Dating of the Lower Pleistocene Vertebrate Site of Tsiotra Vryssi (Mygdonia Basin, Greece): Biochronology, Magnetostratigraphy, and Cosmogenic Radionuclides

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Abstract: Background and scope: The late Villafranchian large mammal age (~2.0–1.2 Ma) of the Early Pleistocene is a crucial interval of time for mammal/hominin migrations and faunal turnovers in western Eurasia. However, an accurate chronological framework for the Balkans and adjacent territories is still missing, preventing pan-European biogeographic correlations and schemes. In this article, we report the first detailed chronological scheme for the late Villafranchian of southeastern Europe through a comprehensive and multidisciplinary dating approach (biochronology, magnetostratigraphy, and cosmogenic radionuclides) of the recently discovered Lower Pleistocene vertebrate site Tsiotra Vryssi (TSR) in the Mygdonia Basin, Greece. Results: The minimum burial ages (1.88 ± 0.16 Ma, 2.10 ± 0.18 Ma, and 1.98 ± 0.18 Ma) provided by the method of cosmogenic radionuclides indicate that the normal magnetic polarity identified below the fossiliferous layer correlates to the Olduvai subchron (1.95–1.78 Ma; C2n). Therefore, an age younger than 1.78 Ma is indicated for the fossiliferous layer, which was deposited during reverse polarity chron C1r. These results are in agreement with the biochronological data, which further point to an upper age limit at ~1.5 Ma. Overall, an age between 1.78 and ~1.5 Ma (i.e., within the first part of the late Villafranchian) is proposed for the TSR fauna. Conclusions: Our results not only provide age constraints for the local mammal faunal succession, thus allowing for a better understanding of faunal changes within the same sedimentary basin, but also contribute to improving correlations on a broader scale, leading to more accurate biogeographic, palaeoecological, and taphonomic interpretations.

Keywords: Villafranchian; Pleistocene; Balkans; southeastern Europe; mammals; biochronology; palaeomagnetism; cosmogenic radionuclides

1. Introduction

The fascinating world of the Pleistocene has long attracted the interest of scientists from different disciplines. The rich mammal record, including iconic animals such as mammoths, saber-toothed cats, giant hyenas, and giant deer; the evolution and dispersals of our own genus *Homo*; and the large-scale global climatic fluctuations are only some

of the highly intriguing research areas that characterize the Pleistocene. The late Villafranchian large mammal age, defined in Europe as starting at ~2.0 Ma [1–3] and ending at ~1.2 Ma [4–6] at the beginning of the subsequent Epivillafranchian, is a crucial period in the evolution of the Early Pleistocene terrestrial ecosystems of Eurasia. The climatic conditions during the late Villafranchian resulted in the (intermittent) expansion of open-forest and savanna-like landscapes from the Transcaucasian to the European peri-Mediterranean regions [7,8]. In turn, this affected the structure and dynamics of the western Eurasian mammal palaeocommunities tremendously, triggering faunal turnovers, extinctions, and dispersal events [2,7,9], including the first arrival of hominins at the gates of Europe [10,11]. Indeed, the fossil record of the northern/eastern peri-Black Sea region and southern Europe documents the arrival during this period of new immigrants of Asian and African origin along with the regional extinction of several, previously well-adapted lineages [1,2,7,12]. The analysis and interpretation of these mammal bioevents and their underlying mechanisms necessitate the establishment of an accurate chronological framework. The discovery of several new fossiliferous localities and the re-assessment of older ones, in combination with improved dating methodologies, have substantially enhanced our knowledge about the Early Pleistocene of Europe. However, there are still several open issues that need to be addressed. For instance, the dating methods (either direct or indirect) that are commonly applied to Quaternary deposits and fossils, have their own assumptions, as well as assets and limitations (see [13] for an overview) that bring uncertainties in age estimations, thus, limiting high-resolution correlations across different sites. Moreover, although Early Pleistocene local European records and faunal successions have been relatively well explored and defined through time, pan-European biogeographic correlations and schemes (large-scale biochronology) are still limited (see also [1]) and poorly supported by an accurate chronological framework, especially for the Balkans and adjacent territories. As a result, our understanding of the palaeoecological conditions, including corridors or barriers that may have enabled or impeded the dispersal of several large mammals in this timeframe, is highly obscured. Additionally, these continental-scale biogeographic extrapolations rely mostly on spot data from sedimentary basins from distant geographic regions, such as Italy, Spain, France, and the Balkans (Figure 1), which, as stated above, are difficult to correlate, resulting in the following uncertainties especially when attempting to resolve: (i) possible discontinuities in the fossil record, both local or composite (faunal units); (ii) the degree of diachrony or synchrony of the various dispersal events in response, for example, to Pleistocene climate variability; and (iii) the different geological, climatic, environmental, and taphonomic conditions at the various sites (see also [14,15]).

Figure 1. Selected sites of the Caucasus, the northern peri-Black Sea territory, and the northern peri-Mediterranean region, attributed to the late Villafranchian and Epivillafranchian, ~2.0–0.8 Ma (map from Natural Earth, naturalearthdata.com).

