on their beams. Like the fallow deer, the Philis deer lacks upper canines. Specimens found by our team belong to at least three different individuals. Their size and morphology corresponds to that described in Heintz (1970), a monograph devoted to the Villafranchian cervids of France and Spain. *E. ctenoides senezensis* is larger; its size is comparable to that of a modern red deer, from which it differs mainly in its antlers. The numerous fossils excavated during our research include one almost complete skeleton and remains of at least two other individuals. Both these subspecies help to define the late Villafranchian in several European countries, including France, Spain and Greece.

As to the two other species, *L. gallicus* represents the oldest elk currently known from Europe. It is characterized by slender limbs and, above all, by its beams, very elongated and horizontally arranged on both sides of the animal. In France, it is only known from the late Villafranchian. *C. ramosus minor* is the smallest deer from Senèze; its dimensions are a little larger than those of a roe deer. It is characterized by its antlers; all the tines grow in the frontal part of the beam and face forward.

Crégut-Bonnoure (2024) analyzed the bovids from Senèze in Chap. 14. This diverse group is the second most common family among the Senèze mammals. The Bovidae have undergone multiple radiations over geological time, making them particularly interesting for biochronological analysis. In the Plio-Pleistocene, the paleoenvironmental changes linked to the onset of climatic instability led to new radiations and major faunal movements, resulting in the establishment of new guilds. The family is represented at Senèze by four tribes (Antilopini, Caprini, Ovibovini and Bovini), and the aim of this analysis is to present and discuss their richness and diversity. Our excavations yielded only seven fragmentary remains, and unfortunately their incomplete nature makes it impossible to compare them significantly with the material from the previous collections.

Eight bovid species were described in the last century. In this chapter, they were all revised, except *Leptobos*, which allowed the correction of some identifications, including many from other localities. As a result, eleven taxa are now identified: *Gazellospira torticornis*, *Procamptoceras brivatense*, cf. *Hemitragus* sp., *Gallogoral meneghinii*, *Pliotragus ardeus*, *Megalovis latifrons*, *Ovis claudiusguerini* nov. sp., *Leptobos etruscus*, *L. furtivus*, *Bison* (*Eobison*) sp. and Bovidae indeterminate. Cf. *Hemitragus* sp. and Bovidae indeterminate are new for the locality, while the previous *Ovis* sp. is now identified as a new species dedicated to the late Claude Guérin. *Bison* (*Eobison*), known from a single specimen donated to the team and whose stratigraphic position is unknown, is younger than the other species and must derive from an otherwise unknown horizon dating to the end of the Early Pleistocene.

Morphological variability can be observed in *Pliotragus*, *Gallogoral* and *Megalovis*, suggesting an evolution of these taxa over time and the possibility of more than one fossiliferous level. However, these possible distinct levels would not be very distant in time (as opposed to that yielding the *Bison*), and it is not possible to distinguish successive bovid assemblages. The bovid fauna from Senèze is clearly younger than those from MN 16 and MNQ 17 localities from the Massif Central.

In Chap. 15, Ménouret and Guérin (2024) discuss the proboscidean from Senèze, *Mammuthus meridionalis meridionalis*. They begin with a taxonomic review of the genus and the species, which ranges in France from MNQ 17 into the early Middle Pleistocene. It is a tall species, with male height at the shoulder between 3.5 and 4.2 m and weight mostly 7–10 tons. The skull presents a concave forehead, inflated parietals, a sharp occipital crest, long and low mandibular corpus and elongated symphysis. The tusks are stocky, curving slightly upward and inward; the M3 is thick and moderately hypsodont.

Following a full list of specimens (including one partial tusk recovered in our fieldwork), each element is described in some detail and compared morphologically and morphometrically to those of other populations of the species (and in some cases to other species of the genus). There is good agreement in general between the Senèze fossils and those of this subspecies from other middle-late Villafranchian sites. Interestingly, two M3s from Colle Mancino (estimated age ca. 1.2 Ma) are the most similar to those from the original skull excavated by Boule (1892) and on exhibit in Paris (see Faure et al. 2024), the only remaining elements of that specimen. The implications of this similarity are unclear, but it seems that this morphology first appeared at Senèze.

