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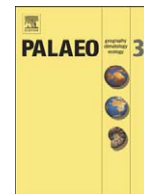
The Pikermian Event: Temporal and spatial resolution of the Turolian large mammal fauna in SE Europe

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ABSTRACT

During the Turolian (late Miocene), the Eastern Mediterranean region is considered to have been part of a single major ecological area, supporting a particular savanna-type large mammal community, referred to as the Pikermian Biome. Analysis of the timing, turnover patterns, biogeographic relations and palaeoecological profile of the Turolian large mammal faunas from either sides of the Aegean Sea failed, however, to confirm the presence of a homogeneous mammal community isotropically behaving through time. For most of the Turolian, the large mammal assemblages from Southern Balkans and Anatolia appear to have existed under different environmental conditions, partly isolated by natural barriers. Overall climatic changes and regional physico-geographic factors, around 7.2 My, allowed the Southern Balkan biogeographic region to be temporarily part of the sub-Paratethyan bioprovince. As a result, significant faunal reorganizations and interchanges triggered the emergence and expansion of the "Pikermian" mammal fauna, which collapsed soon after 7.0 My as a consequence of the early Messinian global changes. The Pikermian Large Mammal Event seems to follow known procedures related with contemporaneous marine and land faunal episodes across the Mediterranean.

1. Introduction

The geographic area that presently incorporates the Southern Balkans, Turkey and part of the South peri-Pontic region, formed during late Miocene the western domain of the so called Greco-Iranian biogeographic province (Bonis de et al., 1992). Classical late Miocene European large mammal sites such as Pikermi, Maragheh, Samos, Salonique, Titov-Veles etc. highlight the spatial extent of this area that provided thousands of fossil remains, relatable to several dozen mammal taxa. Even if the exact late Miocene vegetational character of this land is still called into question, with estimates ranging from sclerophyllus evergreen woodlands to a savanna mosaic (Quade et al., 1994; Cerling et al., 1997; Solounias et al., 1999; Merceron et al., 2004, 2006; Strömberg et al., 2007), a particular mammal community of savanna-like type gradually emerged in the C3-dominated and progressively deforested areas of the Greco-Iranian province during Turolian. Solounias et al. (1999) recognized this ecosystem as a rather homogeneous and isotropically evolved community unit, referred to as the Pikermian Biome.

The ecological character and the timing of the Pikermian Biome have been the subject of several recent studies (Solounias et al., 1999; Spassov, 2002; Fortelius et al., 2006; Bernor, 2007; Strömberg et al., 2007; Costeur and Legendre, 2008; Eronen et al., 2008) without, however, a closer look on its internal structure and its response to

regional physico-geographic factors. In view of this need, the present study analyzes the turnover patterns, the biogeographic relations and the palaeoecological signal of the SE European Turolian large mammal fauna in the western domain of the Greco-Iranian province i.e., the type area of the emergence and acme of the Pikermian Biome.

2. Materials and methods

2.1. The fossil record

Over the last two decades, updated data and new discoveries in the Eastern Mediterranean region have significantly improved our knowledge concerning Turolian large mammal faunas and provided a much more detailed and accurate chronological calibration, based mainly on magnetostratigraphy. The present study focuses on local faunal assemblages (LFAs) from Greece, Bulgaria and Turkey spanning the period 8.7 to 6.7 My, i.e., MN11 and MN12 (Mein, 1999; Steininger, 1999). The studied sample includes a basic group of magneto/radio-chronologically controlled LFAs and a secondary group of bio-chronologically controlled LFAs. The first ones are placed in descending age-order correlated with the European Neogene Mammal zones (MN), after correction of their original age-indication to the Berggren et al. (1995) GeoPolarity Time scale (Fig. 1). Bio-chronologically controlled LFAs are placed on the same scale following the most current available information concerning the evolutionary stage of particular large mammal lineages.

Recent reviews of the entire Samos fauna gave a fine time-resolution of old and new fossil assemblages (Kostopoulos et al., 2003; Koufos et al.,

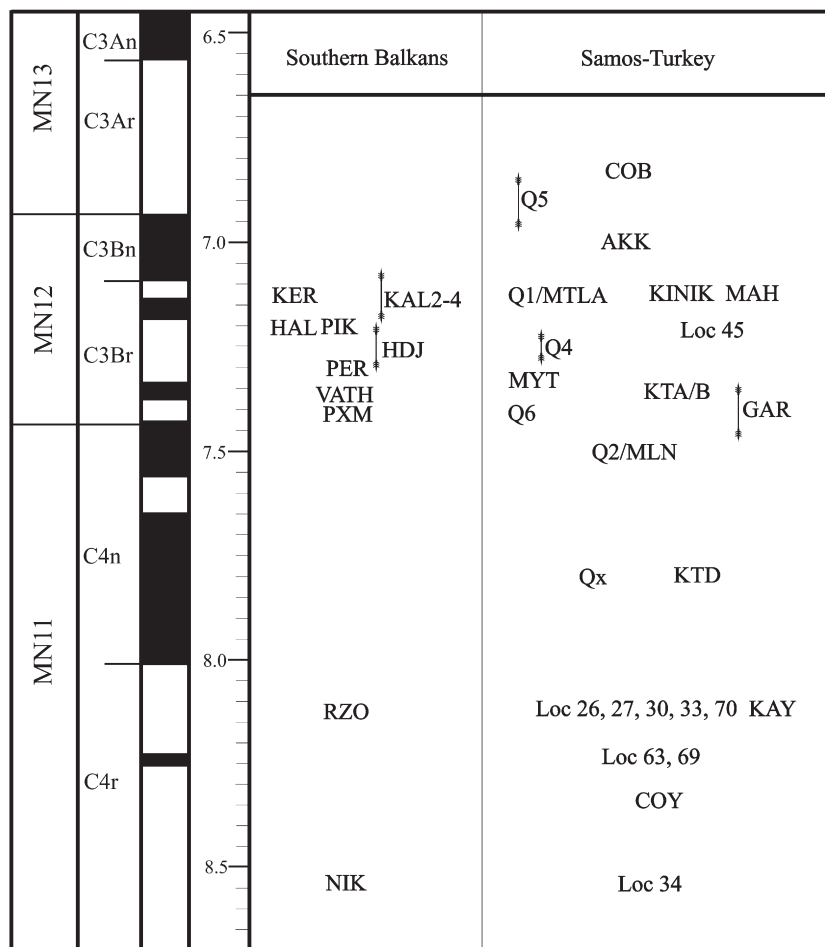*E-mail address:* dkostop@geo.auth.gr.

