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The Late Pliocene–Middle Pleistocene Large Mammal Faunal Units of Greece

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Abstract: Located at the eastern corner of Mediterranean Europe, Greece occupies a critical position for mammal dispersals to/from Europe, Asia, and Africa and constitutes a potential passageway towards Western Europe. During recent decades, numerous fieldwork campaigns in several Pliocene–Pleistocene sites have greatly enriched the fossil record and provided valuable taxonomic and biostratigraphic data. However, a fully developed reference biochronological unit scheme for the Greek record that could contribute to correlations at a continental scale is still pending. In this article, we provide the updated Late Pliocene to Middle Pleistocene large mammal succession, and we introduce the Faunal Units (FUs) of Greece. We define eight FUs, the Milia, Dafnero, Gerakarou, Tsiotra Vryssi, Krimni, Apollonia, Marathousa, and Apidima FUs (from the oldest to the youngest), which are determined by a set of first and last local occurrences. The results form the basis for discussion of already set turnovers, dispersals, and extinction/immigration events and showcase the importance of the local record for the investigation of the European terrestrial ecosystems. By developing the first detailed biochronological scheme for the Pliocene–Pleistocene of Southeastern Europe, this study comprises the basis for an expanded Balkan faunal unit scale and a reference framework for future investigations.



Citation: Konidaris, G.E.; Kostopoulos, D.S. The Late Pliocene–Middle Pleistocene Large Mammal Faunal Units of Greece. *Quaternary* **2024**, *7*, 27. <https://doi.org/10.3390/quat7020027>

Academic Editor: Maria Rita Palombo

Received: 3 April 2024

Revised: 31 May 2024

Accepted: 7 June 2024

Published: 12 June 2024



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Keywords: biochronology; biostratigraphy; Villafranchian; Galerian; faunal units; Pliocene; Pleistocene; Greece

1. Introduction

As one of the most likely passageways from Africa/Levant and as the main gate from Asia to Europe, the Balkans have long been considered crucial in understanding and developing the Neogene/Quaternary European continental biostratigraphy and biochronology (e.g., [1–7]). Greece occupies a critical position at the southernmost tip of the Balkans and at the eastern corner of the Mediterranean Europe, and the region's fossil record is of fundamental importance and interest in this discussion.

Research of fossil vertebrate in Greece has a long tradition for almost two centuries, with numerous sites and finds (e.g., [8,9]) that systematically add to the knowledge of the evolution of the Quaternary continental and insular faunas of Europe. During the last two decades, numerous fieldwork campaigns at multiple sites (e.g., Dafnero, Sesklo, Vatera, Volakas, Libakos, Mygdonia Basin, and Megalopolis Basin) by various paleontological teams have greatly enriched the Late Pliocene to Middle Pleistocene fossil record in Greece and provided valuable taxonomic, biostratigraphic, paleoenvironmental, and taphonomic data. Although basic, local biochronological–biostratigraphic schemes have already been proposed and revised on many occasions (e.g., [6,10–13]), they remain atypical, and no systematic effort has been made so far to manage the available data towards the creation of

a formal and broader local/regional biochronological unit scheme that could contribute to correlations at a continental scale.

Based on previous studies and new data, we provide the updated Late Pliocene to Middle Pleistocene mammal succession in Greece by means of faunal units and discuss key taxa in both the regional and pan-European frame. Using available local chronological markers and biochronological evidence, we time-calibrate the local faunal scale and correlate it with well-dated faunas of Western Europe. The results form the basis for a discussion of already set mammal turnovers, dispersals, and extinction/immigration events and showcase the importance of the local record for the investigation of the European terrestrial ecosystems. We expect this effort to provide a basis for an expanded Balkan Pliocene–Pleistocene faunal unit scale and a reference framework for future investigations.

2. Methods

Our approach focuses on the Villafranchian, Galerian, and Aurelian European Land Mammal Ages (ELMAs) as redefined by Rook and Martínez-Navarro, Bellucci et al., and Palombo [14–16]. The Villafranchian is subdivided into early (ca. 3.5–2.6 Ma), middle (ca. 2.6–2.1 Ma), and late (ca. 2.1–1.2 Ma) periods, while we also recognize the Epivillafranchian (ca. 1.2–0.8 Ma) as a distinct transitional ELMA between those of the Villafranchian and Galerian [17,18]. Our analysis is based on the biochron concept of faunal units (FUs) as introduced by Azzaroli [19], reviewed by Azzaroli et al. [20] and Gliozzi et al. [21], and discussed by many later authors (e.g., [22–24]). A FU corresponds to an assemblage interval biochron sensu Walsh [25]; it represents a local/regional biochron of the lowest rank, including a typical local/regional taxa association or well recognized evolutionary stage(s) of particular phyletic lineage(s) and is defined by clear bioevents (paleobiological events sensu Walsh [25]) such as the first or last local historical appearances of one or more taxa (e.g., [21,22,25]).

Our dataset includes Greek mammal assemblages spanning from ~3.5 to ~0.12 Ma (Late Pliocene to Middle/Late Pleistocene) that include more than three large mammal taxa identified at least at the genus level. Faunal lists of local faunal assemblages (LFAs) derive from a wide range of literature references (e.g., [6,8,9,13,26,27] and references cited). Published and unpublished data recovered from recently described sites and faunas (such as GAS, SES-L, DFN3, KZ, AK, TSR, PLN, KMN, KYP-3, 4, and MAR-1; Table 1), updated lists of already known LFAs (such as DFN, APL, APD, and LIB), and new chronological calibrations (such as for DFN/DFN3, TSR, and MAR-1) are all involved in the analysis in order to achieve the maximum possible information and time control. In some cases, published taxonomic identifications have been updated and/or reviewed according to the current knowledge to reach a basic taxonomic consensus.