Delson (2024) reviews the few Senèze primates in Chap. 16. There are only two specimens known, both cercopithecids found by Philis: a fragmentary ulna and a nearly complete skull. The ulna is referred to *Macaca sylvanus*, of which several subspecies may have sequentially inhabited Europe from the Late Miocene into the Late Pleistocene. The female skull was first described by Depéret (1928), who made it the holotype of *Dolichopithecus arvernensis*, which he thought was a colobine related to *D. ruscinensis* Depéret, 1889 from the mid-Pliocene of Perpignan. Necrasov, Samson and Rădulesco (1961) described a fragmentary face of a cercopithecid from the newly-studied Romanian site of Valea Grăunceanului (usually abbreviated as Grăunceanu) as *Paradolichopithecus geticus*. They thought this taxon also represented a colobine, similar to *D. arvernensis*. Later in the 1960s, several authors recognized that these taxa were synonymous and actually cercopithecines. Thus the Senèze skull is now termed *Paradolichopithecus arvernensis*; additional samples of this species have been described from Grăunceanu, and from Vatera-F, Karnezeika and Dafnero-3 (all in Greece), dating to MNQ 17 (and perhaps 18). Other specimens have been referred to further species of this genus. Emended and differential diagnoses and a general description are presented for *Paradolichopithecus*, and an emended diagnosis for *P. arvernensis*. The Senèze skull is described and illustrated in detail.

There are two major systematic questions regarding *Paradolichopithecus*: is it more closely related to *Macaca* or *Papio*?; and is it a synonym of the east Asian *Procynocephalus* Schlosser, 1924? The arguments on both sides of these questions are presented, and (at least in a preliminary decision), *Paradolichopithecus* is considered a distinct genus of the Macacina. A longer analysis of these problems will be presented along with descriptions of the Grăunceanu and Vatera-F samples in a forthcoming study.

## Analytical Interpretations of the Senèze Fauna

Two chapters analyze broader aspects of the Senèze assemblage, taphonomy and biochronology. In addition, three other related topics can be discussed on the basis of the entire volume's content: composition and proportions of the fauna; assessment of paleoenvironment; and site formation.

Biochronology is discussed by a group of authors in Chap. 17 (Crégut-Bonnoure et al. 2024). Following a brief review of stratigraphy, geochronology and palynology (as discussed above), the implications for relative dating of each mammalian group and the birds are presented, along with a full list of taxa present, separated by origin (Philis and other twentieth century finds vs. our collection). The faunal list is then compared to those from twelve other Massif Central localities dating from MN 16 through MNQ 20, plus Saint-Vallier. It is clear that Senèze falls between sites placed in MNQ 17 and MNQ 19. The lack of *Mammut borsoni* (only MN 16), *Tapirus arvernensis* (mainly MN 16) and *Anancus arvernensis* (MN 16 and MNQ 17) places Senèze younger than MNQ 17. The carnivores *Panthera gombaszogensis* and *Pachycrocuta brevirostris* also do not occur at Senèze: the former appears at Slivnitsa (Bulgaria), which may be slightly younger than Senèze, while the latter only occurs in the Epivillafranchian. Subspecies or "stages" in the lineages of ursids, felids, cervids, bovids, equids and rhinocerotids also set Senèze apart from earlier and later sites. A further faunal comparison was made with a selection of Spanish and Italian sites of MNQ 17 and MNQ 18, as well as with Tegelen (the Netherlands) and Erpfingen (Germany), both MNQ 18. Senèze again shares taxa with early MNQ 18 sites, especially.

A number of the studied localities have been dated recently, so their ages could be compared with those for Senèze. Sites yielding *Anancus arvernensis* are considered to be placed in MNQ 17. These include Chilhac and Le Coupet (France), dating to 2.285 ± 0.046 Ma and 2.274 ± 0.032 Ma and Coste San Giacomo and Pantalla (Italy), with ages of 2.23 ± 0.03 Ma and 2.23 ± 0.18 Ma, respectively. These dates, all preceding 2.20 Ma, combined with the estimate of 2.20 Ma for the base of the Senèze sequence, suggest that the boundary between MNQ 17 and MNQ 18 is close to 2.2 Ma. In turn, Blassac-La Girondie (France) was dated to 1.946 ± 0.029 Ma by Paquette et al. (2021), who considered it to fall in MNQ 19 on the basis of three distinctive cervids not found at Senèze. But those species are not diagnostic of MNQ 19, leading Crégut-Bonnoure et al. (2024) to suggest the site might be of mid MNQ 18 age. They accepted Dmanisi (Georgia) as very late in MNQ 18, with a date of 1.80–1.76 Ma, suggesting that the end of MNQ 18 was ca. 1.75–1.70 Ma.