The Lower Pleistocene fossiliferous localities of the Mygdonia Basin (central Macedonia, Greece) have been known since the end of the 1970s [16–18]. Numerous fieldwork campaigns, carried out for several decades, have led to the discovery of several sites, and to the excavation and study of a great number of fossils. This work has significantly enriched the Pleistocene fossil record of Greece [19–22]. Currently, there are twelve open-air Lower Pleistocene vertebrate sites known in the Mygdonia Basin (Figure 2), located in at least three distinct stratigraphic horizons and correlated to different parts of the late Villafranchian. Owing to their rich and diversified fauna of different evolutionary stages, the Mygdonia sites (1) permit identification and tracking of faunal and evolutionary changes within the stratigraphic succession of the same sedimentary basin, and thus enhance our knowledge on the evolution and taxonomy of several vertebrate taxa and mammal turnovers; (2) allow a more precise biostratigraphic correlation with other fossil assemblages of Greece and southeastern Europe; and (3) contribute to palaeogeographical interpretations and the better understanding of the palaeoenvironmental conditions, offering overall valuable insights into the Early Pleistocene terrestrial ecosystems of Europe. Moreover, Greece and the Balkans in general, located in the southeastern corner of Europe, occupy a critical position for the dispersals of mammals and hominins to and from Europe, western Asia, and the Levant/Africa [22–27], highlighting the need for systematic and deeper investigations in key locations, such as the Mygdonia Basin. Importantly for the Pleistocene continental biostratigraphy of Greece, the late Villafranchian localities of the Mygdonia Basin, together with the older ones from the Aliakmon Basin (e.g., Dafnero) and the younger ones from the Megalopolis Basin (e.g., Marathousa-1 and Kyparissia sites), all of which are characterized by long stratigraphic sequences, altogether cover a rather continuous faunal sequence spanning from the middle Villafranchian to the Galerian [22,28–31], and permit the detailed study of the Early–Middle Pleistocene fossil and palaeoenvironmental record of Greece.
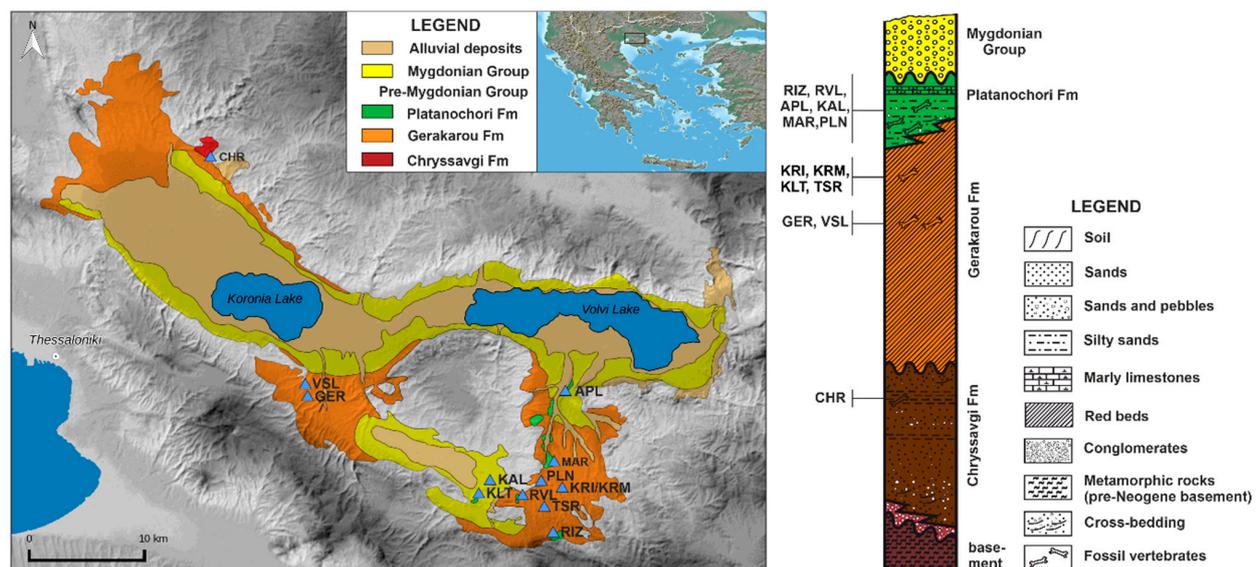
Figure 2. Geological map of the Neogene and Quaternary lithostratigraphic units of the Mygdonia Basin (**left**) and simplified composite stratigraphic column of the basin indicating the position of the fossiliferous localities (**right**). Modified from [21] and data from [19]. Map of Greece from Copernicus Land Monitoring Service (https://land.copernicus.eu/).

In this article, we report the first detailed chronological scheme for the late Villafranchian from southeastern Europe. This has been achieved through a comprehensive and multidisciplinary dating approach (biochronology, magnetostratigraphy, and cosmogenic radionuclides) of the recently discovered Lower Pleistocene vertebrate site Tsiotra Vryssi (TSR) in the Mygdonia Basin. More specifically, the aims of the present study are the following: (1) to precisely constrain the age of the site by means of a combination of dating methods; (2) to follow more thoroughly the regional mammal succession through

time and to enhance our knowledge about the relationships among the various Mygdonia Basin localities; and (3) to correlate TSR with other Lower Pleistocene localities of western Eurasia, thus, placing TSR within the larger discussions on Early Pleistocene mammal diversity and bioevents. As one of the first such studies from the Early Pleistocene of Greece and Southeastern Europe in general, and the first from the Mygdonia Basin, this study aspires to render TSR and the surrounding fossil sites to be a western Eurasian reference region for the chronological correlation of other localities and for the study and comparison of their vertebrate assemblages.

## 2. Geological Setting and Fossiliferous Locality

The Mygdonia Basin is located in central Macedonia (Greece), to the northeast of Thessaloniki, and represents an elongated east-west trending tectonic depression, the formation of which started during the early–middle Miocene with the incipient development of the Pre-Mygdonia Basin (Figure 2). During the Neogene–Early Pleistocene, the basin was filled with fluvial/fluvio-torrential and lacustrine sediments, while at the beginning of the Middle Pleistocene a new tectonic event led to further subdivisions into smaller basins, which were subsequently filled mostly by lacustrine sediments [32]. These Neogene to Quaternary deposits were subdivided into two high-rank lithostratigraphic units, namely the Pre-Mygdonian Group (Neogene to Early Pleistocene) and the Mygdonian Group (Middle Pleistocene to Holocene). The Pre-Mygdonian Group can be further subdivided into three successive lithostratigraphic formations (Fm), the Chryssavgi Fm, the Gerakarou Fm and, the Platanochori Fm [19]. The following six Lower Pleistocene fossiliferous sites have been discovered, to date, in the upper part of the Gerakarou Fm: Gerakarou-1 (GER), Vassiloudi (VSL), Krimni-1 and -2 (KRI and KRM), Kalamoto-2 (KLT), and Tsiotra Vryssi (TSR). The study of their assemblages indicated that, although the localities are not isochronous, all of them can be correlated to the first part of the late Villafranchian (Early Pleistocene) [19–21]. The overlying Platanochori Fm includes six more fossiliferous sites, i.e., Apollonia-1 (APL), Ravin of Voulgarakis (RVL), Riza-1 (RIZ), Marathoussa (MAR), Kalamoto-1 (KAL), and Platanochori-1 (PLN) (Figure 2), which are correlated to the second part of the late Villafranchian [19–21]. More information on the stratigraphy and the fossiliferous sites can be found in [19] and [21].

TSR (GPS coordinates 40°31′23.2″ N, 23°26′07.5″ E and elevation 250 m a.s.l.) is situated in the Gerakarou Fm, the most widely exposed sedimentary unit across the Mygdonia Basin (Figure 2) with a thickness in excess of 100 m. The Gerakarou Fm consists of red-brown sands, gravels, sandy silts, and clays, deposited in a fluvial/fluvio-torrential environment [19]. TSR was discovered in 2014 during a targeted survey by a joint team from the Aristotle University of Thessaloniki and the Paleoanthropology working group at the Eberhard Karls University of Tübingen [21]. It has since yielded a wealth of large mammal fossils (Figure 3), as well as some micromammals, reptiles, and birds. The ~1 m thick fossiliferous unit Geo 2a (Figure 4) consists of pale brown-dark yellowish brown poorly sorted silts, locally intercalated by cm-thick lenses of medium-coarse grained sands and is relatively more clayey in its uppermost part. The spatial taphonomic analysis of the faunal remains and the sedimentological and micromorphological studies indicated multiple dispersion events and recurrent spatial rearrangement of a lag, (peri)autochthonous assemblage, consistent with the cyclical lateral switching of a braided fluvial system [33]. The large mammal assemblage is rich and diversified and, so far, comprises 14 species ([21,34–36] and unpublished data; a cranium belonging to the felid *Megantereon* was discovered in the excavation season of 2018, whose complete study is pending, however, the genus is included in the herein updated faunal list). The fauna is dominated by horses (*Equus*), but also includes several other herbivore taxa, such as bovids (*Leptobos*, *Bison*, *Pontoceros*), deer (*Cervus*, *Praemegaceros*), rhinos (*Stephanorhinus*), mammoths (*Mammuthus*), and giraffids (*Palaeotragus*). Carnivores are well represented and include wolf-like dogs (*Canis*), giant hyenas (*Pachycrocuta*), bears (*Ursus*), and saber-toothed cats (*Megantereon*) (Table 1). TSR has yielded more than 2000 mammalian bones and teeth to date, which are stored at the Museum of Geology, Palaeontology, and Palaeoanthropology of the

Laboratory of Geology and Palaeontology at the Aristotle University of Thessaloniki, Greece (LGPUT).