Fig. 1. Correlation of Turolian large mammal assemblages from SE Europe (excluding Dytiko 1–3, ~6.5 My) with GPTS (Berggren et al., 1995) and MN-zones (Mein, 1999; Steininger, 1999). Data from Güleç et al. (2007), Kappelman et al. (2003), Karadenizli et al. (2005), Kostopoulos et al. (2003), Koufos (2006), Koufos et al. (2006b, in press), Spassov (2002). Abbreviations. NIK: Nikiti-2, Greece; RZO: Ravin des Zouaves 5, Greece; PXM: Prochoma, Greece; VATH: Vathylakkos 1–3, Greece; PER: Perivolaki, Greece; HDJ: Hadjidimovo, Bulgaria; HAL: Halmyropotamos, Greece; PIK: Pikermi, Greece; KAL2-4: Kalimantsi 2–4, Bulgaria; KER: Kerassia, Greece; DYTI: Dytiko 1–3, Greece; Loc 34, 63, 69, 26, 27, 30, 70, 45: Middle Sinap, Turkey; Loc 33—KAV: Kavakdere, Middle Sinap, Turkey; Loc 42—COB: Çobanpinar, Middle Sinap, Turkey; COY: Çorak Yerler, Turkey; KAY: Kayadibi, Turkey; Qx: Quarry x, Samos; KTD: Kemiklitepe D, Turkey; Q2/MLN: Quarry 2–Mytilinii 4, Samos; Q6: Quarry 6, Samos; GAR: Garkin, Turkey; KTA/B: Kemiklitepe A/B, Turkey; MYT: Mytilinii 3, Samos; Q4: Quarry 4, Samos; KINIK: Kinik, Turkey; MAH: Mahmutgazi, Turkey; Q1/MTLA: Quarry 1–Mytilinii 1, Samos; AKK: Akkaşdaği, Turkey; Q5: Quarry 5, Samos.

in press). The LFAs of Ravin des Zouaves 5, Vathylakkos and Prochoma, in the lower Axios valley of Northern Greece are also magnetochronologically dated (Kondopoulou et al., 1992; Sen et al., 2000 and corrections by Koufos et al., 2006b). The Perivolaki LFA in Thessaly, Central Greece provided poor magnetostratigraphic resolution but enough in order to be linked with those of the Axios valley (Koufos et al., 2006b). Nikiti-2 LFA (NIK, Chalkidiki, northern Greece) is biochronologically placed between the latest Vallesian *Ouranopithecus* bearing site Nikiti-1, which is placed a few meters below (Koufos, 2006), and Ravin des Zouaves-5 (RZO, Axios valley, Greece). The famous Pikermi LFA near Athens is certainly of middle Turolian age and, although diverging opinions about its exact dating do exist (Bernor et al., 1996; Koufos, 2006), the evolutionary stage of most large mammal lineages suggest a younger age than Perivolaki/Vathylakkos and closer to Q1/MTLA of Samos. The age of the LFA of Halmyropotamos (Evia) is not easy to determine since faunal identifications are old; most taxa show, however, greatest similarity with the Pikermi LFA (Koufos, 2006). Kerassia is a relatively new and not profoundly studied site, located in Evia. Although two fossil horizons have been recognized (Theodorou et al., 2003; Koufos, 2006), their faunal composition does not show, at the moment, significant biochronological differences. The entire faunal assemblage and especially the presence of *Samotherium major* imply great similarities with the Samos upper fossil horizons and therefore Kerassia is placed at the same level with Q1/MTLA. The presence of cf. *Mesopithecus monspessulanus* at Dytiko sites

(lower Axios valley) together with some advanced herbivores (Koufos, 2006; Bouvrain and Bonis de, 2007) indicate an age somewhat younger than the rest of Axios valley but older than the Maramena site that is dated to the end of the Turolian (Schmidt-Kittler et al., 1995).

Spassov (2002) and Spassov et al. (2006) register several Turolian large mammal faunas from Bulgaria. Among them, Hadjidimovo and Kalimantsi 2, 3 and 4 show the most complete faunal lists and have been studied in greatest detail. Hadjidimovo is certainly older than Kalimantsi 2, 3 and 4 but biochronological data appear contradicting concerning its precise dating. Hadjidimovo is thought to be of early middle Turolian age (Spassov, 2002) and the presence of *Mesopithecus* cf. *delsoni* (Koufos et al., 2003) is rather in favor of such a designation. Yet, the *Hipparion* assemblage of this locality and some bovids indicate a higher evolutionary stage, slightly earlier than Pikermi (Hristova et al., 2002, 2003; Geraads et al., 2003). Kalimantsi 2, 3 and 4 are probably the same as Pikermi or slightly younger.

Middle Sinap Turolian sites, Turkey (Loc. 34, 63, 69, 26, 27, 30, 33 = Kavakdere, 70, 45, 42 = Çobanpinar) are finely calibrated by magnetostratigraphy (Kappelman et al., 2003). The same is true for Kemiklitepe D and A/B (Sen et al., 1994), even though their ages appear slightly older in the Berggren et al. (1995) time-scale. Akkaşdaği is radiometrically dated at 7.0 ± 0.1 My (Karadenizli et al., 2005). Recent studies at Çorak Yerler (Ünay et al., 2006; Güleç et al., 2007) bring to light the primate *Ouranopithecus turkae* and suggest a MN 11 age, probably between Loc. 34

and Loc. 63 of Middle Sinap. The Kayadibi LFA is slightly younger and at about the same evolutionary level as Loc. 33 (= Kavakdere) of Middle Sinap. Garkin is usually dated at MN11 but a latest MN11/earliest MN12 age seems more appropriate. The LFAs of Kinik and Mahmutgazi are more or less at the same evolutionary level with Samos Q1/MTLA, and certainly older than Akkaşdaği and Çobanpinar.