The composition of the Senèze mammalian assemblage has not been discussed earlier in this volume. Many authors provide lists of all specimens in their taxa of interest, allowing the number of separate fossils to be estimated. Specimens with the same catalogue number or those known to be part of a single individual were counted only once. Valli (2024) did not review the large number of cervids recovered prior to our research, so Heintz (1970) was consulted to estimate similar counts for *Eucladoceros ctenoides senezensis* and *Metacervoceros rhenanus philisi*. The total summed the number of specimens with antlers (and separate skulls), number of teeth (sum of largest numbers for any position in upper and lower permanent and deciduous rows), and half the sum of estimated numbers of each major postcranial element tabulated by Heintz. The resulting estimates by species, family and order are presented in Table 19.1, and values by family are illustrated in Fig. 19.1. The total of 2200+ mammal specimens is clearly dominated by cervids (over 63%). *Metacervoceros rhenanus philisi* and *Eucladoceros ctenoides senezensis* each are represented by more specimens than any other order. Bovidae, Rhinocerotidae and Equidae are well-represented (with roughly 13.8, 9.3 and 8.9 %, respectively), but far behind the two cervids. Other families and orders are rare at Senèze, never reaching 2% of the mammal specimens. Birds account for slightly <1% of the tetrapod total. These frequencies will be discussed again when considering paleoenvironmental indications below.

An alternative way of looking at the size of the total Senèze collection is to consider the number of catalogue numbers at each major institution. In some cases multiple

**Table 19.1** List of numbers per taxon for the fauna from Senèze

| Taxon | FGD 2001–06 | Previous finds | Total by species | FGD 2001–06 | Previous finds | Total by family | Percent by family | FGD 2001–06 | Previous finds | Total by order | Percent by order |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Mammalia | | | | | | | | 140 | 2098 | 2238 | |
| Lagomorpha | | | | | | | | | 10 | 10 | 0.45 |
| Leporidae | | | | | 10 | 10 | 0.45 | | | | |
| *Oryctolagus* cf. *lacosti* (number estimated—see Masson 1943) | | 10 | 10 | | | | | | | | |
| Rodentia | | | | | | | | 2 | 22 | 24 | 1.07 |
| Sciuridae | | | | | 1 | 1 | 0.04 | | | | |
| Sciuridae indet. aff. *Eutamias* | | 1 | 1 | | | | | | | | |
| Arvicolidae | | | | 1 | 21 | 22 | 0.98 | | | | |
| *Mimomys pliocaenicus-M. ostramosensis* group | | 10? | 10 | | | | | | | | |
| *Mimomys pitymyoides* (group) | 1 | 11? | 12 | | | | | | | | |
| Hystricidae | | | | 1 | | 1 | 0.04 | | | | |
| *Hystrix refossa* | 1 | | 1 | | | | | | | | |
| Carnivora | | | | | | | | 2 | 42 | 44 | 1.97 |
| Felidae | | | | 1 | 16 | 17 | 0.76 | | | | |
| *Dinofelis* sp. | | 1 | 1 | | | | | | | | |
| *Acinonyx pardinensis* | 1 | 3 | 4 | | | | | | | | |
| *Homotherium crenatidens* | | 7 | 7 | | | | | | | | |
| *Megantereon cultridens* | | 5 | 5 | | | | | | | | |
| Hyaenidae | | | | 1 | 8 | 9 | 0.40 | | | | |
| *Chasmaporthetes lunensis* | | 3 | 3 | | | | | | | | |
| *Pachycrocuta perrieri* | | 5 | 5 | | | | | | | | |
| Hyaenidae indet. (not counting coprolites) | 1 | | 1 | | | | | | | | |
| Canidae | | | | | 12 | 12 | 0.54 | | | | |
| *Vulpes alopecoides* | | 3 | 3 | | | | | | | | |
| *Nyctereutes megamastoides* | | 4 | 4 | | | | | | | | |
| *Canis arnensis* | | 3 | 3 | | | | | | | | |
| *Canis* sp. | | 2 | 2 | | | | | | | | |
| Ursidae | | | | | 6 | 6 | 0.27 | | | | |
| *Ursus etruscus* | | 6 | 6 | | | | | | | | |
| Primates | | | | | | | | | 2 | 2 | 0.09 |
| Cercopithecidae | | | | | 2 | 2 | 0.09 | | | | |
| *Paradolichopithecus arvernensis* | | 1 | 1 | | | | | | | | |
| Cf. *Macaca sylvanus* | | 1 | 1 | | | | | | | | |
| Cetartiodactyla | | | | | | | | 126 | 1598 | 1724 | 77.03 |
| Suidae | | | | | 2 | 2 | 0.09 | | | | |
| *Sus strozzii* | | 2 | | | | | | | | | |
| Cervidae | | | | 119 | 1295 | 1414 | 63.18 | | | | |
| *Metacervoceros rhenanus philisi* | 40 | 640 | 680 | | | | | | | | |
| *Croizetoceros ramosus minor* | | 12 | 12 | | | | | | | | |
| *Eucladoceros ctenoides senezensis* | 59 | 441 | 500 | | | | | | | | |
| *Cervalces gallicus* | | 2 | 2 | | | | | | | | |
| Cervidae indet | 20 | 200 | 220 | | | | | | | | |
| Bovidae | | | | 7 | 301 | 308 | 13.76 | | | | |
| *Gazellospira torticornis* | | 37 | 37 | | | | | | | | |
| *Procamptoceras brivatense* | | 16 | 16 | | | | | | | | |
| *Ovis claudiusguerini* | | 1 | 1 | | | | | | | | |
| Cf. *Hemitragus* sp. | | 3 | 3 | | | | | | | | |
| *Megalovis latifrons* | 2 | 13 | 15 | | | | | | | | |