A hierarchical cluster analysis based on presence/absence data at the genus level was applied to a subset of the 23 most complete Greek LFAs (number of recorded genera ≥ 5) and 43 genera of large mammals (Supplementary Material) in order to test their best possible grouping(s) by means of faunal synthesis consistency and correlate clusters with particular time slices. The analysis was performed using PAST [28]. The Q-mode dendrogram [following UPGMA: unweighted pair group method with arithmetic mean algorithm] was obtained by applying several similarity indices, which provided consistent final groupings; the results of the Raup–Crick similarity index, which is used to statistically test presence/absence data through a randomization method [29], were selected for presentation. We excluded, however, a posteriori Aghia Kyriaki (AK; N genera = 6) as it stands as an outlier in most of the runs.

Distinct Greek faunal units (GFUs) have been defined within each cluster based on a species-level analysis on the whole set of data. Local first and last historical appearances (hereinafter referred to as first and last local occurrences, FLOs and LLOs, respectively) of large mammal taxa have been used for the definition of each GFU. Fossiliferous sites included in this study along with their location and selected references are provided in Table 1.

Table 1. Fossiliferous sites included in the study including their abbreviations, locations, and selected references.

Abbreviation	Fossiliferous Site	Location	Selected References
ALK-VOL	Halykes-Volos	Thessaly	[26,30]
AK	Aghia Kyriaki	Aetoloakarnania	[31]
APD-A, B	Apidima Caves A, B	Peloponnese	[5,32]
APL	Apollonia-1	Mygdonia Basin, Macedonia	[33–36]
APO	Apolakkia	Rhodes Island	[26,37,38]
DAM	Damatria	Rhodes Island	[11,26]
DFN, DFN3	Dafnero 1, 3	Haliakmon valley	[39–41]
GAS	Gephyra	Axios valley	[42]
GER	Gerakarou-1	Mygdonia Basin	[6,43]
KAF	Kaiafas	Peloponnese	[11]
KAL, KLT	Kalamoto 1, 2	Mygdonia Basin	[44]
KPT	Kapetanios	Haliakmon valley	[45]
KRI, KRM KMN	Krimni 1, 2, 3	Mygdonia Basin	[46]
KSR	Kastritsi	Thessaly	[47]
KYP-3, 4	Kyparissia 3, 4	Megalopolis Basin, Peloponnese	[48–50]
KZ	Karnezeika	Peloponnese	[51,52]
LIB	Libakos	Haliakmon valley	[45]
MAR	Marathoussa	Mygdonia Basin	[53]
MAR-1, 2	Marathousa 1, 2	Megalopolis Basin	[50,54,55]
MIL	Milia	Haliakmon valley	[56,57]
MKN	Makinia	Aetoloakarnania	[47]
SES-L	Sesklo (Lower Level)	Thessaly	[58,59]
SES-U	Sesklo (Upper Level)	Thessaly	[58,59]
PEC	Petalona Cave	Chalkidiki peninsula	[60–62]
PLN	Platanochori-1	Mygdonia Basin	[63]
POL	Polylakkos	Haliakmon valley	[45]
PYR	Pyrgos	Peloponnese	[26]
RVL	Ravin of Voulgarakis	Mygdonia Basin	[43]
RIZ	Riza	Mygdonia Basin	[43]
TB-2–5	Tourkovounia 2–5	Attica	[64,65]
TSR:	Tsiotra Vryssi	Mygdonia Basin	[63,66]
VAT	Vatera	Lesvos Island	[67,68]
VOL	Volakas	Drama Basin	[11,69]
VSL	Vassiloudi	Mygdonia Basin	[43]

3. Results

The cluster analysis provided three main groups of LFAs (similarity index ≥ 0.5) that roughly correspond to recognized ELMAs. Galerian and Aurelian LFAs (KYP-3, 4, MAR-1, APD-A, B; cluster “A” in Figure 1) are clearly separated from those of the Villafranchian–Epivillafranchian (cluster “B” in Figure 1) based on the *Homo* + *Palaeoloxodon* + *Cervus* s. str. + *Dama* + *Hippopotamus* large mammal association. Subcluster “a1” can be dated between 780 and ca. 450 ka as it includes the sites KYP-4 (lower part of the Middle Pleistocene <780 ka [70,71], MAR-1 (ca. 450 ka, correlated to Marine Isotope Stage 12 [72]), and KYP-3 (intermediate stratigraphic position between KYP-4 and MAR-1 [70]). Subcluster “a2” is represented in the analysis only by APD-A and B LFAs and corresponds broadly to the late Middle Pleistocene; the crania of *Homo* from Apidima Cave A provided ages of ca. 210 and 170 ka [5], and a comparable or slightly younger age can be assumed for Apidima Cave B.

Cluster “B” incorporates Villafranchian and Epivillafranchian LFAs (Figure 1). Within subcluster “b1”, the LFA grouping largely follows the informal scheme of the early (“b1.a”), middle (“b1.b”), and early late (“b1.c”) Villafranchian subdivision, whereas late Villafranchian (“b2.a”) and latest Villafranchian–Epivillafranchian (“b2.b”) assemblages are incorporated in subcluster “b2”. The “b1.a” subcluster includes the LFAs of MIL, SES-L, and APO, characterized by the co-occurrence of *Anancus* + *Hipparion* in contrast to any other group of LFAs included in the analysis. Vlachos et al. [57] correlated the best-

documented Milia (MIL) faunal assemblage with MN16a, suggesting an approximate age of 3.0–2.8 Ma [73]. We find the link of this cluster with “b1.c” artificial and therefore of very low credibility; it is mainly based on the common presence of *Sus* and *Gazella*, though species-level taxonomy is sharply different in these two sets of faunas.