Large-scale diversity analyses of the European late Miocene usually bring together Greece and Turkey as representing a single biogeographical ensemble (Bernor et al., 1996; Fortelius et al., 1996; Solounias et al., 1999; Costeur et al., 2004; Fortelius et al., 2006). Albeit these two areas show strong geographic affiliation during late Miocene, as expected, their faunal fusion allows underestimation of the divergence signal that is still indicated in the same global analyses (e.g., Costeur et al., 2004: Fig. 3). We treat, therefore, Greece and Turkey separately, roughly following the regional scheme of Maridet et al. (2007) and Costeur and Legendre (2008), but introduce two main modifications: (1) the Bulgarian faunal assemblages are pooled with the Greek ones, as dictated by the late Miocene physiogeography of Southern Balkans, in which Northern Greece and Southern Bulgaria are connected through an extensive valley-system, and (2) as the Late Miocene Samos territory is part of Asia Minor, the Greek faunal assemblages from Samos island are clustered together with the Turkish ones. Hence, the local faunal assemblages (LFAs) are divided in two working groups: the first one represents the "western block of LFAs" including Greek and Bulgarian faunas and the second the "eastern block of LFAs" including the Samos and Turkish assemblages. A taxa-per-locality data matrix has been produced based on available bibliography and personal data. According to standard practices, the present paper follows faunal homogenization procedures, correcting possible synonymy problems; minor changes, additions and modifications on the original faunal lists have been performed. Species originally referred to as "cf." are a priori included into the nominal taxon. In cases of monospecific genera or genera represented by a single species during the Turolian, species referred to as "aff." or "sp." are also included into the nominal taxon, except if convincing arguments to the opposite exist. Based on the matrix, range charts of 124 important Turolian SE European large mammal taxa have been drawn out (Appendix A) separately for the eastern and western blocks of LFAs.

2.2. Sampling biases

Sampling efforts and inequality of time intervals may significantly alter diversity analysis. To avoid the effects of the second type of bias, the present analysis of turnover and biogeographic patterns is based on pre-fixed time-slices of 100 Ky for the time span between 8.7 and 6.7 My. Barry et al. (2002) mention that the 100 Ky-level might be the finest possible resolution for terrestrial faunas.

Because regional species richness and number of localities vary noticeably in the analysed fossil record (1–50 species per locality and 0–7 localities per time interval), sampling bias might be introduced. Range-throughs can significantly improve the condition, eliminating sampling effects. Least square regression analysis after range-through process (Fig. 2), indicates that variation in number of localities explains no more than one-third of the variation in species richness per time interval ($r^2 = 0.304$, $p = 0.011$; Spearman's rs = 0.475, $p = 0.034$). The results are totally compatible with those of Maridet et al. (2007) and Costeur and Legendre (2008), suggesting that raw diversity is largely interpretable.

2.3. Methods

Following the pre-fixed time intervals of 100 Ky, the first and last occurrence data (FOD, LOD), the relative turnover index (RT = (FOD + LOD)*10/2), the standing richness (Nsr, following Maas et al., 1995), and the Rate Quotiens of first and last occurrences (RQF and RQL respectively for intervals of equal duration, following Gingerich, 1987 and Barry et al.,
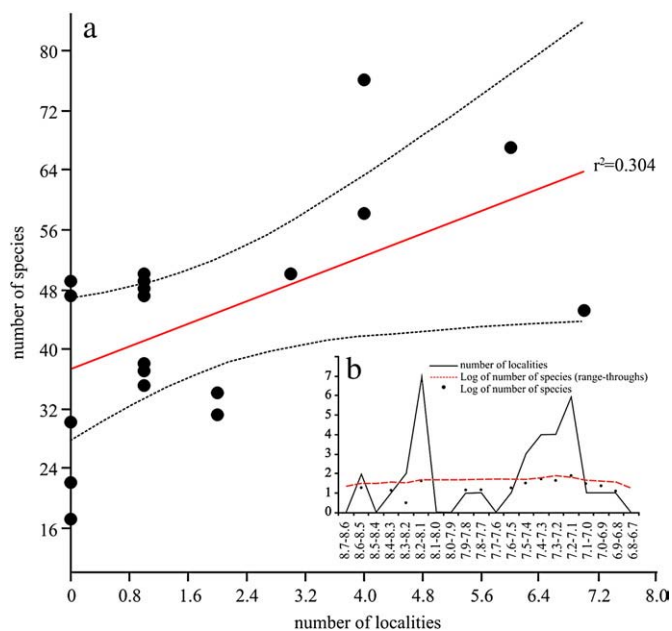

Fig. 2. Linear regression analysis (a) between number of species after range throughs (ordinate) and number of localities (abscissa) and correlation (b) of the number of localities per time interval to the row diversity counts.

1995) have been estimated separately for the eastern and western blocks of LFAs, as well as, for the entire fossil record (marked as "total").

Biogeographic relationships between the eastern and western blocks of LFAs are expressed by a commonality index (CI = Common species/Uncommon species %) per time interval. Furthermore, a parcimony analysis using Branch and Bound algorithm is performed (PAST® free software; Hammer et al., 2001) among successive eastern and western SE European chronofaunas that have been treated as terminal taxa (Appendix B). Each chronofauna groups together eastern or western LFAs following an unequal time interval approach. A species is considered to be present in the chronofauna even if it occurs in only one LFA of the cluster. Each species is regarded as a character of the chronofauna. The cladogram has been rooted to a hypothetical ancestral chronofauna, in which pre-Turolian species are mentioned as present (state 1) and their persistence into Turolian chronofaunas is regarded as primitive. If the species does not occur earlier, then state "0" credits the outgroup and the presence of the species in a chronofauna is regarded as advanced (state 1). In a few cases, in which successive evolutionary steps inside a genus were recognizable, a multiple state coding is used. As the entrance of a species into a chronofauna can only happen once, Dollo optimization criteria have been adopted (Hammer et al., 2001; Hammer and Harper, 2006).

Palaeoecological inference relies on taxonomical composition of successive chronofaunas, eliminating sampling bias of individual fossil sites. The palaeoecological profile is detected by Principal Component Analysis (PAST® free software; Hammer et al., 2001) on the basis of counts of species in distinct taxonomical categories, ranging from genus up to family/subfamily level. Although species ecology might significantly vary within higher taxa, strong signal of particular categories in combination could inform about ecological distinctiveness/similarity among fossil communities.

3. Results

3.1. Turnover patterns

3.1.1. Standing richness

Standing richness (Nsr) is a conservative expression of species diversity changes through time (Maas et al., 1995; Azanza et al., 2000).
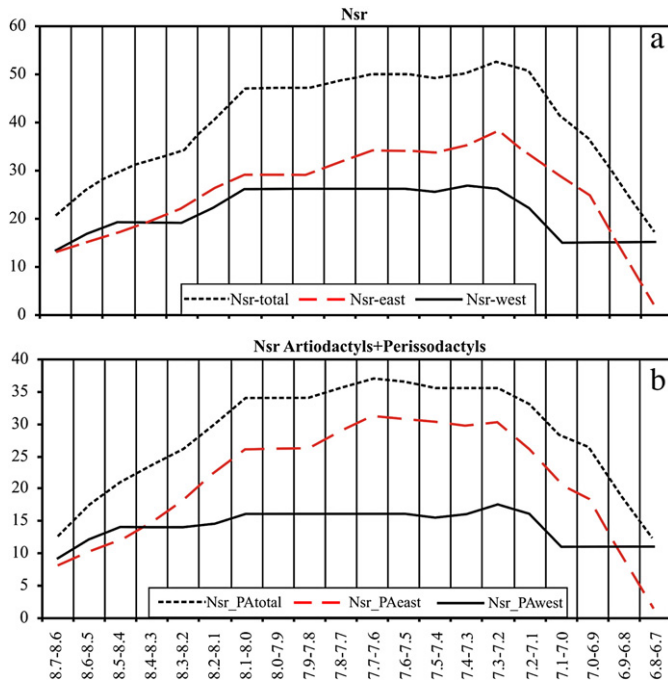
Fig. 3. Rates of standing species richness for (a) the complete Turolian SE European large mammal record and (b) the Artiodactyls+Perissodactyls subset (abscissa: 0.1 My time-slices).