(continued)

**Table 19.1** (continued)

| Taxon | FGD 2001–06 | Previous finds | Total by species | FGD 2001–06 | Previous finds | Total by family | Percent by family | FGD 2001–06 | Previous finds | Total by order | Percent by order |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Pliotragus ardeus* | 1 | 55 | 56 | | | | | | | | |
| *Gallogoral meneghinii* | 1 | 90 | 91 | | | | | | | | |
| *Leptobos* | 3 | 84 | 87 | | | | | | | | |
| Bovidae indet | | 2 | 2 | | | | | | | | |
| Perissodactyla | | | | | | | | 9 | 398 | 407 | 18.19 |
| Equidae | | | | 4 | 195 | 199 | 8.89 | | | | |
| *Allohippus senezensis senezensis* | 3 | 174 | 177 | | | | | | | | |
| *Allohippus major* | 1 | 16 | 17 | | | | | | | | |
| Possible additional equids known from phalanges and/or metapodials: | | | | | | | | | | | |
| (1) Larger than the average for *Allohippus stenonis vireti* | | 2 | 2 | | | | | | | | |
| (2) Cf. Valdarno *Allohippus stehlini* | | 1 | 1 | | | | | | | | |
| (3) Cf. small ?*Allohippus* of Pyrgos | | 2 | 2 | | | | | | | | |
| Rhinocerotidae | | | | 5 | 203 | 208 | 9.29 | | | | |
| *Dicerorhinus etruscus etruscus* | 5 | 203 | 208 | | | | | | | | |
| Proboscidea | | | | | | | | 1 | 26 | 27 | 1.21 |
| Elephantidae | | | | 1 | 26 | 27 | 1.21 | | | | |
| *Mammuthus meridionalis meridionalis* | 1 | 26 | | | | | | | | | |
| Aves | | | | | | | | | 21 | 21 | [0.93][1] |
| Ciconiiformes | | | | | | | | | | | |
| Ciconiidae | | | | | | | | | | | |
| *Ciconia nigra* | | 1 | | | | | | | | | |
| Anseriformes | | | | | | | | | | | |
| Anatidae | | | | | | | | | | | |
| *Tadorna* cf. *ferruginea* | | 1 | | | | | | | | | |
| *Anas clypeata* | | 2 | | | | | | | | | |
| *Aythya* sp. | | 1 | | | | | | | | | |
| *Mergus* cf. *merganser* | | 1 | | | | | | | | | |
| *Mergellus* sp. size of *M. albellus* | | 1 | | | | | | | | | |
| Anatidae indet | | 1 | | | | | | | | | |
| Accipitriformes | | | | | | | | | | | |
| Accipitridae | | | | | | | | | | | |
| *Haliaeetus albicilla* | | 1 | | | | | | | | | |
| *Buteo* sp., size of *Buteo buteo* or *Buteo lagopus* | | 1 | | | | | | | | | |
| Galliformes | | | | | | | | | | | |
| Tetraonidae | | | | | | | | | | | |
| *Tetrao* cf. *partium* | | 1 | | | | | | | | | |
| Phasianidae | | | | | | | | | | | |
| *Pavo bravardi* | | 1 | | | | | | | | | |
| *Alectoris* cf. *graeca* | | 3 | | | | | | | | | |
| Gruiformes | | | | | | | | | | | |
| Otididae | | | | | | | | | | | |
| *Otis* sp. size of *Otis tarda* | | 1 | | | | | | | | | |
| Strigiformes | | | | | | | | | | | |
| Strigidae | | | | | | | | | | | |
| *Bubo* sp. | | 2 | | | | | | | | | |
| *Surnia robusta* | | 1 | | | | | | | | | |