Figure 3. Tsiotra Vryssi site and excavation photos. (**a**) General view of the site; (**b**) Closer view of the site; (**c**) Cranium of a bear (*Ursus etruscus*); (**d**) Complete front limb of a horse (*Equus* sp.); (**e**) Accumulation of isolated and articulated bones of a large bovid, a horse, and a rhino (*Stephanorhinus* sp.); (**f**) Skeletal remains of a mammoth (*Mammuthus meridionalis*).
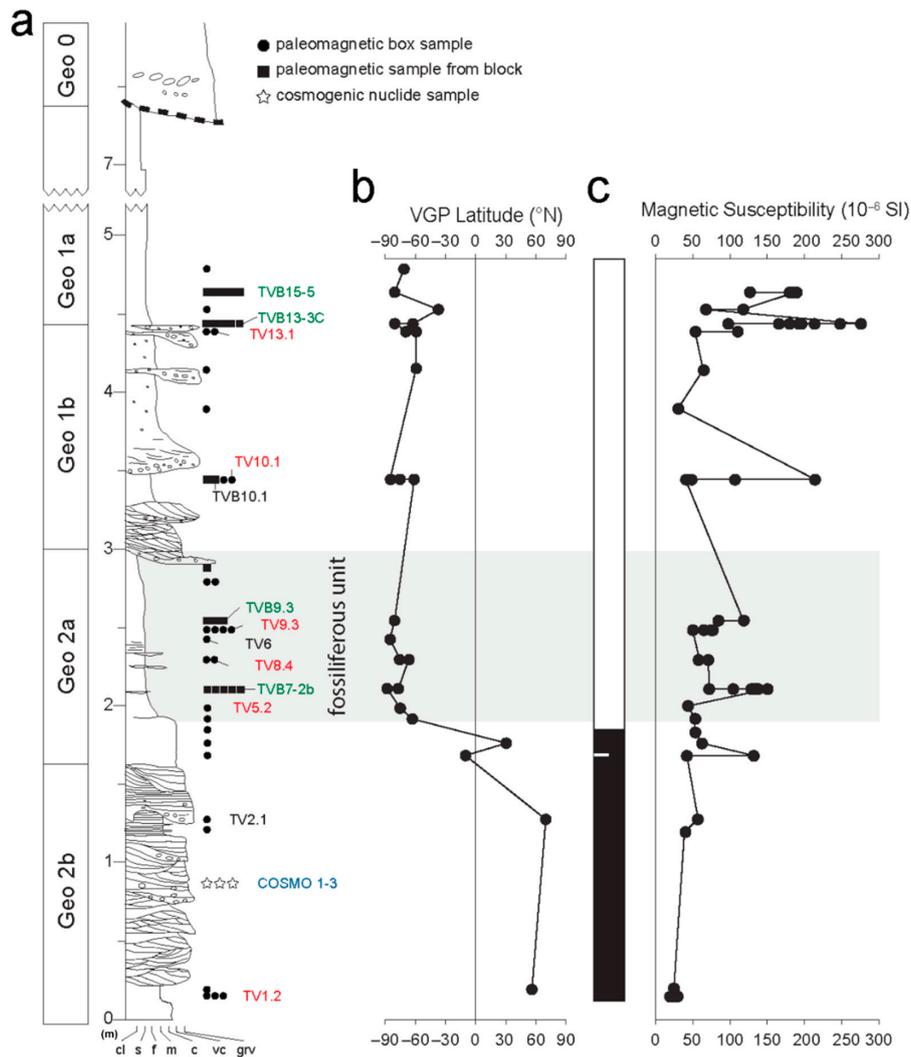
Figure 4. (**a**) Stratigraphic log (modified from [33]) of the Tsiotra Vryssi section with location of the samples for magnetostratigraphy and experiments for rock magnetism, and for cosmogenic radionuclides dating; (**b**) Latitude of the virtual geomagnetic poles (VGP) with interpreted magnetostratigraphy (black is normal polarity, white reverse polarity); (**c**) Magnetic susceptibility κ.

Table 1. Preliminary faunal list of the large mammals from Tsiotra Vryssi (excavation seasons 2014–2019). Faunal list updated from [21], based on [34–36] and unpublished data.

Order	Family	Genus	Species
Proboscidea	Elephantidae	*Mammuthus*	*meridionalis*
Carnivora	Canidae	*Canis*	sp.
	Ursidae	*Ursus*	*etruscus*
	Hyaenidae	*Pachycrocuta*	*brevirostris*
	Felidae	*Megantereon*	sp.
Perissodactyla	Equidae	*Equus*	sp. (medium-sized)
		Equus	sp. (large-sized)
	Rhinocerotidae	*Stephanorhinus*	sp.
Artiodactyla	Giraffidae	*Palaeotragus*	sp.
	Cervidae	*Cervus*	sp.
		Praemegaceros	sp.
	Bovidae	*Pontoceros*	sp.
		Leptobos	sp.
		Bison	cf. *degiulli*

3. Methodology

Cosmogenic radionuclides: Pairs of in situ-produced cosmogenic radionuclides analyzed in fluvial sediment can be used for burial dating based on different decay rates of the two isotopes (e.g., [37,38]). Age determination of sediment deposition in the study area makes use of simple burial dating with in situ-produced ^{26}Al and ^{10}Be concentrations in quartz (e.g., [39]). Three sand samples from the same stratigraphic depth located at ~1 m below the bottom of the Geo 2b fossiliferous layer (Figure 4a) were sieved to 0.25 to 0.50 mm. Quartz was separated and cleaned to reach Al concentrations of ~100 ppm. Al and Be were extracted according to protocols outlined in [40]. The ^{26}Al/^{27}Al and ^{10}Be/^{9}Be ratios of samples, blanks, and standards were measured at the AMS facility of Cologne (Germany). The ^{26}Al and ^{10}Be concentrations of samples were corrected for chemistry blanks of 1.93×10^5 and 4.97×10^4 atoms, respectively. Standards used for calibration of the ^{26}Al/^{27}Al and ^{10}Be/^{9}Be ratios were KN01-5-3 and KN01-4-3 [41], as well as KN01-6-2 and KN01-5-3 [42], respectively. All sample preparation was conducted at the University of Tübingen.