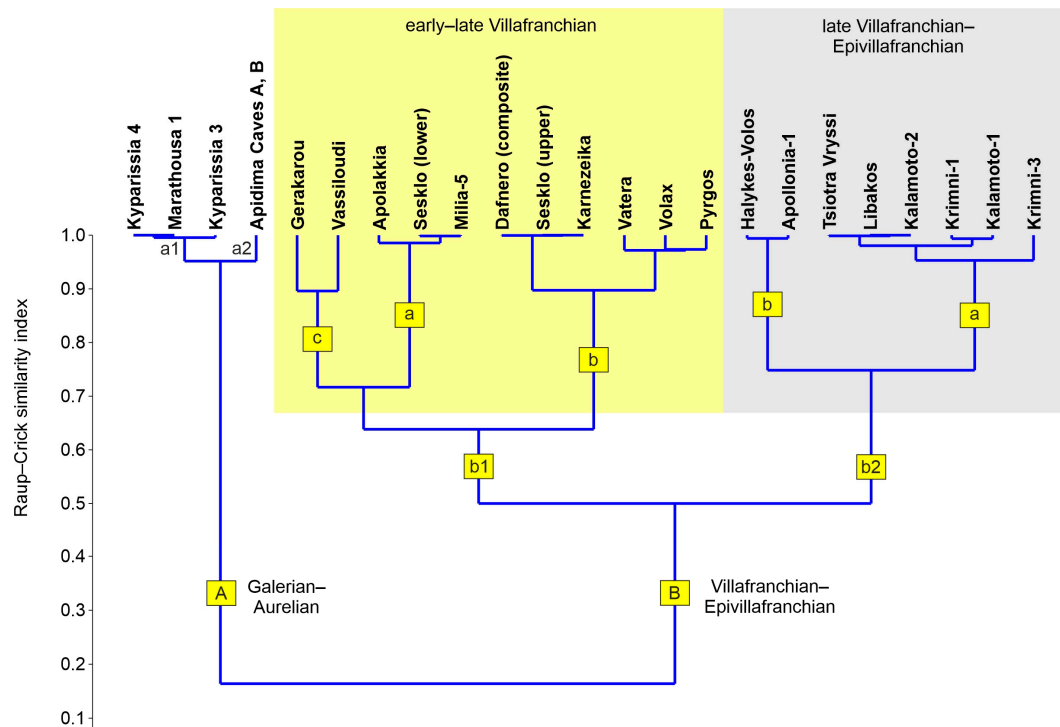


Figure 1. Hierarchical cluster analysis at the genus level showing the faunal similarities among selected Villafranchian to Aurelian large mammal assemblages of Greece.

Subcluster “b1.b” includes the LFAs of DFN/DFN3, SES-U, VAT, VOL, KZ, and PYR (Figure 1). With the exception of Pyrgos (PYR), this faunal assemblage is characterized by the association of *Nyctereutes* + *Equus* + *Palaeotragus* + *Gazella* + *Gazellospira* + *Gallogoral*, while *Paradolichopithecus* is also present in three out of the remaining five LFAs. Based on magnetochronology of the DFN/DFN3 sites [39], this group of LFAs is dated around 2.4–2.3 Ma. The PYR LFA, rather, has to be excluded from this subcluster and is likely associated with “b1.c”, as suggested by the lack of basic taxa of this association (e.g., *Gallogoral*, *Nyctereutes*) and evidenced by the species-level taxonomy of its equid content [74].

The subcluster “b1.c” includes the LFAs of GER and VSL (Figure 1) and is characterized by the association of *Equus* + *Sus* + *Gazella* + *Leptobos*. Although *Canis* is recorded only in GER LFA, we suggest it is part of this association, and its absence from VSL is due to the limited material from this LFA. Both GER and VSL belong to the same stratigraphic levels of Mygdonia Basin, below the TSR LFA which provided a maximum age of 1.78 Ma [66]. Hence, we estimate an age of about 2.0 Ma for this faunal group, confirmed by the common presence of *Pliocrocuta* and *Pachycrocuta* in GER.

Within “b2”, the subcluster “b2.a” includes the LFAs of TSR, LIB, KLT, KRI, KAL, and KMN (Figure 1). The faunal assemblage is characterized by the co-occurrence of *Mammuthus* + *Equus* + *Stephanorhinus* + *Hippopotamus* + *Dama*-like deer and, although not present in every single LFA, by *Canis* + *Pachycrocuta* and the coexistence of *Leptobos* and *Eobison*. Based on TSR [66], this cluster of LFAs is dated between 1.78 and ca. 1.5 Ma.

The subcluster b2.b includes the LFA of APL and most likely ALK-VOL (Figure 1). At the genus level, it is defined by the association of *Equus* + *Canis* + *Hemitragus* and likely *Pachycrocuta*, *Mammuthus*, and *Pontoceros*. The large mammal association at the genus level appears quite similar to that of the previous assemblage, but key taxa such as *Palaeotragus*

and *Leptobos* are missing. Although no geochronological evidence is available for this assemblage, it is safely placed between 1.5 and 0.8 Ma and likely around 1.2 Ma [6].