(continued)

**Table 19.1** (continued)

| Taxon | FGD 2001–06 | Previous finds | Total by species | FGD 2001–06 | Previous finds | Total by family | Percent by family | FGD 2001–06 | Previous finds | Total by order | Percent by order |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Passeriformes | | | | | | | | | | | |
| Turdidae | | | | | | | | | | | |
| Cf. Turdidae, size of *Turdus merula* | | 1 | | | | | | | | | |
| Corvidae | | | | | | | | | | | |
| *Corvus corax antecorax* | | 1 | | | | | | | | | |
| Osteichthyes | | | | | | | | 5 | 1 | 6 | |
| Cypriniformes | | | | | | | | | | | |
| Cyprinidae | | | | | | | | | | | |
| *Tinca* sp. | | 1 | | | | | | | | | |
| Perciformes | | | | | | | | | | | |
| Percidae | | | | | | | | | | | |
| *Perca fluviatilis* | 5 | | | | | | | | | | |

[1] Percentage of birds among all tetrapods (birds + mammals). FGD: the Faure/Guérin/Delson fieldwork of 2001–2006

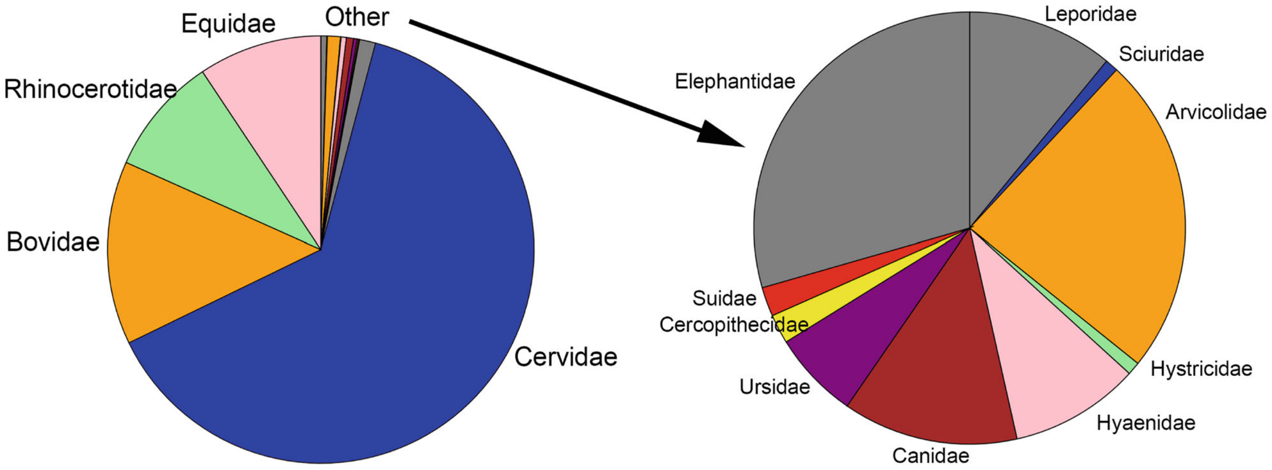

**Fig. 19.1** Frequency of occurrence of mammalian families and two higher taxa in the Senèze assemblage. Data from Table. 19.1. This figure was produced with the PAST statistical program (v 4.03), see Hammer et al. (2001)

numbers were given to single fossil individuals, so the total is greater than that given in Table 19.1. There are 1860 numbers for Senèze mammals (and 20 for birds) in the Naturhistorisches Museum Basel; 826 (of which 63 are indeterminate) in the Université Claude Bernard-Lyon 1 and about 100 in the Institut de Paléontologie, Muséum national d'Histoire naturelle, Paris. Our sample from 2001–2006 includes 1314 numbers for mammals (identified or indeterminate), plus 20 coprolites and 5 fish; every element of a partial skeleton has a separate number.

There are also mounted skeletons (see Faure et al. 2024) of a number of taxa in the Basel and Lyon collections: *Homotherium crenatidens*, *Megantereon cultridens* (now dismounted), *Sus strozzii*, *Metacervoceros rhenanus philisi* (2), *Eucladoceros ctenoides senezensis* (2), *Cervalces gallicus*, *Gallogoral meneghinii* (2), *Leptobos etruscus, Allohippus senezensis* (3, plus one unmounted) and *Dicerorhinus etruscus* (2). Our fieldwork recovered four additional partial skeletons (with more than a dozen elements each): *Eucladoceros ctenoides senezensis, Allohippus senezensis* (2) and *Dicerorhinus etruscus*.