Simple burial dating was performed with a MatLab script modified from [40] based on [39]. Decay constants used for ^{26}Al and ^{10}Be were $(9.830 \pm 0.250) \times 10^{-7}$ [43] and $(4.997 \pm 0.043) \times 10^{-7}$ [44,45]. The sea level and high latitude (SLHL) production rates for ^{26}Al were 28.54, 0.84, and 0.081 atoms/(g$_{(qtz)}$ yr) for nucleonic, stopped muonic, and fast muonic production, respectively [46,47]. The SLHL production rates used were 3.92, 0.012, and 0.039 atoms/(g$_{(qtz)}$ yr) for nucleonic, stopped muonic, and fast muonic ^{10}Be production, respectively [46,47]. The ^{26}Al/^{10}Be ratio of production at SLHL was ~7.4. The SLHL production rates were scaled to the sample location with the online calculator of Marrero et al. [48] using the scaling procedure "SA" based on Lifton et al. [49]. Production rates at individual sampling depths were calculated based on nucleonic, stopped muonic, and fast muonic adsorption lengths, which were 157, 1500, and 4320 g/cm^2, respectively [46]. Overburden was assumed to be at least 3000 cm with a constant density over time of 2.0 ± 0.1 g/cm^3. This overburden results in a calculated simple burial age, which can be considered to be a minimum burial age [39]. The production rate at the sample location was used as the production rate of the sediment source area, because the production rate of the palaeo-sediment source area was unknown. Therefore, this production rate is considered to be a minimum production rate for a source area located at higher elevation, and hence results in a maximum calculated burial age. Thus, based on the above, the calculated simple burial age has the potential to be either younger or older than the actual age, and we interpreted it to be the best estimate of the actual burial age given with available constraints.

Palaeomagnetism: A total of 52 standard (10 cc) samples were recovered from 4.5 stratigraphic meters of the Tsiotra Vryssi section (Figure 4a), either by manually inserting plastic boxes in the outcrop section (32 specimens) or by hand-sampling six oriented blocks, each yielding up to 5 specimens, which were subsequently consolidated and cored in the laboratory. All analyses were conducted at the Alpine Laboratory of Paleomagnetism (ALP) of Peveragno (Italy), with the exception of the thermal demagnetization experiments, which were performed at the Department of Geophysics of the Aristotle University of Thessaloniki.

The low-field magnetic susceptibility (κ) was measured with an AGICO KLY-3 Kappabridge. Then, samples were AF (Alternating Field) demagnetized in steps of 5–10 mT up to 100 mT with a 2G Enterprises AF Degausser. The natural remanent magnetization (NRM) was measured after each demagnetization step with a 2G Enterprises 755 DC-SQUID cryogenic magnetometer located in a magnetically shielded room. The directions of the NRM were plotted on standard vector end-point demagnetization diagrams and the characteristic remanent magnetization (ChRM), where present, was isolated with standard principal component analysis on selected data. Isothermal remanent magnetization (IRM) acquisition experiments were performed on 6 representative samples using an ASC Scientific IM-10-30 impulse magnetizer and an AGICO JR-6 spinner magnetometer. Finally, thermal demagnetization experiments of a three-component IRM adopting 2 T, 0.5 T, and

0.1 T orthogonal fields were performed on another set of 4 samples with a Minispin spinner magnetometer (Molspin) at the Department of Geophysics of the Aristotle University of Thessaloniki.

Faunal similarity analysis: In order to examine the similarities and relationships of TSR with other Early Pleistocene localities, we performed hierarchical cluster analysis at the genus level. Twenty-four faunas/sites were selected ranging geographically from Georgia to Spain and spanning chronologically from ~2.5 to ~0.8 Ma (middle Villafranchian to Epivillafranchian). A total of 56 genera of large mammals (excluding primates) were considered. The analysis was conducted with the PAST software, version 4.04 [50]. The Q-mode dendrogram (with unweighted pair-group average (UPGMA) algorithm) was acquired by applying the similarity index Raup-Crick, which is used to statistically test presence and absence data through a randomization method [51]. The faunal assemblages considered are Fonelas P-1 [52], Untermassfeld [53,54], Gerakarou-1, Krimni-1, Apollonia-1, Libakos [55], Slivnitsa [56], Poggio Rosso [57], Kalamoto-2 [20], Dmanisi [11], Pirro 10 [58], Sima del Elefante (TE-) Lower Red Unit (LRU) TE8–14 [59], Vallparadís Estació Middle Unit, Layers EVT6–VT8 [60,61], Venta Micena [62], Val di Chiana [9], Pietrafitta [9], Trlica 11–10 [63], Vallonnet [64], Fuente Nueva 3 [62], Barranco León [62], Pantalla [65], Dafnero [66] and Taurida [67], with faunal updates and taxonomical reviews by us for the Greek sites.

## 4. Results

4.1. Cosmogenic Radionuclides

In situ produced cosmogenic radionuclide concentrations of ^{26}Al and ^{10}Be from three samples (Figure 4a) range from (31.88 ± 1.74) to $(37.07 \pm 1.91) \times 10^4$ atoms/g$_{(qtz)}$ and (9.40 ± 0.33) to $(10.51 \pm 0.42) \times 10^4$ atoms/g$_{(qtz)}$. The ^{26}Al/^{10}Be ratios are 3.53 ± 0.23, 3.18 ± 0.20, and 3.39 ± 0.22 for the three samples from the same stratigraphic layer. These ratios result in simple burial ages of 1.88 ± 0.16 Ma, 2.10 ± 0.18 Ma, and 1.98 ± 0.18 Ma, respectively (Table 2).

Table 2. Cosmogenic radionuclide information for samples from the stratigraphic layer Geo 2b of Tsiotra Vryssi.

Sample ID	Lab ID	Grain Size (µm)	Qtz Dissolved (g)	m(^{27}Al) (ppm)	^{26}Al/^{27}Al	1σ Error (%)	^{26}Al Conc. 10^4 atoms/g$_{(qtz)}$	m(^{9}Be) (mg)	^{10}Be/^{9}Be	1σ Error (%)	^{10}Be Conc. 10^4 atoms/g$_{(qtz)}$	^{26}Al/^{10}Be	Simple Burial Age (Myr)
COSMO 1	GL11	250–500	46.76	121	1.39×10^{-13}	4.46	37.07 ± 1.91	0.3397	2.16×10^{-13}	3.60	10.51 ± 0.42	3.53 ± 0.23	1.54 ± 0.10
COSMO 2	GL7	250–500	76.52	81	1.80×10^{-13}	5.23	32.48 ± 1.70	0.2868	4.10×10^{-13}	3.34	10.23 ± 0.34	3.18 ± 0.20	1.75 ± 0.10
COSMO 3	GL8	250–500	55.97	65	2.20×10^{-13}	5.44	31.88 ± 1.74	0.2874	2.76×10^{-13}	3.51	9.40 ± 0.33	3.39 ± 0.22	1.62 ± 0.10