4. Discussion

4.1. Establishment of the Greek Faunal Units

Based on the cluster analysis results and the local stratigraphic, biostratigraphic, biochronologic, and geochronologic evidence, the entire set of Greek Late Pliocene to Middle Pleistocene LFAs were reclassified chronologically based on the degree of faunal consistency (Figure 2, fourth column). A species-level analysis within and between successive LFA clusters allow eight GFUs to be recognized, which are (from the base to the top): the Milia FU, Dafnero FU, Gerakarou FU, Tsiotra Vryssi FU, Krimni FU, Apollonia FU, Marathousa FU, and Apidima FU (Figure 2, fifth column). Each GFU is defined by a set of FLOs and LLOs (Figure 3).

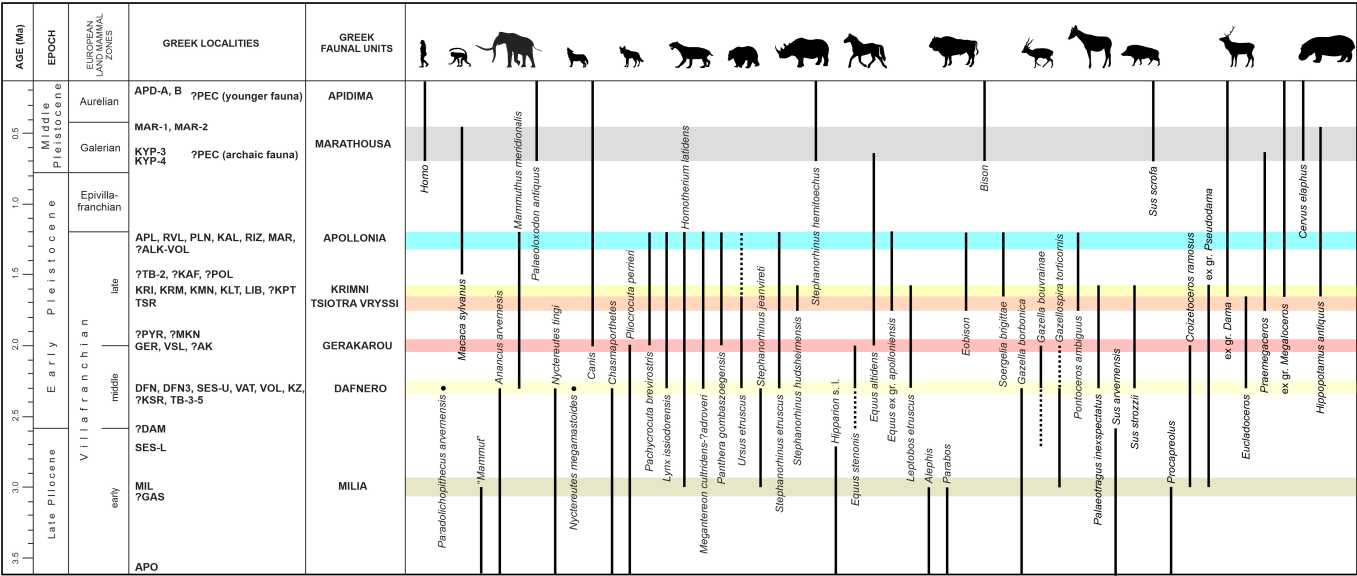


Figure 2. The Late Pliocene–Middle Pleistocene (Villafranchian to Aurelian) large mammal faunal units of Greece, the examined fossiliferous localities, and biochronological range of selected large mammals (silhouette images from [PhyloPic](#), [phylopic.org](#)).

The lack of solid, local evidence concerning early to early/middle Villafranchian LFAs from Greece and the rather sparse record allow only the Milia FU to be recognized within this interval at about 3.0 Ma, including MIL and possibly GAS LFAs (e.g., [42,56,75]). The Milia FU is marked by the LLOs of “*Mammuth*”, *Alephis*, *Parabos*, and *Procapreolus* and the FLOs of *Ursus*, *Homotherium latidens*, *Stephanorhinus jeanvireti*, *Gazellospira torticornis*, *Croizetoceros ramosus*, and cervids of the “*Pseudodama*” lineage (Figure 2). *Mammuthus* might also firstly occur in this FU [76], though data are rather sporadic and not well time-controlled. The older Apolakkia (APO) LFA from Rhodes Island bears very few large mammals and mostly micromammals, the latter indicating a latest Ruscinian (MN15) age [26,37,38]. It is therefore quite possible that at least one more FU can be established below the Milia FU, but data are currently insufficient. Due to the absence of *Equus*, the Sesklo lower level (SES-L) LFA is certainly dated before the Pliocene/Pleistocene boundary [58]. It shares with Milia several common taxa at the genus level (Figure 2), but the large and advanced *Plesiohipparion* and the possible presence of *Gazella bouvraiae* [58] indicate a younger (MN16b) age, and the assemblage might represent a distinct FU between those of Milia and Dafnero, occupying the uppermost part of the early Villafranchian.