rises again getting its highest values between 7.3 and 7.2 My. From 7.2 My onwards, Nsr drops drastically down, reaching its minimum after 6.8 My. The overall Nsr pattern is generally followed by both the western and eastern records with some interesting modifications. The western Nsr line (Fig. 3a) shows lower fluctuations over time than the eastern one. The 7.8–7.2 My flip-flop period of increasing Nsr observed in the total and particularly in the eastern record is much less exaggerated at the western one, which appears almost stable for a very long period of time (Fig. 3a). After 7.2 My the standing richness of the western record decreases and rather stabilizes at the levels of early Turolian, while the Nsr of the eastern record shows a much more dramatic decline reaching significantly lower levels than the western one.

Although similar in a general way, the Nsr values obtained only from the Artiodactyls-plus-Perissodactyls sub-set give some additional information (Fig. 3b). For the 8.4 to 6.9 My time span, the differences between West and East are much greater than those for the complete faunal records because of the lower values attained by the western record. This rather suggests that the influence of carnivores, primates, probiscideans etc. is more significant at the West than at the East. Furthermore, at the eastern record an additional peak at 7.7 My appears, reaching slightly higher Nrs values than the 7.2 My one, implying that maximum Turolian diversification of artiodactyls and perissodactyls had been reached slightly earlier than that of the rest fauna (Fig. 3b).

3.1.2. Turnover

Both the western and eastern records illustrate some similar successive fluctuations of the relative turnover index (RT) between 8.7 and 8.0 My, followed by a period of stability until 7.5 My, which is interrupted at the East by an additional turnover event at 7.8–7.7 My (Fig. 4a). From 7.5 to 6.7 My both records show more pulsed turnover than previously,

Standing richness of the total record ("east + west," Fig. 3a) gently increases from 8.7 to 8.3 My and more rapidly between 8.3 and 8.0 My, reaching a first maximum and stabilizing there till 7.4 My. Then, Nsr
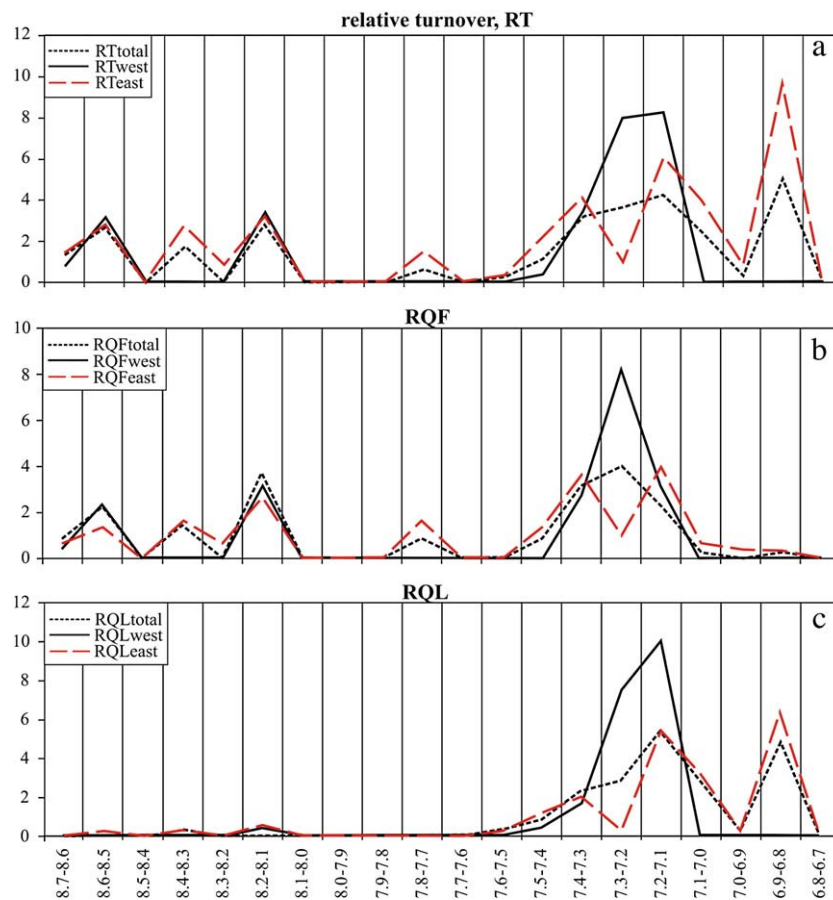

Fig. 4. Rates of relative turnover, RT (a) and rate quotients (number of events divided by the average number of events) for first, RQF (b) and last, RQL (c) occurrences of SE European large mammals during Turolian (abscissa: 0.1 My time-slices).
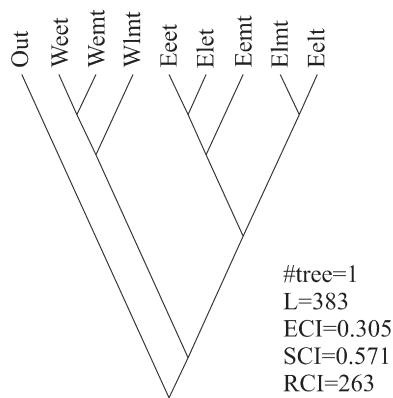
Fig. 5. Single most parcimonious cladogram resulted from the analysis of SE European Turolian chronofaunas. E for east, W for west; eet: early early Turolian, 8.7–8.0 My; let: late early Turolian, 8.0–7.5 My; emt: early middle Turolian, 7.5–7.25 My; lmt: late middle Turolian, 7.25–7.0; elt: early late Turolian, 7.0–6.7 My; L: tree length; ECI: ensemble consistency index; SCI: stratigraphic consistency index; RCI: relative completeness index.

following, however, different patterns (Fig. 4a). The western record indicates a single major turnover lasting from 7.5 to 7.0 My with its peak at around 7.2 My (Fig. 4a). At the same time (7.5–7.0 My) the turnover signal at the East is double and it is succeeded by an even stronger turnover at 6.9–6.8 My (Fig. 4a). Interestingly, at the time of maximum RT at the West there is minimum RT at the East.