4.2. Magnetic Properties

Values of κ are relatively low all along the section (Figure 4c), with an average value of 105×10^{-6} SI. Samples from the basal part of the sequence, between 0 and 2 m from the base, show the lowest values $(15–60 \times 10^{-6}$ SI), whereas peak κ values were measured from samples collected at 2 m (ca. 150×10^{-6} SI), 3.5 m (ca. 215×10^{-6} SI), and 4.5 m (ca. 275×10^{-6} SI). The IRM acquisition curves indicate the dominance of low to medium coercivity phases (80 to 400 mT) with saturation reached at 2500 mT, suggesting the presence of a mixture of magnetite/maghemite and hematite (Figure 5A). The three-axis IRM experiments [68] show that the medium (0.5 T) and high-coercivity (2 T) curves have maximum unblocking temperatures of 650–675 °C (Figure 5B), consistent with the presence of hematite. The low-coercivity (0.1 T) curve declines at a rather constant pace from room temperature up to 350–400 °C, before recording a rapid decrease at ~600 °C, followed by a slower decrease up to 650–675 °C (Figure 5B); this behavior could be interpreted to reflect progressive oxidation of an original maghemite/magnetite phase into a secondary hematite.
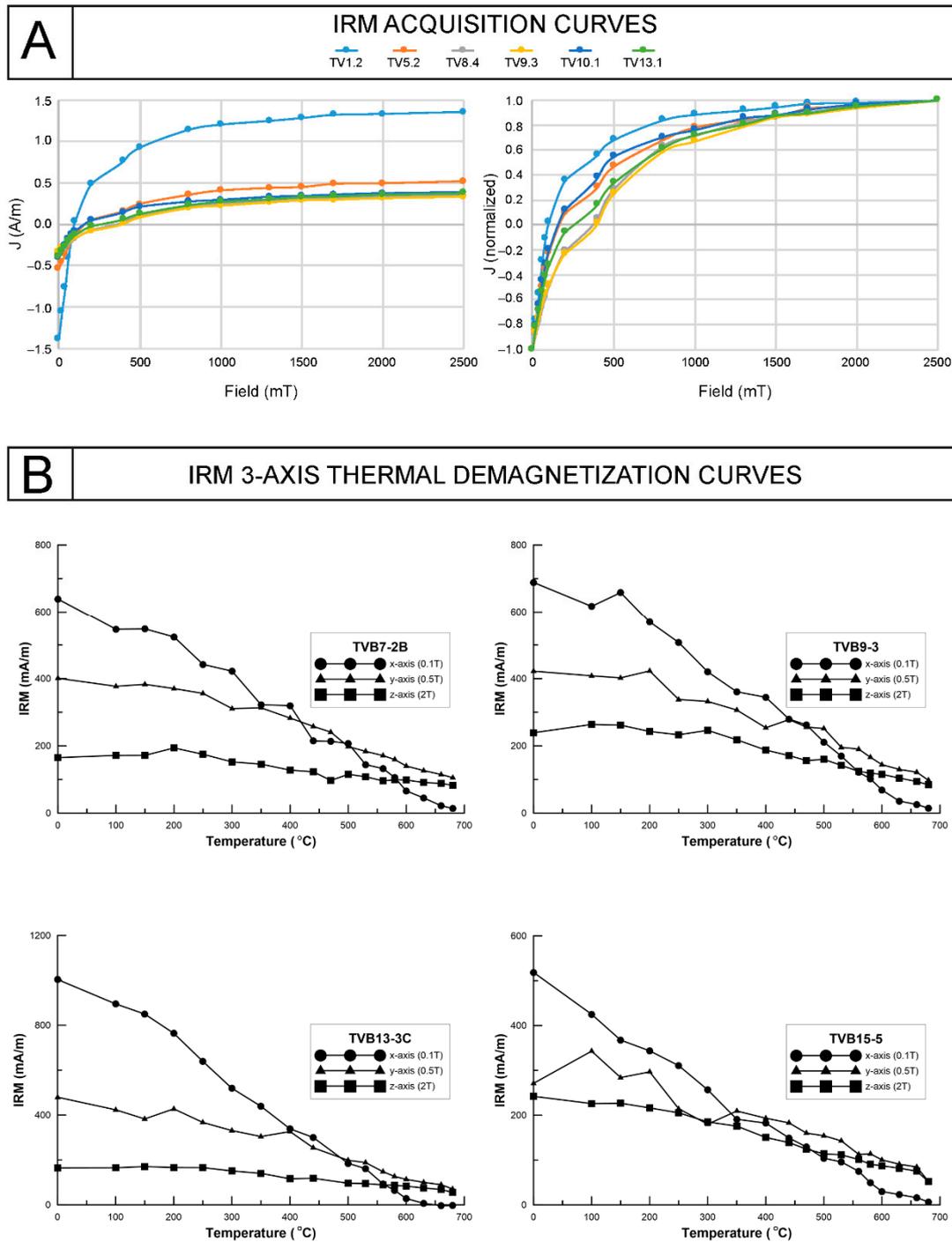
Figure 5. (**A**) Isothermal remanent magnetization (IRM) backfield acquisition curves and (**B**) thermal decay curves of three-axis IRM of selected samples from Tsiotra Vryssi (see Figure 4 for location).

4.3. Magnetostratigraphy

Bipolar ChRM component directions, oriented north-and-down or south-and-up in in situ coordinates and within a field range of ~10–70 mT, were isolated in 23 of 38 demagnetized samples from the Tsiotra Vryssi section (Figure 6). The mean ChRM direction, calculated by applying standard Fisher statistics on n = 23 ChRM directions (declination = 176.8 °E, inclination = −40.5°, α_{95} = 10.7°, Table 3 and Figure 7), led to a palaeomagnetic pole position of latitude 72.4 °N and longitude 213.2 °E (A_{95} = 7.8°). The McFadden and McElhinny [69] reversal test applied to the ChRM component directions in in situ

coordinates result was indeterminate (k1 ≠ k2, type I), probably due to the small number of components used.
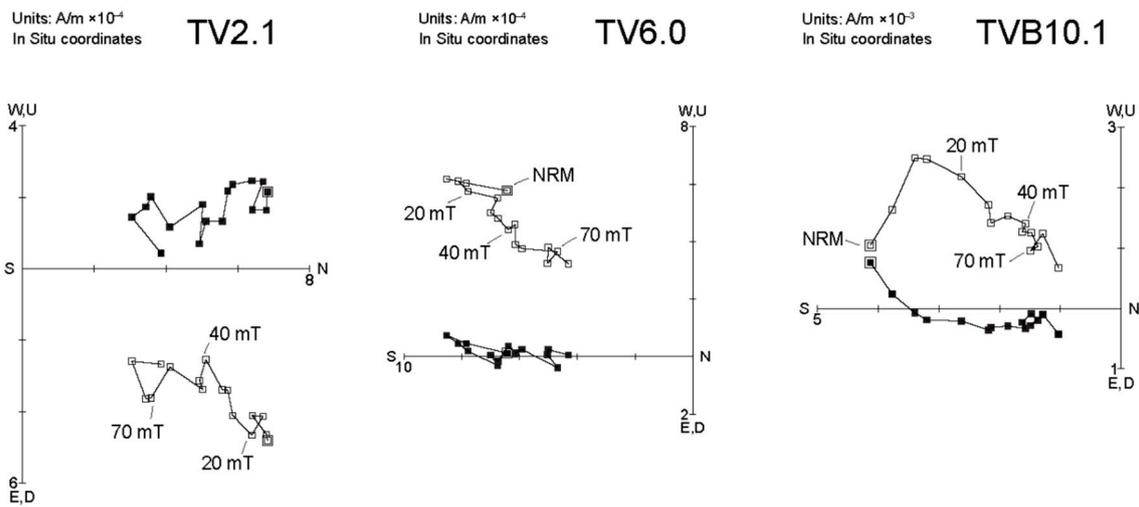
Figure 6. Vector end-point demagnetization diagrams of key samples from the Tsiotra Vryssi section in in situ coordinates. Closed squares are projections onto the horizontal plane, and open squares are projections onto the vertical plane. Applied AF covers a range 0–100 mT with steps of 5 mT up to 50 mT and of 10 mT up to 100 mT.