AGE (Ma)	EPOCH	EUROPEAN LAND MAMMAL ZONES	GREEK LOCALITIES	GREEK FAUNAL UNITS	FIRST OCCURENCE	LAST OCCURENCE
0.5	Middle Pleistocene	Aurelian	APD-A, B ?PEC (younger fauna)	APIDIMA	<i>Felis silvestris</i> , <i>Lynx lynx</i> , <i>Canis lupus</i> , <i>Ursus arctos</i> , <i>Dama dama</i> , <i>Capra ibex</i>	<i>Palaeoloxodon antiquus</i> , <i>Panthera pardus</i> , <i>Panthera spelaea</i> , <i>Crocota crocuta</i> , <i>Ursus spelaeus</i> , <i>Stephanorhinus hemitoechus</i> , <i>Bison priscus</i> , <i>Megaloceros</i> , <i>Hippopotamus amphibius</i>
1.0	Middle Pleistocene	Galerian	MAR-1, MAR-2 KYP-3 KYP-4 ?PEC (archaic fauna)	MARATHOUSA	<i>Homo</i> , <i>Lutra simplicidens</i> , <i>Panthera spelaea</i> , <i>Crocota</i> , <i>"Hyaena" prisca</i> , <i>Ursus deningeri</i> , <i>Palaeoloxodon</i> , <i>Mammuthus trogontherii</i> , <i>Stephanorhinus hemitoechus</i> , <i>Cervus</i> , <i>Dama</i> , <i>Sus scrofa</i> , <i>Bison</i> , cf. <i>Bos</i>	<i>Macaca sylvanus</i> , <i>Lutra simplicidens</i> , <i>Equus altidens</i> , <i>Praemegaceros</i> , <i>Hippopotamus antiquus</i>
1.5	Pleistocene	EpiVillafranchian				
2.0	Early Pleistocene	late	APL, RVL, PLN, KAL, RIZ, MAR, ?ALK-VOL ?TB-2, ?KAF, ?POL KRI, KRM, KMN, KLT, LIB, ?KPT TSR	APOLLONIA KRIMNI TSIOTRA VRYSSI	<i>Soergelia</i> , <i>Megaloceros</i> , <i>Hippopotamus</i> , <i>Dama</i> group, <i>Equus</i> ex gr. <i>apolloniensis</i> , <i>Stephanorhinus hundsheimensis</i> , <i>Pontoceros</i> , <i>Eobison</i> , <i>Praemegaceros</i>	<i>Mammuthus meridionalis</i> , <i>Lynx issiodorensis</i> , <i>Panthera gombaszoegensis</i> , <i>Megantereon</i> , <i>Homotherium</i> , <i>Pachycrocuta</i> , <i>Ursus etruscus</i> , <i>Stephanorhinus etruscus</i> , <i>Equus</i> ex gr. <i>apolloniensis</i> , <i>Pontoceros</i> , <i>Soergelia</i> , <i>Eobison</i>
2.5	Early Pleistocene	middle	?PYR, ?MKN GER, VSL, ?AK	GERAKAROU	<i>Pachycrocuta brevirostris</i> , <i>Canis</i> , <i>Canis (Xenocyon)</i> , <i>Panthera gombaszoegensis</i> , <i>Equus altidens</i>	<i>Pliocrocuta</i> , <i>Equus stenonis</i> s. str., <i>Gazella bouvrinae</i> , <i>Gazellospira</i> , <i>Croizetoceros</i>
3.0	Late Pliocene	early	DFN, DFN3, SES-U, VAT, VOL, KZ, ?KSR, TB-3-5 ?DAM SES-L MIL ?GAS	DAFNERO MILIA	<i>Paradolichopithecus</i> , <i>Ursus etruscus</i> , <i>Lynx issiodorensis</i> , <i>Megantereon cultridens</i> lineage, <i>Mammuthus meridionalis</i> , <i>Stephanorhinus etruscus</i> , <i>Sus strozzii</i> , <i>Eucladoceros</i> s. l., <i>Palaeotragus inexpectatus</i> , <i>Leptobos etruscus</i> <i>Ursus</i> , <i>Homotherium latidens</i> , <i>Stephanorhinus jeanvireti</i> , <i>Gazellospira torticornis</i> , <i>Croizetoceros ramosus</i> , "Pseudodama" lineage	<i>Anancus</i> , <i>Nyctereutes</i> , <i>Stephanorhinus jeanvireti</i> "Mammul", <i>Alephis</i> , <i>Parabos</i> , <i>Procacpreolus</i>
3.5			APO			

Figure 3. Biostratigraphic table of the large mammal localities and faunal units of Greece with the first and last local occurrences of the various taxa.

Apart from the well-known LFAs of DFN/DFN3, SES-U, VAT, VOL, and KZ (e.g., [6,40,51,58,67,69]), the Dafnero FU may also include TB 3-5 and possibly KSR, both known for limited large mammal remains [11,47,65]. The Dafnero FU is characterized by the presence of *Paradolichopithecus arvernensis* and *Nyctereutes megamastoides*; the LLOs of *Anancus*, *Nyctereutes tingi*, *Chasmaporthetes*, *Stephanorhinus jeanvireti*, and *Gazella borbonica*; and the FLOs of *Lynx issiodorensis*, *Megantereon cultridens* lineage, *Ursus etruscus*, *Mammuthus meridionalis*, *Stephanorhinus etruscus*, *Sus strozzii*, *Palaeotragus inexpectatus*, *Eucladoceros* s. l., and *Leptobos etruscus*. The Damatria (DAM) LFA from the upper part of the homonymous Damatria Formation in Rhodes Island is more difficult to assess within this scheme, due to the puzzling evidence arising from the combination of small and large mammals, which are broadly assigned to MN16 [11,26,77]. Local biostratigraphic evidence places the Plio-Pleistocene boundary in the lower part of the overlying Kritika Formation ([78] and references therein). Hence, the presence of *Equus* and *Sus strozzii* (if this latter is confirmed) suggest that the DAM LFA slightly predates or roughly corresponds to the early/middle Villafranchian transition and could potentially be included in the Dafnero FU, which is suggested to last from ca. 2.3 to ca. 2.5 Ma.