Since the relative turnover index and the species richness are an account of both First (FOD) and Last Occurrence Data (LOD) indiscriminately, the ratio of observed turnover to the expected one (rate quotiens), estimated separately for the first (RQF) and last (RQL) occurrences, would give more details on the quality of the record (Maas et al., 1995) (Fig. 4b, c). The 8.7–8.0 My increase of standing richness and pulsed turnover period is associated in both records by low RQL values (Fig. 4c) and strong pulsed RQF values (Fig. 4c), rather higher than the expected ones, suggesting a time of dispersal due to both origination and immigration; it is worth noting, however, that 60% of new appearances at the West represent carnivores while 90% at the East refers to artiodactyls. A short dispersal phase also occurs later at the East (7.8–7.7 My) characterized mostly by new appearances of multiple hipparionine lineages (Fig. 4b). Thus, the long 8.7–7.5 My period is characterized at both the western and eastern records as a time of new appearances in rather successive waves.

At the West, the high RT signal around 7.2 My is combined to weak increase of standing richness and extremely high RQF and RQL values (Fig. 4b, c), suggesting a rather anagenetic pseudoturnover, i.e. a renewal of the large mammal fauna. At the East the double turnover signal at 7.4–7.1 My is more complicated (Fig. 4b, c). From 7.4 to 7.3 My the standing richness increases and the RQF values are high (Fig. 4b), while the RQL ones, even higher than expected, are rather low (Fig. 4c); all together implying a dispersal phase mainly of (pseudo-)origination. Next follows a short period of stability (7.3–7.2 My) and then a phase of declined standing richness (7.2–7.1 My) associated by extraordinarily high RQL values (Fig. 4c) but also high RQF ones (Fig. 4b), marking an extinction–pseudoextinction and emigration period for perissodactyls and artiodactyls in combination with immigration of western carnivores. This event is directly succeeded at the East by a true extinction phase around 6.8 My with very low RQF and high RQL values (Fig. 4b, c) and rapidly declining standing species richness (Fig. 3a). Thus, the signal at the East seems to follow a triple phase pattern of (pseudo-)origination (7.4–7.3 My)—immigration/emigration (7.2–7.1 My)— and true extinction (6.9–6.8 My).

3.2. Biogeographic patterns

3.2.1. Parsimony analysis

The single most parsimonious cladogram (Fig. 5) indicates that eastern and western Turolian chronofaunas are well segregated in two geographically controlled crown assemblages with sister group relationships between them. Each local Turolian chronofauna shows sister group relationships with the preceding one(s) from the same geographic sector. The results suggest that the western and eastern large mammal chronofaunas, evolved rather locally, keep a high degree of independency over early and middle Turolian times. This is quite interesting, given that common characters (species) between East and West do exist, particularly during middle Turolian.

3.2.2. Commonality index

Commonality index is considered to be an expression of the faunal interchanges or isolation between eastern and western LFAs per time interval. Commonality index (Fig. 6a) remains low until 7.4 My with minor positive elevations at 8.5 and 8.2 My. Uncommon species increase steeply from 8.7 to 8.0 My and then stabilize till 7.4 My (Fig. 6b). At the same period common species are less than 10, weakly fluctuating over time (Fig. 6b); interestingly, a great percentage of them correspond to pre-Turolian or end-Vallesian faunal elements.
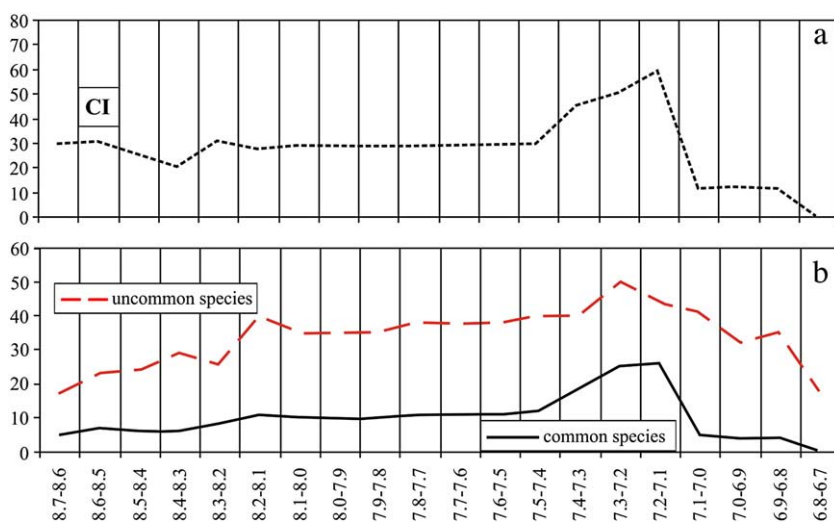

Fig. 6. Rates of commonality index, CI (a) and its analysis into common and uncommon species (b) between western and eastern Turolian SE European LFAs (abscissa: 0.1 My time-slices).

From 7.4 My commonality index increases drastically reaching its maximum at about 7.2–7.1 My (Fig. 6a). This appears to be the result of a slight decrease of uncommon species associated by a strong increase of the common ones (Fig. 6b), suggesting an extensive faunal interchange between the western and eastern sector. From 7.1 My onwards commonality index drops down abruptly, getting lower values than at the beginning of Turolian (Fig. 6a). Uncommon species decrease rather gradually after 7.1 My, while common ones decline dramatically (Fig. 7b).

The overall pattern is completely followed by the main mammal groups (artiodactyles, perissodactyls and carnivores) until 7.4 My (Fig. 7). From 7.4 to 7.2 My common artiodactyls increase and uncommon ones decline approaching each other at about 7.2 My; they diverge again between 7.1 and 6.8 My (Fig. 7a). Perissodactyls show a rather significant increase of uncommon species around 7.3 My, followed by a decrease between 7.3 and 7.2 My with contemporary increase of common elements (Fig. 7b). From 7.4 to 7.2 My uncommon and common carnivore species increase simultaneously (Fig. 7c). Common species keep increasing till ~7.1 My, while uncommon ones slop quickly down after 7.2 My and until the end of the studied period.

The increase of commonality at ~7.2 My has all the characters of an event; it is short, abrupt and happens after a long period of steadiness, affecting in different ways the spatial distribution of basic groups of large mammals.