Table 3. Palaeomagnetic mean direction and pole form the Tsiotra Vryssi characteristic remanent magnetization (ChRM) component directions. N, number of samples; k, Fisher precision parameter; α_{95}, radius of the cone of 95% confidence; Dec., mean declination of the ChRM component; Inc., mean inclination of the ChRM component; Lat., latitude of palaeomagnetic pole; Long., longitude of palaeomagnetic pole; A_{95}, radius of the cone of 95% confidence around the palaeomagnetic pole.

Mean Directions In Situ					Palaeopole		
N	k	α_{95}	Dec.	Inc.	Lat.	Long.	A_{95}
23	9.0	10.7°	176.8 °E	−40.5°	72.4 °N	213.2 °E	7.8°
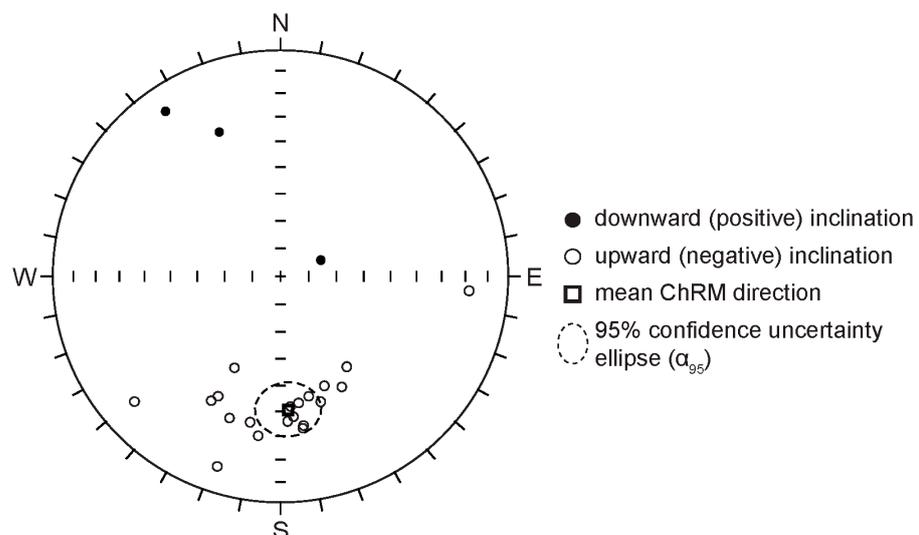
Figure 7. Equal-area projections of the ChRM component directions from the Tsiotra Vryssi section (see Table 3 for mean direction).

When plotted versus stratigraphic depth, the latitude (positive for normal polarity, negative for reverse polarity) of virtual geomagnetic poles (VGPs) calculated for each ChRM component direction (Figure 4) define a lower incomplete normal magnetic polarity interval overlain by an incomplete reverse polarity interval (Figure 4).

4.4. Biochronology

The presence of the large-sized hyena *Pachycrocuta brevirostris* in the TSR fauna indicates a post-middle Villafranchian age, as the migration of this species to Europe, referred to as the "*Pachycrocuta brevirostris* event", is tentatively dated at ~2.0 Ma [3] and marks the beginning of the late Villafranchian [2]. Approximately at the same time, *Canis sensu stricto* also becomes widespread [70,71]. This taxon's earliest occurrences in the Balkan Peninsula are traced at Slivnitsa (Bulgaria) and Gerakarou 1, correlated to the middle/late Villafranchian boundary [24,72,73]. The bear *Ursus etruscus* from TSR differs from the middle Villafranchian specimens of Saint-Vallier (France) and is more similar to the typical *U. etruscus* from Upper Valdarno (Olivola and Tasso Faunal Units (FUs) of Italy); however, it is most similar to the specimens from Pietrafitta (Farneta FU) [36], tentatively dated at ca. 1.7–1.5 Ma [1,3,74]. The large-sized deer *Praemegaceros* and the spiral-horned antelope *Pontoceros* first occur at Dmanisi and are present soon after in the northern peri-Black Sea region and the Balkan Peninsula [75,76], while *Praemegaceros* appears in Italy during the Farneta FU [1] and in Spain after ~1.6 Ma, at the Orce sites [77]. The giraffid *Palaeotragus* is well recorded during the middle Villafranchian, and is also present in the late Villafranchian of Fonelas P-1, Dmanisi, Libakos, and Denizli-Kocabaş [78], but has not been documented, as yet, in the fossil-rich Pirro Nord, the Orce sites, Apollonia 1, or Untermassfeld, collectively correlated to the second half of the late Villafranchian and Epivillafranchian [1,7]. The strongest biochronological indicator recovered so far from TSR is the co-existence of the large-sized bovids *Leptobos* and *Bison*. *Leptobos* was present in Europe during the early and middle Villafranchian but also survived during the first part of the late Villafranchian (e.g., [65,79]). The earliest record of bisons in western Eurasia is documented at Dmanisi (~1.8 Ma), while they subsequently dispersed into peri-Mediterranean Europe from ~1.7–1.5 Ma onwards (e.g., Farneta FU, Orce sites, Pirro Nord, Apollonia-1, Sima del Elefante-TE9). The *Leptobos-Bison* co-existence is relatively rare; apart from TSR, it is recorded in Mygdonia Basin at Krimni-1 and Kalamoto-2, as well as further afield at Trlica 11–10 in Montenegro, the Taurida Cave in Russia and Pietrafitta in Italy [35,67,75,79,80].

In order to examine more comprehensively the overall faunal relationships and similarities between TSR and other middle Villafranchian–Epivillafranchian localities of western Eurasia, we conducted hierarchical cluster analysis at the genus level. The resulting Q-mode dendrogram (Figure 8) clusters the faunas chronologically (rather than geographically). Two main clusters emerge, reflecting the significant faunal reorganization (even at genus level) close to ~2.0 Ma at the middle/late Villafranchian boundary, i.e., cluster A, including the middle and middle/late Villafranchian faunas (Dafnero and Slivnitsa) and cluster B encompassing the late Villafranchian to Epivillafranchian ones. Cluster B is further divided into two subclusters, i.e., B1 consisting of the late Villafranchian to Epivillafranchian faunas younger than ~2.0–1.9 Ma and B2 including those faunas that are at or slightly after the middle/late Villafranchian boundary, at ca. 2.0 (Fonelas P-1 and Gerakarou-1). Subcluster B1 is separated into B1.1 of the late Villafranchian to Epivillafranchian faunas of Europe and B1.2 of Dmanisi. The former is further divided into B1.1.1 (~2.0–1.5 Ma) and B1.1.2 (after ~1.6–1.5 Ma). This distinction signifies the small-scale reorganization of the faunas at the genus level during the middle part of the late Villafranchian, leading to the faunas (B1.1.2) of the second part of the late Villafranchian and the Epivillafranchian, which have "lost" middle Villafranchian relics and have mostly "renewed" their faunal elements. B1.1.1 is separated into B1.1.1a, which includes the 2.0–1.8 Ma faunas of Poggio Rosso and Pantalla (both within Olivola/Tasso FUs [1,81]; and B1.1.1b, with the faunas dated between ~1.8 and ~1.5 Ma. B1.1.1b, including TSR, represents the time interval, which documents the co-existence of *Leptobos* and *Bison*, the earliest occurrences of *Praemegaceros* in Europe, and