## Paleoenvironment

Most of the paleontological contributions have provided some information on the paleoenvironmental implications of the taxa studied. We will bring these together and then attempt to summarize an overall conclusion.

J. Argant (2024) analyzed the pollen collected at various points across the site, especially in contact with skeletons, confirmed by the content of hyaenid coprolites. Leafy trees dominated the pollen assemblages, especially *Quercus*, *Corylus* and *Alnus*; conifers were less common, including *Pinus*, *Abies*, *Cedrus* and *Juniperus*. Non-arboreal pollen was often less frequent than arboreal, but Poaceae (grasses) is always present and *Plantago* and *Rumex* are also found on occasion. This led her to interpret an environment with both open spaces and wooded areas, with climate relatively temperate or cool temperate.

Of the fish, assuming the fossils had similar adaptations to their extant congeners, *Tinca* (found in the core) lives on muddy and grassy bottoms in quiet rivers and ponds, while *Perca* (excavated in lakeshore deposits) is found in water plant communities of rivers and lakes.

A number of birds provide information about their habitat preferences; each species is known by only 1–3 specimens. Many taxa live on the water or its banks, in forests with lakes or gallery forest along watercourses. *Tetrao* and *Surnia* inhabit forest edges or lower altitude forests. *Alectoris* and *Otis* are found in more open environments, grassy plains or bushland. Some forms are migratory and winter in the tropics, south and southeast Asia and eastern Africa. Senèze would have been more humid and wooded than Saint-Vallier, with no indication of a cooler climate than today's.

Among the mammals, deer, especially elk, generally prefer wooded environments, although *Eucladoceros*, like the red deer, had a flexible diet which allowed it to also inhabit more open environments. *Sus strozzii* indicates a forested area under a wet and probably warm climate. Bovids are almost entirely open-country species, with a wide range of climatic preferences. Short muzzles and deep, not very robust, metapodials like those of *Allohippus senezensis* are usually found in equids living in rather dry conditions like extant *Equus hemionus* and *E. przewalskii*. *Dicerorhinus etruscus* probably preferred wooded savanna and moist climate. *Mammuthus meridionalis* also preferred wooded savanna, but under temperate or cooler conditions in a relatively dry environment. The modern *Macaca sylvanus* feeds and travels on the ground in open to mixed woodland and into grassland but sleeps in trees. Its environments are wet and cold in winter, with warm and dry summers. *Paradolichopithecus arvernensis* postcrania (from other sites) are similar to those of *Papio* and *Mandrillus*, suggesting a high degree of terrestriality, perhaps in open terrain to woodland. Carnivores often have a wide range of environmental tolerance, although the felids found at Senèze also occur in other sites which were close to large streams, lakes or fluvio-paludal environments.

As discussed, deer are the most common mammals at Senèze, with antelope, rhino and horse far behind. This suggests that the environments preferred by these animals would likely be the most common around the maar lake. Deer prefer wooded habitats and rhino wooded savanna, but bovids are open-country animals, and *Allohippus* is suggested to inhabit dry (and open) areas. Of the rarer species, *Sus* prefers forest, *Mammuthus* wooded savanna, the primates open country but perhaps with trees in which to sleep. This suggests a mixture of habitats with forest to woodland dominant. Perhaps more open steppe/savanna existed outside the maar itself. This agrees well with the palynological results, with leafy trees dominant, conifers and grasses present but less frequent. The climate would presumably have been warmer than today, and moist especially close to the lake.

Several MIS cycles spanned the 2.20–2.08 interval, and they would also have impacted the climate and vegetation around the maar. According to Channell et al. (2020) following dates in Lisiecki and Raymo (2005), the Feni correlated to MIS 81 (quite warm), MIS 80 (cooler) and into MIS 79 (warm). The broadly warm interval continued to the Huckleberry Ridge, when a sharp cooling occurred. The Réunion was also cool (MIS 84), followed by a warmer interval (MIS 83) and a cold phase (MIS 82) before the Feni. This implies that the two intervals when we suggest fossils were found in our fieldwork, ca. 2.20–2.18 Ma and 2.10–2.08 Ma, were both warmer times linked to MIS 83 and MIS 81, with the strongly cold MIS 82 between them and the cool MIS 84 and MIS 80 on either side. Debard (2024) has proposed that the slope deposits in Trenches 5–7 represented a colder interval, which might instead be correlated to MIS 84 and the Réunion excursion, which was not captured in the paleomagnetic sampling.