3.2.3. Isolation and communication markers

Omitting single species occurrences (Appendix A), several taxa show geographic isolation between the eastern and western sector. The colobine monkey *Mesopithecus* is well known at the West during the entire Turolian but it is missing from the East. *Chasmaporthetes bonisi* is a rather endemic exclusively West faunal element, present in the whole Turolian succession. According to the current knowledge the middle Turolian *Machairodus aphanistus* and *Belbus beaumonti* are restricted to the East, while *Paramachaerodus orientalis*, *Plessiogulo crassa*, *Simocyon primigenius* and *Thalassictis robusta* to the West. It is worth noticing that all western carnivore dwellers seem to have northern affinities. During early Turolian *Choerolophodon anatolicus* occupies the eastern territories and *Choerolophodon pentelici* the western ones. Chalicotheres (*Chalicotherium goldfusii* and *Macrotherium macedonicum*) do not appear at the East, while they are present during middle Turolian at the West. Although the taxonomy of chilotheres remains unresolved, they do not occur at the West during Turolian, whereas multiple lineages are present at the East. The middle Turolian *Cremohipparion mediterraneum* seems to be a western dweller while *Hipparion dietrichi* an eastern one. *Hipparion* "*dietrichi*" from the early-early middle Turolian of Southern Balkans has different origin and needs systematic revision (Vlachou and Koufos, in press). Among giraffids, the early Turolian *Samotherium boissieri* is an eastern dweller whereas *Bohlinia attica* has a long but scrappy record at the West till MN13; yet, it is missing from the East except perhaps at the very beginning of the Turolian. Ovibovine-like bovids (*Criotherium*, *Plesiaddax*, *Urmiatherium*) are scarce but well documented at the East; among them only *Criotherium* appears so far in the Balkans probably at the same time as at the East (early Turolian) but its primitive state suggests the occurrence of two distinct lineages in the Eastern Mediterranean (Geraads and Spassov, 2008). The early Turolian *Tragoreas oryxoides* and *Majoreas elegans/woodwardi* and the middle Turolian *Gazella mytilinii*, *Oioceros wegneri* and *Prostrepsiceros zitteli* occur only at the East, whereas the early Turolian *Prostrepsiceros axiosi* and the middle Turolian *Protoryx carolinae* are present only at the West.

An additional group of large mammals indicates extension of their territories over time in either direction. Three extensional waves can be
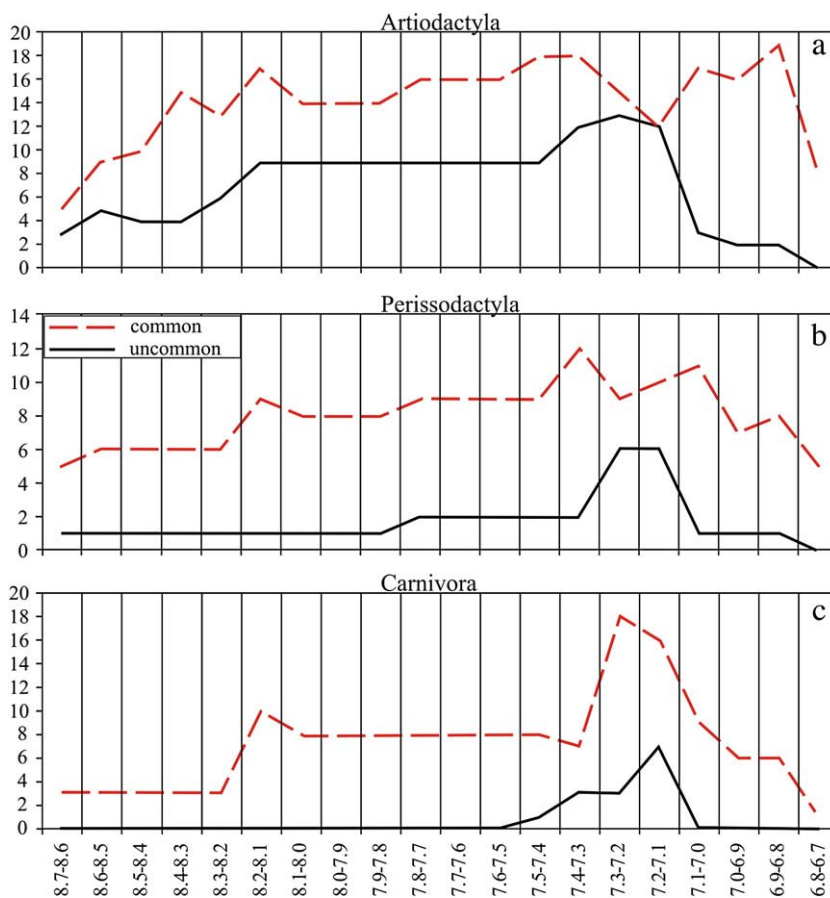

Fig. 7. Rates of common and uncommon species for artiodactyls (a), perissodactyls (b) and carnivores (c) between western and eastern Turolian SE European LFAs (abscissa: 0.1 My time-slices).

detected. At 8.1–8.2 My there is a territorial expansion of western dwellers toward the East. *Helladotherium duvernoyi*, *Nisidorcas planicornis*, *Tragoportax rugosifrons* and *Gazella pilgrimi* appear for the first time at the East (but also at the north, Vislobokova, 2005) and most of them survived longer here than in the Balkans. At around 7.3 My a second wave allows mostly an introduction of eastern elements into the western domain; *Promephitis larteti*, *Adcrocuta eximia*, *Choerolophodon pentelici*, *Dihoplus pikermiensis*, *Pliohyrax*, *Samotherium*, *Skoufotragus* (=*Pachytragus*), *Sporadotragus Palaeoryx pallasi*, *Palaeoreas lindermayeri*, *Oioceros rothii*, *Gazella capricornis*, and small *Lucentia*-like cervids appear for the first time at the West. A last wave of West to East direction occurred at about 7.1 My and includes mainly carnivores (*Ictitherium viverinum*, *Metailurus parvulus*, *Plioviverops obrigni*, *Promeles palaeattica*, and probably *Thalassictis robusta* and *Ursavus depereti*); *Zygolophodon* may also be added to this wave.

3.3. Palaeoecological profile

The first and second principal components explain ~44% and ~26% of the total variance respectively (Fig. 8). The West and East chronofaunas are well separated along the second component; the western chronofaunas are characterized by stronger signal of primates, spiral-horned antelopes, hyaenids, giraffines, and suids, while the eastern ones by caprine- and ovibovine-like bovids, aceratheriines, cremohipparions, phiohyracids, palaeotragines and gazelles. Furthermore, in both sectors there is a clear gradient from early early Turolian to late middle Turolian chronofaunas, driven mainly by the increasing positive loadings of carnivores, caprine-like bovids and hippotherium-type horses. The analysis indicates that similar taxonomic categories contribute differently in contemporaneous chronofaunas from West and East, suggesting ecological divergence.