is overall characterized by the mixture of middle ("archaic") Villafranchian components and "modern" late Villafranchian newcomers.
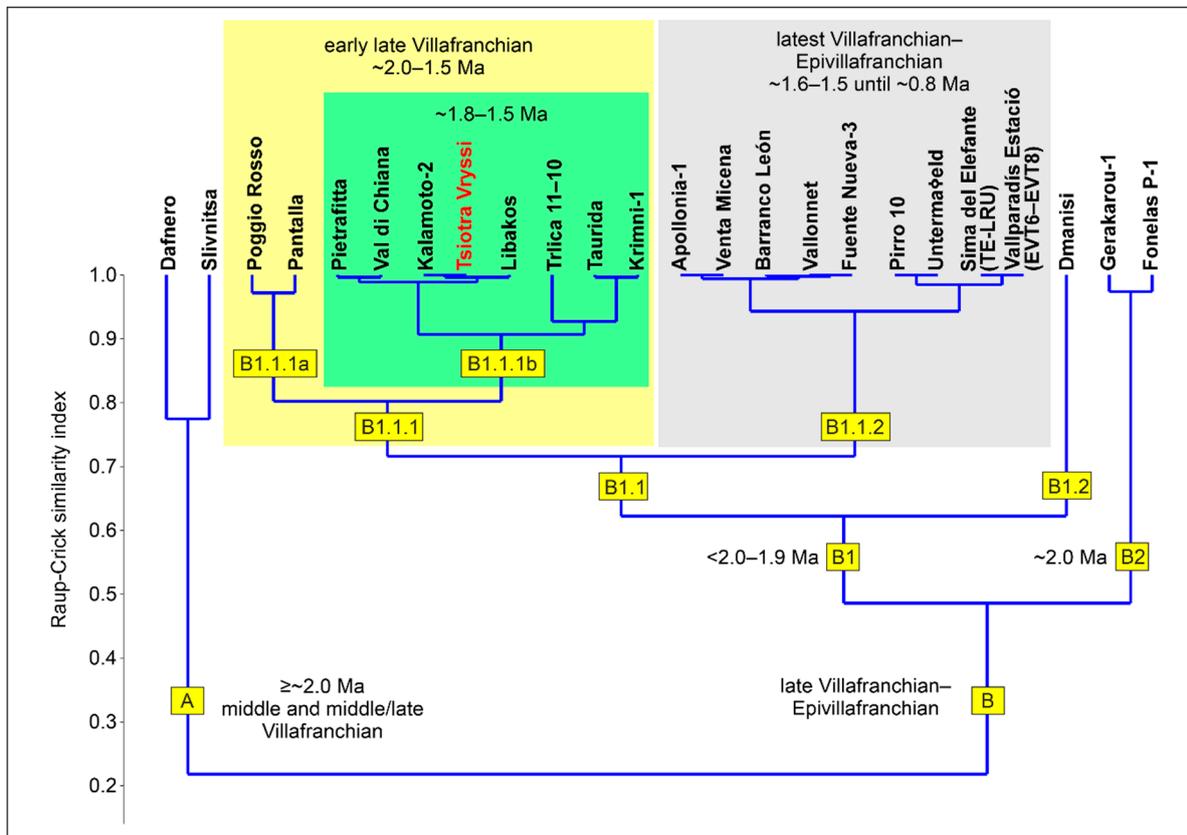

Figure 8. Hierarchical cluster analysis at the genus level showing the faunal similarities among selected middle Villafranchian to Epivillafranchian mammal assemblages of western Eurasia.

Considering all biochronological data, TSR is younger than the middle Villafranchian (~2.6–2.0 Ma) faunas and older than the latest Villfranchian and Epivillafranchian ones (~1.5–0.8 Ma, e.g, the Orce sites, Apollonia-1, Pirro Nord, Untermassfeld, and Vallonnet). On the basis of the large mammals, a biochronological age between ~1.8 and 1.6–1.5 Ma is expected for TSR.

5. Discussion

5.1. Age Estimation: Age Constraints

The minimum burial ages (1.88 ± 0.16 Ma, 2.10 ± 0.18 Ma, and 1.98 ± 0.18 Ma) provided by the cosmogenic radionuclide method indicate that the normal magnetic polarity interval encompassing Geo 2b and the bottom part of Geo 2a correlates to the Olduvai subchron (1.95–1.78 Ma, C2n). As a result, the whole magnetic polarity sequence corresponds to the late part of the Olduvai and the early part of the succeeding Matuyama Chron, whose base is currently dated to 1.78 Ma [82]. Therefore, an age younger than 1.78 Ma is indicated for the fossiliferous layer (the bulk of Geo 2a), which was deposited during reverse polarity chron C1r. These results are in very good agreement with the biochronological data, which also indicate an upper age limit at ~1.5 Ma for the fossil accumulation. Therefore, an age between 1.78 and ~1.5 Ma (within the first part of the late Villafranchian) is proposed for the TSR fauna (Figure 9).
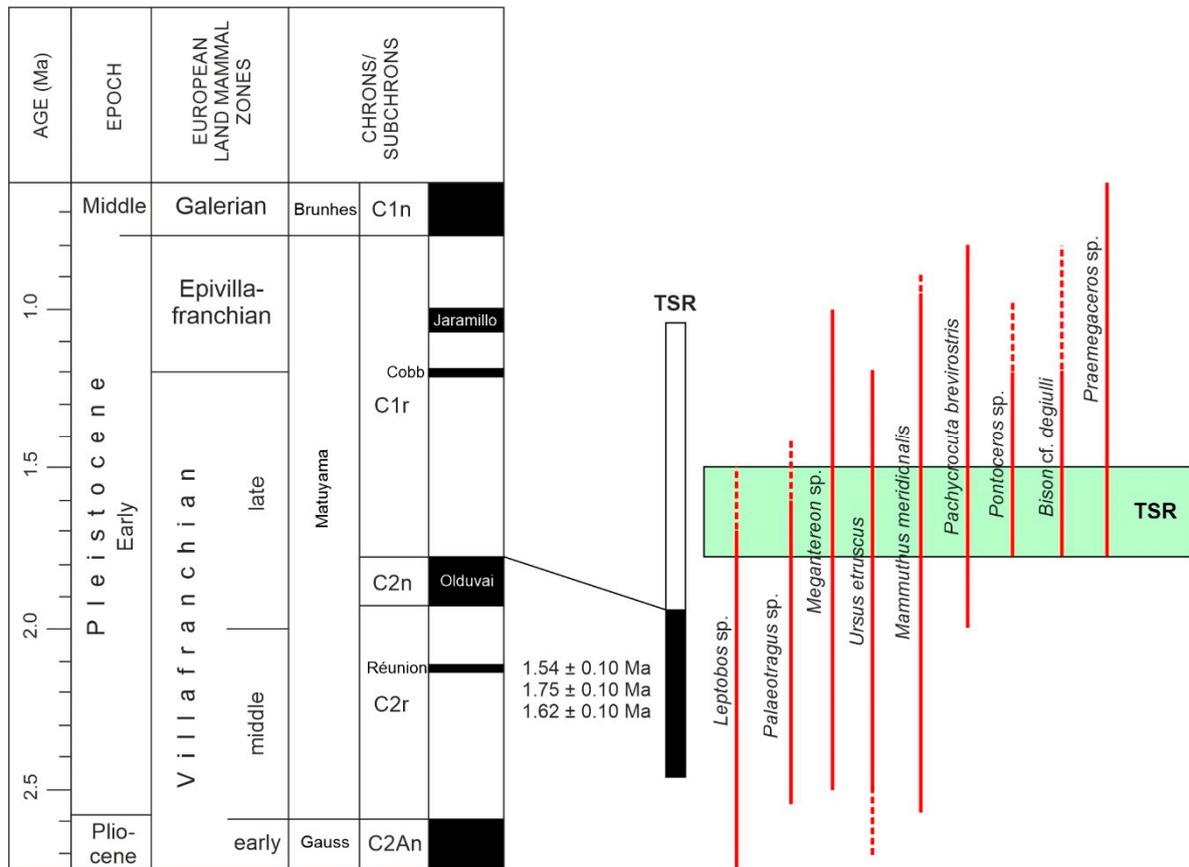
Figure 9. Correlation with the geomagnetic polarity time scale (GPTS) [82], simple burial ages provided by cosmogenic radionuclides, and biochronological range of selected large mammals from Tsiotra Vryssi.