## Taphonomy

Fernández-Jalvo et al. (2024, Chap. 18) report research on the taphonomic history of the Senèze large-mammal assemblage recovered in our excavations and some older finds housed in the paleontology collection of the Laboratoire de Géologie, Université Claude Bernard-Lyon 1. Five hundred twenty-seven fossils from the 2003–2006 seasons of our work were studied and classified according to taxon, age, body part and size class. Fractures, peeling and other surface modifications such as punctures, gnaw marks, cracks, friction marks (such as trampling), soil corrosion and pathology were noted for each element. Experiments were undertaken to replicate deformation and compression damage.

Sediment analysis on fossils revealed slight differences in sediment distribution, oxide deposits, and coloration, suggesting varying depositional conditions, possibly related to seasonal changes. Manganese staining on many bones indicates immersion in damp sediment. The distribution of this manganese on fossils, with most bones completely black, except for the stain-free articular surfaces, indicated that skeletal elements were in anatomical connection during deposition and possibly burial.

Several individuals exhibit almost complete and anatomically connected skeletons, suggesting a fast burial and/or prolonged period of permanent water immersion. This environment likely facilitated quicker decay of ligaments, resulting in rib and vertebrae detachment before limbs. A number of individuals showed significant pathology indicating arthritis in the limbs and especially distal extremities (carpals, tarsals, metapodials and phalanges).

The formation of the Senèze site was attributed mainly to gravitational forces, with blocks falling down the inner slope, and colliding with skeletonized carcasses, causing fracture and compression. The absence of hydrodynamic abrasion, size selection, or piles of fossils, together with diagenetic breakage and fragments still in anatomical connection reinforces the idea that re-sedimentation or reworking did not occur. There is often minimal bone dispersion, indicative of underwater decay. Plastically deformed long bone shapes, cracks with curled edges (associated with humid environments), manganese and iron oxides, fossils arranged on site both horizontally or almost vertically, together with the absence of rodent chewing or weathering support an underwater burial process. Only in very rare cases some fossils from the upper part of the excavation (upper part of the slopes) show signs of weathering, rodent chewing and the presence of hyena coprolites, indicating that these bones were exposed subaerially on the shore of the lake.

Patterns of bone breakage, compression and deformation, most likely caused by falling blocks and boulders due to sediment compaction and mudflows, were investigated. There was no clear evidence for carnivore activity, with potential mimics caused by abiotic means. Pseudo-carnivore tooth marks caused by falling block impacts on the bone surfaces, soil corrosion and pressure marks on coarse sediments were discussed in detail, emphasizing the need for careful differentiation of such marks according to their origin. There is also no evidence for human activity at the site, which is reasonable as it is older than Dmanisi and all sites in western Europe with signs of human occupation.

## Site Formation

One of the primary goals of the taphonomic research was to determine the most likely processes which formed the Senèze fossil accumulations. Paleontologists often assume that assemblages of large mammal bones may be the result of carnivore kills or geological events such as flooding. There do not seem to be any specific suggestions about the origin of the Senèze assemblage until 1989, when Couthures (1989: 210) proposed that “Only sudden and repeated asphyxia could have been responsible for the particular ecological disaster of Senèze and for the abnormal mixing of animal fossils.” It is not clear why he thought this or what he meant by “abnormal mixing”.

The next alternative was proposed by Debard in Delson et al. (2006, p. 287): “mud or debris slides down the inner slopes from the local summits (possibly related to local faulting evidenced in the trench sequences) which engulfed large animals either while still alive or soon after death. The resulting cadavers could have been washed into the lake margin before they could be preyed upon by any of the local carnivores and would have remained in anatomical connection at least during the early phases of preservation.”

The big question is why so many almost complete skeletons have been recovered from the crater lake at Senèze, especially without any indication of carnivore ravaging. A. Argant (2024) has suggested that predators attacked herbivores coming to drink at the lake, either on the shore or as they moved down the hillside. But this idea is unlikely given the lack of carnivore damage (rather only pseudo-carnivore tooth marks as noted above) on any bones studied by Fernández-Jalvo et al. (2024).

Instead, both Debard (2024) and Fernández-Jalvo et al. (2024) have proposed that the larger mammals fell into the lake and drowned when they were unable to climb out. Debard offered slightly different scenarios in colder or warmer intervals. During the cold phases, dead or still living animals could be dragged by solifluction to be trapped in the icy waters of the lake. The association of remains with pebbles and blocks (frequent in the southeastern sector, Trenches 5–7) may reflect very cold conditions where the surface of the lake, partly frozen and covered with stony pavement, could yield under the weight of heavier animals, causing their death by drowning. During the warmer phases, as seen in the western lake beds (Trenches 1–3), they could simply slip on the slope while coming to drink; because the stiffness of the sedimentary layers resulted in bluffs 0.5–1.5 m high at the edge of the lake and due to the instability of the waterlogged sediments, the animals could not get back up onto the bank and drowned. Fernández-Jalvo et al. (2024) emphasized the common presence of joint pathologies on many of the associated skeletons, which would have made it harder for such animals to extract themselves from the lake.