A closer look on Pikermi and Samos (referred only to Q1/MTL level; Kostopoulos et al., 2003), the two most characteristic and rather contemporaneous LFAs of the Pikermian Biome, supports the previous remarks. Although 43% of the 51 species recorded at Pikermi also exist at Samos, occupying 58% of its fauna (38 species), the two mammal assemblages give a strikingly different ecological profile. The tree-dwelling semi-terrestrial *Mesopithecus* (Koufos et al., 2003; Youlatos, 2003) flourish at Pikermi but is missing from Samos. Apart from seven

common carnivores, felids and mustelids appear much more diversified at Pikermi than at Samos. Ursids are represented by the carnivorous *Indarctos* at Pikermi instead of the omnivorous *Ursavus* at Samos. Browsing-depended proboscideans have weaker signal at Samos than at Pikermi. Unlike Pikermi, the grazing *Diceros neumayri* prevails over the browsing *Dihoplus pikermiensis* at Samos (Giaourtsakis et al., 2006). The mix-feeding *Cremohipparion mediterraneum* of Pikermi is replaced at Samos by the grazing *Cr. proboscideum*, whereas hipparionine horses as a whole appear highly diversified at Samos (5 species instead of 2 at Pikermi) (Vlachou and Koufos, in press). The browsing giraffe *Helladotherium* that prevails among large herbivores in Pikermi, is supplanted at Samos by the grazer *Samotherium major* (Solounias et al., 1999 and literature therein). Except for gazelles, small to medium-sized bovids with browse to intermediate feeding preferences (*Palaeoreas*, *Protragelaphus*, *Oioceros*, *Prostrepsiceros*) are much more diversified at Pikermi than at counterpart levels of Samos, where grazing ovibovine-like bovids occur (*Urmiatherium*) (Solounias et al., 1999; Merceron et al., 2006 and literature therein). On the other hand, gazelles are much more diversified at Samos than in Pikermi. Browsing and mix-feeding boselaphines predominate among large bovids at Pikermi, whereas grazing to mix-feeding caprine-like bovids dominate at Samos.

4. Discussion

4.1. The MN12 boundaries

Steininger (1999) defines middle Turolian (MN12) as the interval between the base of Chron C4n.2n and the top of C3An.2n, ranging from 8.0 to 6.6 My but alternative views (Mein, 1999; Agusti et al., 2001; van Dam et al., 2001 and literature therein) correlate the base of middle Turolian with Chron C4n.1n at 7.50 My. The Turolian SE European large mammal record suggests that no important turnover occurs at 8.0 My. At that time standing species richness remained stable, while first and last occurrences traced one another closely at very low levels. Both conditions are unlike those expected for the beginning of a land mammal zone. At about 7.5 My and after a relatively long period of rather faunal stability, last occurrences exceeded first ones and species richness started to increase as a result of the forthcoming significant raise of first occurrences. This pattern
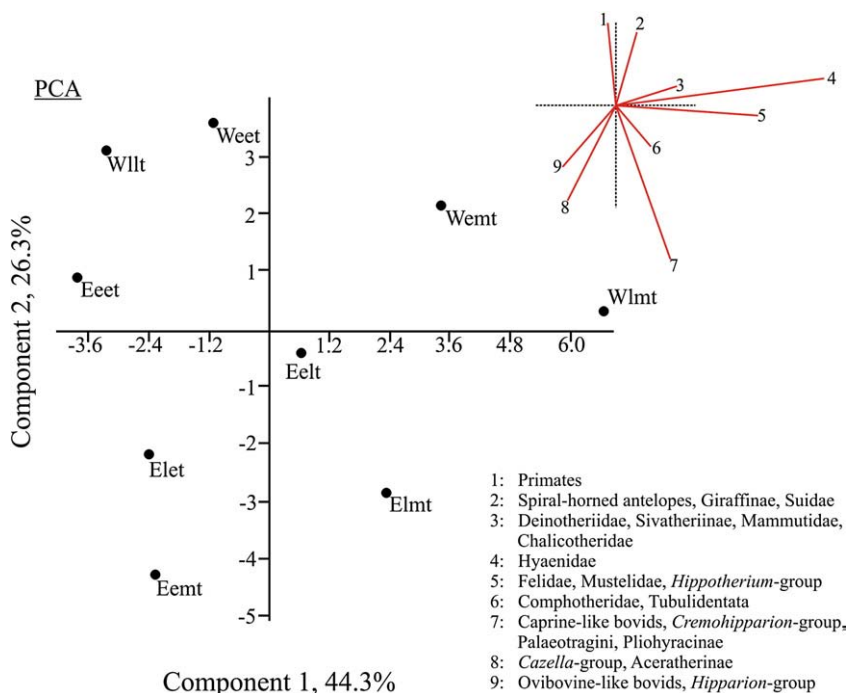
Fig. 8. Principal component analysis of Turolian SE European chronofaunas according to their taxonomic composition. Abbreviations as in Fig. 5.

PCA

1: Primates
2: Spiral-horned antelopes, Giraffinae, Suidae
3: Deinotheriidae, Sivatheriinae, Mammutidae, Chalicotheridae
4: Hyaenidae
5: Felidae, Mustelidae, *Hippotherium*-group
6: Comphotheridae, Tubulidentata
7: Caprine-like bovids, *Cremohipparion*-group, Palaeotragini, Pliohyracinae
8: *Cazella*-group, Aceratherinae
9: Ovibovine-like bovids, *Hipparion*-group

Component 2, 26.3%

Component 1, 44.3%

agrees with the concept of a land mammal boundary and thus the 7.5 My limit between MN11 and MN12 is also confirmed for Eastern Mediterranean. Kostopoulos et al. (2003) suggest correlating the lower MN12 boundary with C3B/C4n limit, at 7.43 My in good agreement with the present results.

The upper MN12 boundary is more difficult to be traced. The 6.6 My upper limit of Steininger (1999) seems to postdate the faunal events. Other authors (Sen, 1997; Garcés et al., 1998; Agusti et al., 2001) suggest bracketing the MN12/MN13 boundary between chrons C3Ar and C3Bn, i.e. between 6.6 and 7.1 My. In the Eastern Mediterranean, an end-zone pattern appears between 7.0 and 6.8 My; during this period last occurrences exceeded first ones and species richness strongly declined. A 6.8–6.9 My upper MN12 boundary seems also to fit the West European record (van Dam, 1997).