5.2. Placement of TSR within the Greek and European Context

The TSR fauna lacks typical middle Villafranchian (~2.6–2.0 Ma) large mammal associations, including the cervids *Croizetoceros*, *Metacervocerus*, and *Eucladoceros*; the bovids *Gazella*, *Gazellospira*, and *Gallogoral*; the canid *Nyctereutes*; and the hyaenids *Chasmaporthetes* and *Pliocrocuta*, present in the Saint-Vallier FU, Varshets (Bulgaria), as well as in the Greek fossil record, for example, in Dafnero, Sesklo, Vatera, and Volax [1,22,56,83]. TSR also appears younger than the "*Canis*" or "*Panthera*" sites of the Costa San Giacomo FU, Senéze (France), La Puebla de Valverde (Spain) and Slivnitsa, correlated close to the middle/late Villafranchian boundary, and which preserve most of the genera mentioned above [56,61,81,84]. However, TSR retains some middle Villafranchian taxa, which also survived until the beginning of the late Villafranchian, such as *Leptobos* and *Palaeotragus*. On the other hand, the TSR fauna includes several late Villafranchian newcomers, such as *Pachycrocuta*, *Pontoceros*, *Bison* and *Praemegaceros*. The association *Palaeotragus + Praemegaceros* (+ *Leptobos* in [85]) is so far only recorded in Fîntîna lui Mitilan (Romania, [86]), the association *Leptobos + Bison + Pontoceros + Praemegaceros* + two *Equus* species is documented to date only in Trlica 11–10 [75], while the association *Leptobos + Bison + Pontoceros* + two *Equus* species in Taurida Cave [67]. TSR is also close to Dmanisi, whose faunal record includes *Palaeotragus*, *Bison*, *Pontoceros*, *Praemegaceros*, and two *Equus* species [11]. With respect to localities of the central/western sector of the Mediterranean region, TSR is chronologically younger than Fonelas-P1, Poggio Rosso, and Upper Valdarno localities, all correlated to the beginning of the late Villafranchian (ca. 2.0–1.8 Ma), and it is older than Venta Micena, Pirro Nord, Fuente Nueva-3, and Barranco León, collectively dated after ca. 1.6–1.5 Ma, fitting best with the Farneta FU of Italy.

Within the regional faunal succession, TSR is younger than Gerakarou 1 yielding the late Villafranchian "marker" *Pachycrocuta brevirostris*, but otherwise still retaining a more "middle Villafranchian character" in its fauna including the bovid *Gazella* (in Italy not later than the Costa San Giacomo FU [79,87]) and the suid *Sus strozzi* (see [88]). On the other hand, TSR is older than Apollonia 1, where middle Villafranchian relics are absent, and typical late Villafranchian components are present, such as *Canis apolloniensis* (*Canis* ex gr. *mosbachensis*), *Bison*, *Praemegaceros,* and *Pontoceros*, accompanied by various caprines/ovibovines [22], the latter, so far, absent from TSR. The current data indicate that TSR is perhaps chronologically close (although faunal and perhaps chronological differences do exist) with Krimni-1 and Kalamoto-2, where leptobovine bovids also coexist with bisons. Outside the Mygdonia Basin, Libakos (Aliakmon Basin) might be of comparable age to TSR. Libakos has yielded *Leptobos*, *Palaeotragus*, *Pachycrocuta*, *Pontoceros*, *Equus altidens*, and two *Canis* species, in association, however, with the more "modern" *Hippopotamus antiquus*, and the cervids *Praedama savini* and *Dama vallonnetensis* [22,89].

6. Conclusions

Cosmogenic radionuclide dating provides numerical age constraints on the normal polarity detected from the magnetostratigraphic analysis below the fossiliferous layer, correlating it to the Olduvai Subchron. The reverse polarity interval identified in the fossiliferous layer, combined with the biochronological data, indicate that the TSR sediments were deposited during the early part of the Matuyama Chron, between 1.78 and ~1.5 Ma. Overall, TSR presents faunal similarities with Dmanisi, the Farneta FU, Trlica 11–10, Taurida, and the Greek faunas of Libakos, Krimni-1, and Kalamoto-2. Our results not only provide constraints for the age of the local mammal faunal succession, but also help to improve correlations on a broader scale between northern Mediterranean and peri-Black Sea sites, thus, leading to more accurate biogeographic, palaeoecological, and taphonomic interpretations during a crucial interval of time for mammal/hominin migrations and faunal turnovers.

The dating of TSR at ca. 1.78–1.5 Ma places the site close to (or shortly after) the age of Dmanisi, which documents the earliest presence of hominins in western Eurasia. Additionally, this interval records the last occurrences of a number of Villafranchian taxa, as well as the onset of a gradual displacement of other taxa by large mammals that characterize the following Epivillafranchian and Galerian large mammal ages [1,7,9]. Inter-regional differences in the timing and extent of faunal renewals, dispersals, and changes in the structure of mammal palaeocommunities reflect the variability in biotic responses to ecological stimuli according to the geographic setting and prevailing environmental conditions [9,90]. Chronological frameworks serve as the building blocks that allow us to assess potential synchroneity, asynchrony, or diachrony in faunal dynamics. Such detailed studies have been lacking until recently for the Pleistocene of the Greek peninsula. Together with the current investigations for the middle Villafranchian [31,66], our study contributes to filling this gap by providing, for the first time, palaeomagnetic and radiometric constraints to a late Villafranchian locality in the Balkans, and in the Mygdonia Basin in particular, which is one of the most important and richest fossiliferous basins in southeastern Europe. Further refinement of the chronostratigraphic framework of the Mygdonia Basin would provide a better understanding of faunal changes within this sedimentary basin and help calibrate biochronological correlations with other, supra-regional faunal complexes.

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