The succeeding Gerakarou FU at around 2.0 Ma includes GER, VSL, AK, and possibly PYR and MKN LFAs (e.g., [6,26,31,47] and references cited). The FLOs of *Canis* s. str. along with *Panthera gombaszoegensis*, *Pachycrocuta brevirostris*, and *Equus altidens* are found here, whereas *Pliocrocuta perrieri*, *Equus stenonis* s. str., *Croizetoceros ramosus*, *Gazella bouvrinae*, and most likely *Gazellospira* appear for the last time in the Greek record (Figure 2).

The Tsiotra Vryssi FU follows at about 1.8–1.6 Ma, represented only by the homonymous LFA from Mygdonia Basin (e.g., [63,66]). The faunal assemblage incorporates most taxa that first occurred in the previous GFU but also includes the FLOs of *Stephanorhinus hundsheimensis*, *Equus* ex. gr. *apolloniensis*, *Praemegaceros*, *Eobison*, and *Pontoceros* (and perhaps a smaller-sized *Megantereon*), indicating the beginning of an important renewal of the mammal community. At the same time, canids related to the *Canis mosbachensis* lineage, alongside *Canis (Xenocyon)* [79], also appear in this GFU.

The following Krimni FU, centered around 1.6–1.5 Ma, includes the LFAs of KRI, KRM, KMN, LIB, and KLT and possibly KPT, POL, TB-2, and KAF, the latter two attributed mainly based on their micromammal content (e.g., [11,44–46,64,65]). This GFU is characterized by the LLOs of *Sus strozzi*, *Palaeotragus*, *Leptobos*, and *Eucladoceros* s. l. and by the FLOs of *Soergelia*, the *Megaloceros* lineages, *Hippopotamus*, and perhaps *Macaca sylvanus*, while cervids of the ex gr. “*Pseudodama*” are replaced by those of true *Dama*.

The Apollonia FU includes APL, RVL, PNT, KAL, MAR, and RIZ LFAs from Mygdonia Basin (e.g., [6,33,43,44,63]) and most likely ALK-VOL from Thessaly [26,30,59]. No new FLOs occur in this assemblage, yet the absence of middle (“archaic”) Villafranchian relics (i.e., *Palaeotragus*, *Leptobos*) and the presence of mostly late Villafranchian newcomers indicate the more “modern” characteristics of the fauna. On the other hand, this GFU documents the LLOs of several large mammal taxa, such as *Mammuthus meridionalis*, *Pachycrocuta*, *Lynx issiodorensis*, *Homotherium*, *Megantereon*, *Panthera gombaszoegensis*, *Ursus etruscus*, *Stephanorhinus etruscus*, *Equus* ex gr. *apolloniensis*, *Eobison*, *Soergelia*, and *Pontoceros*. The age of the Apollonia FU is currently estimated at about 1.2 Ma, but it is also possible that the herein included LFAs may cover a wider time span from ca. 1.5 up to 0.9 Ma; alternatively, the scarcity/absence of Greek LFAs from this time interval may obscure the potential presence of an additional “ghost” GFU.

The overlain Marathousa FU, dated between <0.80 and ca. 0.45 Ma, includes LFAs from the Megalopolis Basin in Peloponnese (e.g., KYP-3, 4, MAR-1, 2; [48–50,54,55,80]) and most probably the older (attributed to the early Middle Pleistocene) faunal assemblage from Petralona cave in Chalkidiki Peninsula (e.g., [60,61]). This GFU encompasses the Galerian faunas and is marked by an important reorganization of the fauna including the FLOs of *Homo*, *Palaeoloxodon antiquus*, *Lutra simplicidens*, *Stephanorhinus hemitoechus*, *Bison*, *Sus scrofa*, the *Cervus elaphus* lineage, and possibly *Bos*, while, considering the Middle Pleistocene fauna of Petralona this FU may also include the FLOs of *Ursus deningeri*, *Panthera spelaea*, *Crocota crocuta*, and “*Hyena*” *prisca* (the latter as *Pliocrocota perrieri* in [62]). In addition, the presence of a *Panthera* sp., possibly *Panthera pardus*, at KYP-3 [48] could also potentially represent the FLO of this species, as could also be the case for *Mammuthus trogontherii* from Loussika and other localities (e.g., [81]). On the other hand, the Marathousa FU documents the LLOs of *Macaca sylvanus*, *Equus altidens*, *Hippopotamus antiquus*, and *Praemegaceros* as well as of *Lutra simplicidens*.

The uppermost, Apidima FU, represents the establishment of modern faunal elements at the end of the Middle Pleistocene but can practically be extended to the Late Pleistocene as the large mammal fauna does not evidence any renewal during the latter epoch, besides several disappearances towards its end. In addition to the LFA of the Apidima cave complex (APD-A, B) several other LFAs can be included in this FU, for instance, the caves of Petralona (younger fauna), Vraona, Diros, Agios Georgios, Almopia, Kalamakia, Lakonis, Klissoura, Franchthi, Mavri Spilia, and Melitzia as well as Penios valley (e.g., [82–93]). The possibly oldest LFAs of this FU, APD-A and B [5], mark the beginning of the faunal modernization documenting *Capra ibex*, *Dama dama*, *Lynx lynx*, *Vulpes vulpes*, and *Felis sylvestris* ([32]; the red fox and the wildcat could have already been present in the Marathousa FU) while other modern species such as *Ursus arctos* and *Canis lupus* are present in the other LFAs. The Apidima FU includes the LLOs of *Palaeoloxodon antiquus*, *Panthera pardus*, *Panthera spelaea*, *Crocota crocuta*, *Ursus spelaeus*, *Stephanorhinus hemitoechus*, *Bison prisca*, *Megaloceros*, and *Hippopotamus amphibius*.