Among his several suggestions, A. Argant (2024) proposed a slightly different version of the same general idea, opining that some herbivores fled instinctively away from carnivores down the slopes and into the water. Unlike in Africa, there was no fear of crocodiles to deter them. Some would have swum to safety, others would have drowned. After a while their corpses would have risen back to the surface and drifted according to the direction of wind and current. Some of these would end up on the shore and be accessible to scavengers. Others would have sunk once again to the bottom of the lake and been preserved.

Fernández-Jalvo et al. (2024) compared Senèze with other maar-related sites such as Eckfeld, Messel and Camp dels Ninots, where gas emissions from volcanic lakes and fumaroles have been suggested as a possible cause of mass mortality and subsidence. In the case of Senèze, rare gas emissions could have had an influence and could have caused some of the deaths, but its maar was characterized by abrupt slopes, highly plastic sediments that allow slumping and mudflows and most of the skeletons with varying degrees of pathology. This pattern suggests that at Senèze, the instability of the sediment could have caused animals to fall into the water and slide down the slope, making it difficult for them to escape from sinking underwater. The herbivore remains decomposed under water without emitting odors that could attract scavengers. Falling boulders and landslides were frequent, as evidenced by the steep inclination of the strata. The site acted as a natural trap, active for decades or centuries at a time, during multiple intervals over perhaps 100,000 yr at the broad lakeshore area, which explains the high number of complete skeletons, without the need of invoking catastrophic events. The faunal assemblage represents a past biocoenosis shaped by the metabolic necessity of drinking and the (in)ability to escape, rather than by selective collection. This scenario is also consistent with the complementary hypothesis that mud or debris engulfed large animals at Senèze, preserving skeletons in anatomical association during early phases of fossilization.

Taken together, these suggestions envisage various large mammals, especially individuals with limb joint pathologies, drowning under a range of circumstances and their cadavers being preserved in anatomical connection to be discovered by P. Philis and later paleontologists searching at Senèze.

## Epilogue

The Franco-American Senèze Research Project began as the result of a recognition among the three team leaders (and now editors of this book) that Senèze was a famous but poorly documented site typical of the western European late Villafranchian. We planned the research to throw greater light on the local stratigraphy, provide chronometric dates, recover additional specimens of rare taxa and revise the systematics of known species, understand the taphonomy and site formation processes and reconstruct the paleoenvironment. The chapters in this book, summarized above, show that almost all these goals were realized. The stratigraphy of two main sectors of the maar was clarified, and a combination of argon-argon ages and magnetostratigraphic sequences allowed the fossiliferous layers sampled by the team to be precisely dated. No new primates were found, and despite screen washing of several tons of sediment, only two micromammal teeth were recovered. But a number of well-preserved partial skeletons were excavated and two taxa new to the site were identified: *Hystrix refossa* and Hyaenidae indet. The fauna was demonstrated to be homogeneous, refuting the previous suggestion that two distinct assemblages could be identified. On the other hand, one specimen of *Bison* (*Eobison*) sp. collected on the surface from an unknown horizon by local amateur A. Consigny did demonstrate the local presence of Epivillafranchian or later sediments. Five other taxa were identified through systematic revision, and a previously known but indeterminate species was named for one of the team leaders: *Ovis claudiusguerini*. The total assemblage fits neatly between those of MNQ 17 (middle Villafranchian) and later MNQ 18-MNQ 19. Senèze is well justified to be considered the primary reference locality for the earlier part of MNQ 18 and the start of the late Villafranchian.

Findings from taphonomy and stratigraphy clarified that the many associated skeletons were probably preserved as a result of animals falling into the lake under different circumstances and drowning before their bones could be disturbed. Cervids were by far the most common animals recovered at Senèze, followed more distantly by bovids, rhinocerotids and equids. Combining information about the paleoenvironment from the likely habitat preferences of these groups and the results of palynological analysis indicates that a wide range of habitats were present in the Senèze neighborhood: forest, woodland, gallery forest and open plains, but where each of these were located is not yet known.

In sum, the project has been highly successful, justifying the financial and logistical support provided by many agencies and people. We hope that we have made Senèze more accessible and comprehensible and that our data will be of use to many colleagues in the years to come.

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