4.2. The Greek Faunal Units in the European context

Based on available data from Italy, France, and Spain [14,21,73,94,95], the Milia GFU roughly corresponds to the Triversa FU of Italy and Viallete LFA level in France (Figure 4). The Dafnero GFU is correlated to the St. Vallier FU of Italy and France and the Huelago/Fuente Nueva-1 LFA level in Spain (Figure 4). The Gerakarou GFU is placed between the Costa St. Giacomo and Olivola FU of Italy, Senèze LFA level in France, and La Puebla de Valverde LFA level in Spain (Figure 4). The Tsiotra Vryssi GFU corresponds to

the Tasso FU or to the late Tasso/early Farneta FUs of Italy and the Villanueva di Pitamo LFA level in Spain (Figure 4). The Krimni GFU corresponds to the Farneta FU in Italy and the Venta Micena/Fuente Nueva-2 LFA level in Spain (Figure 4). The Apollonia GFU is placed between the Pirro Nord and Colle Curti FUs of Italy and correlates with the Fuente Nueva-3/Barranco León 5/Sima del Elefante LFA level in Spain (Figure 4). The Marathousa GFU represents a unit within the Isernia and Fontana Ranuccio FUs in Italy and also corresponds to the Gran Dolina TD8, Sima de los Huesos, L'Escafe and Arago CM LFAs in Spain and France, respectively (Figure 4). Finally, the Apidima FU can be correlated to several European localities collectively dated to the end of the Middle–Late Pleistocene.

AGE (Ma)	EPOCH	EUROPEAN MAMMAL ZONES	GREEK LOCALITIES	GREEK FAUNAL UNITS	ITALIAN FAUNAL UNITS	ITALY	LOCALITIES		
							SPAIN	FRANCE	
0.5	Middle Pleistocene	Aurelian	APD-A, B ?PEC (younger fauna)	APIDIMA	VITINIA	Casal de' Pazzi, Torre in Pietra 2			
			MAR-1, MAR-2		TORRE IN PIETRA	La Polledrara			
1.0	Pleistocene	Galerian	KYP-3 ?PEC (archaic fauna)	MARATHOUSA	FONTANA RANUCCIO	Fontana Ranuccio, Castel di Guido	Sima de los Huesos	Lunel Viel	
			KYP-4		ISERNIA	Malagrotta		Arago CMII	
1.5	late	Epivilla-franchian			PONTE GALERIA	Isernia		L'Escale	
					SLIVIA	Ponte Galeria 1			
2.0	middle	Villiafranchian	APL, RVL, PLN, KAL, RIZ, MAR, ?ALK-VOL	APOLLONIA	COLLE CURTI	Colle Curti	Gran Dolina TD8	Saint-Prest	
							Valloparadis Estació (MU)		
2.5	early		?TB-2, ?KAF, ?POL		PIRRO NORD	Pirro Nord	Cal Guardiola (UU)	Le Vallonnet	
			KRI, KRM, KMN, KLT, LIB, ?KPT TSR	KRIMNI	FARNETA	Pietrafitta, Val di Chiana	Valloparadis Estació (LU)		
3.0	Late Pliocene		?PYR, ?MKN	TSIOTRA VRYSSI	TASSO		Fuente Nueva 3		
			GER, VSL, ?AK	GERAKAROU	OLIVOLA	Coggio Rosso	Barranco León 5		
3.5			DFN, DFN3, SES-U, VAT, VOL, KZ, ?KSR, TB-3-5		C.S. GIACOMO	Casa Frata	Incarcal		
			?DAM	DAFNERO	ST. VALLIER	Panfalia	Venta Micena		
			SES-L		MONTOPOLI	Olivola	Fonelas P1	Saint Vallier	
			MIL ?GAS	MILIA			La Puebla de Valverde	Chilhac II	
					TRIVERSA	Montopoli	Huélago	Perrier Les Etouaires	
							Villarroya	Senèze	
								7Fardines	
								Rocaneyra	
						Santa Barbara	Las Higueraulas	Violette	

Figure 4. Correlation of the large mammal localities and faunal units of Greece with those of Italy, Spain, and France (data from [14,16,95,96]).

Several authors discuss the problem of diachrony/asynchrony in transcontinental correlations based on mammals and the establishment of mammal dispersal bioevents (e.g., [23,97,98]). The progressive and often longitudinally or latitudinally directed ($N \leftrightarrow S$, $E \leftrightarrow W$) environmental changes, the geographical proximity/distance to neighboring regions that are potential reservoirs of new taxa (such as Africa and Asia for Europe), and the changing geographical barriers/routes to and from target regions (such as the three peninsulas of Southern Europe) accentuate local diversification and create basic conditions for diachronicity. On the other hand, discontinuities and gaps in the local faunal record (sampling effect), spatiotemporal imbalances in the distribution of LFAs at local, regional and interregional scales, asymmetries in the density of available geochronologic age estimates, and long-lasting taxonomic inconsistencies (e.g., discussion on species-level systematics of European *Canis*, *Eucladoceros*, *Megantereon*, “*Pseudodama*”, and *Equus* species-level systematics) inhibit or even prohibit the recognition of mammal dispersal events and the ascertainment/control of their possible diachronicity. At present it seems rather unreasonable to try to interpret the S. European Pliocene to Pleistocene data at a finer scale than the temporal resolution corresponding to a full FU (100–200 kyr).

Even under these unfavorable conditions, the Greek record provides supporting evidence for already well-known and long-established mammal dispersal events such as those of *Equus* at 2.6–2.5 Ma (as redefined by [98]) and *Pachycrocuta* at ~2.0 Ma [99]. The former is recorded between SES-L and DAM LFAs (or between Milia and Dafnero GFUs). From the Balkan to the Iberian Peninsulas at least, the *Equus* event coincides with the

decline of hipparionine horses [58,100], the replacement of *Sus arvernensis* by *Sus strozii* (e.g., [101]), and the appearance of *Mammuthus meridionalis* (e.g., [102]).

The arrival and rapid expansion of *Pachycrocuta* in Europe is associated with the last occurrences of *Pliocrocuta*, both events recorded in the Gerakarou GFU, which also documents the occurrence of *Panthera gombaszoegensis* [103] that entered Europe roughly at the same time as the giant hyena (e.g., [104]). Although the simultaneous and widely discussed *Canis* event (“wolf event” of [105]) is largely abolished due to the diachronous early evidence of wolf-like taxa across Eurasia (e.g., [14,106–109]), the south European record rather agrees with the firm establishment of cursorial pack-hunting canids (*Canis* ex gr. *etruscus* and *Canis arnensis*) between 2.1 and 2.0 Ma (e.g., [110,111]). It is immediately followed (2.0–1.8 Ma) by the last European occurrences of *Gazella* and *Gazellospira* among herbivores. At the same time *Equus altidens* makes its first appearance in Eastern Europe/the Balkans (e.g., [112,113]).

The next complex bioevent of similar duration starts at 1.7–1.6 Ma. All across Southern Europe, *Leptobos* was replaced by *Eobison*, cervids of the *Praemegaceros*-lineage expanded, *Stephanorhinus hundsheimensis* first occurred in the East [14,46,114], and *Pontoceros* expanded from the north peri-Pontic to the south Balkan territories. At the same time or slightly after (1.6–1.5 Ma), a smaller *Megantereon* replaced the previous larger, one and *Hippopotamus* was firmly established in the northern Mediterranean area (although the genus had sporadically occurred earlier; see [115] and references therein).

A major large mammal turnover is evident in the beginning of the Middle Pleistocene as part of the faunal reorganization close the Early/Middle Pleistocene transition that is associated with the period generally called the “Mid-Pleistocene Revolution” (e.g., [96] and references therein). This event encompasses at the (South) European scale the disappearance of several Villafranchian–Epivillafranchian taxa (e.g., *Mammuthus meridionalis*, *Pachycrocuta*, *Ursus etruscus*, *Megantereon*, *Panthera gombaszoegensis*, and *Soergelia*) and the arrival of several Galerian newcomers (e.g., *Palaeoloxodon*, *Mammuthus trogontherii*, *Crocuta*, *Panthera spelaea*, *Panthera pardus*, *Sus scrofa*, and *Stephanorhinus hemitoechus*). At the Greek scale, this turnover is noticeable in the transition from the Apollonia FU to the Marathousa FU.

5. Conclusions

Low-rank biochronological scales such as FUs have a restricted significance, representing a summary/synthesis of local to regional (bio-)chronological ordering and evolution of the mammalian network under the pressure of climatic/environmental oscillations. In light of the common and multifactorial diachrony/asynchrony phenomena across wide physical and ecological boundaries, the role of FUs appears, however, to be crucial for understanding the dynamics of mammalian dispersal in larger geographical scales and for monitoring bioevents of broader significance (e.g., [14,16,98,116,117]). As local biochronological resolution is based on continuous or adjacent and therefore relatively well-correlated sedimentary sequences, FU scales may provide complementary data to interregional/continental scale correlations, especially in the discontinuous and highly fragmentary terrestrial environments. As such, they facilitate the detection, definition, and control of important bioevents, which in turn lead to the establishment of higher-rank biochronological units/scales.

Previous and ongoing investigations in the Greek Pliocene and Pleistocene allow us to generate a first attempt for a local faunal unit scale (GFU) representing the evolution of large mammal communities from Mid-Pliocene to the Late Pleistocene. Each one of the eight recognized Greek faunal units is defined by a set of first and last local occurrence data, though the latest Pliocene and latest Early Pleistocene are still poorly resolved. Additionally, both the local record as well as those from the south of Western Europe (Italy, France, Spain) suggest that the temporal resolution cannot be improved by current knowledge below a critical interval of 100–200 kyrs, which equals the duration of a full FU. Comparison of the GFU scheme with Western European ones indicates a good correspondence in several dispersal events of particular large mammal taxa. Nevertheless, both the early to middle Villafranchian transition at ~2.6 Ma and the Epivillafranchian faunal reorganization at ca.

1 Ma, thoroughly discussed in the literature (e.g., [14,95,118]), are not expressed as clearly in the large mammal record of Greece as in other Southern European countries due to inadequate data.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/quat7020027/s1>, Table S1: Presence/absence data (genus/locality) used for the hierarchical cluster analysis shown in Figure 1.

Author Contributions: Conceptualization, methodology, investigation, resources, D.S.K. and G.E.K.; validation, formal analysis, data curation, visualization, G.E.K.; writing—original draft preparation, D.S.K.; writing—review and editing, G.E.K. All authors have read and agreed to the published version of the manuscript.

Funding: G.K. is supported by the Deutsche Forschungsgemeinschaft (DFG Project no. 463225251, “MEGALOPOLIS”).

Data Availability Statement: All data used in the present analysis are from published resources or provided as Supplementary Material.

Acknowledgments: We thank all colleagues that throughout the years enriched and studied the large mammal fossil record of Greece and for the various discussions that improved several perspectives of the article. We also thank the four reviewers for their comments and suggestions that improved the manuscript.

Conflicts of Interest: The authors declare no conflicts of interest.

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