4.2. Relations with Mediterranean palaeoclimate and palaeogeography

Several works dealing with mammal turnover set off the importance of climatic changes as a major forcing factor (e.g., Barry et al., 1995; Alroy, 1996; Cerling et al., 1997; Azanza et al., 2000; Barry et al., 2002; Fortelius et al., 2006; van Dam et al., 2006). On the other hand, the palaeogeographic impacts on the timing and pattern of mammal dispersals might be also crucial (e.g., Costeur et al., 2004; Agusti et al., 2006; van der Made et al., 2006; Maridet et al., 2007). It is, however, difficult to address accurate correspondence between climatic/palaeogeographic shifts and changes in the large mammal structure for the time and spatial scale the present study deals with.

During late Tortonian, the Mediterranean enters into an arid-warm phase that seems to be already well-established at the East (Koufos, 2003; Fortelius et al., 2006; Strömberg et al., 2007; Böhme et al., 2008). As a response to the delayed aridity expansion from East to West (Fortelius et al., 2006), and to the emergence of modern post-Alpine European topography, eastern mammal taxa rarely or very late invade Central and South-Western Europe, while north-occidental mammal taxa only occasionally extend their territory south-eastwards (e.g., Vislobokova, 2005; van der Made et al., 2006). The condition implies a clear ecological disparity between Turolian mammal communities from western and eastern Mediterranean Europe, as it has been already shown by several authors (Fortelius et al., 1996; Costeur et al., 2004; Koufos et al., 2006a; Costeur and Legendre, 2008).

At the same time, the large mammal community of the western domain of the Greco-Iranian province appears neither homogeneous nor isotropically behaved, in contrast to previous considerations. The present analysis indicates that the early Turolian large mammal association of SE Europe (i.e., the Southern Balkans), though it follows general trends, it seems to absorb most of the environmental vibrations that provide more vigorous reactions at the eastern sector (i.e., Anatolia). While Anatolia experienced during this period a phase of increasing species richness, mainly controlled by successive immigration/origination waves of perissodactyls and artiodactyls, the western sector shows a remarkable faunal stability. At the same time, faunal exchanges between Southern Balkan and Anatolia appear to be low, implying a kind of geographic isolation. Strömberg et al. (2007) summarize earlier views supporting a climatic and vegetational gradient across Greco-Iranian province with increasing aridity and decreasing tree-coverage toward the East. Although a climatic gradient might well have existed, it seems insufficient to fully explain the observed faunal differences and the apparent faunal-swap restrain between Southern Balkans and Anatolia. Other lines of evidence point to a real physiogeographic barrier between these two geographic sectors.

The Southern Balkans and Anatolia underwent a long-standing geographic separation, due to the development of the Eocene–middle-late Miocene subduction accretion complex, passed through the central Aegean region and traced along the nowadays Pindos-Pontides

mountain belt (Mercier et al., 1989; Tranos, in press). During the Vallesian, the inherited physio-geography still prevented extensive faunal exchanges between the south-eastern "lowlands" and the north-western forearc "highlands." Although phytolith evidence (Strömberg et al., 2007) and mammal data from European Thrace (Kostopoulos and Sen, in press) failed to confirm the original Eastern Aegean Province hypothesis of Geraads et al. (2005), the presence of a Vallesian forested corridor along the mountainous remnant of the accretion prism seems possible.

During the late Vallesian–early Turolian, the newly developed NE–SW extensional tectonic regime in the Southern Balkans (Tranos, in press) resulted in the formation of an extensive NW–SE graben-system, which probably facilitated the middle Tortonian/Maeotian marine transgression to reach, through the newly formed Aegean Sea, the Eastern Parathethys (Steininger and Rögl, 1984; Kojumdgieva, 1987; Mercier et al., 1989; Rögl, 1999; Meulenkamp and Sissingh, 2003; Vasiliev et al., 2004; Popov et al., 2006). The presence of such an unstable shallow marine basin between the Southern Balkans and Anatolia maintained the geographic isolation of the two sectors, as indicated by the local large mammal record (Fig. 9). The Anatolian large mammal fauna experienced during this period (~7.8 My) a phase of replenishment due mostly to equid appearances; at the same time the Siwaliks record indicates a faunal shift from equid-dominated to more evenly balanced assemblages (Barry et al., 2002).

From 7.5 to 6.9 My the large mammal faunas of both areas under study entered a period of significant reorganization and faunal exchange centred around 7.2 My. The observed turnover is correlated with the strong latest Tortonian glaciation at 7.3–7.2 My and the severe restriction of the Rifean Corridor that significantly eliminated water mass exchanges between Mediterranean and the Atlantic Ocean (Sierro et al., 1993; Hodell et al., 1994; Seidenkrantz et al., 2000; Kouwenhoven and van der Zwaan, 2006). Nonetheless, the turnover patterns at the East and West of the Aegean were not traced together, as one would expect. The climatic change that started at ~7.5 My in the Mediterranean region might have allowed a first renewal of the large mammal fauna at the eastern sector at 7.4–7.3 My. The following 7.3–7.2 My cooling and consequent drop of the Mediterranean Sea should have severely affected the Aegean marine channel (Fig. 8), allowing an extended faunal migration from East to West and a complete renewal of the Southern Balkan large mammal community. Though the western fauna is relatively balanced after 7.1 My, a migration carnivore wave from the (?north-)western sector occurred, associated with a large extinction phase at the East around 6.9 My. As a result, a dramatic drop of the eastern faunal diversity, similar to that observed at the Siwaliks (Barry et al., 1995, 2002) appeared. The fall of the middle Turolian (i.e., 'Pikermian') large mammal community at 6.9–6.8 My seems to be correlative with the early Messinian glaciation (7.0–6.9 My) and the opposite trend in terrestrial/oceanic carbon shift, that marks the worldwide expansion of C4 ecosystems, even though C3 vegetation still dominated at higher latitudes as in the Mediterranean (Hodell et al., 1994; Quade et al., 1994; Cerling et al., 1997; Barry et al., 2002; Krijgsman et al., 2002; Strömberg et al., 2007 and literature therein). The Pikermian turnover event coincides with the SM12A micromammalian event of van Dam and Weltje (1999), the West European first Messinian Mammalian Event (MME1) of Agusti et al. (2006) and the Siwaliks "7.3–7.0 My event" of Barry et al. (2002). Furthermore, all these faunal episodes seem to fit pretty well in the model of great turnover during 400 Kyr-eccentricity minima of Milankovich climate oscillations (van Dam et al., 2006) and the related large changes in species' geographical distributions (Dynesius and Jansson, 2000).

The scarce late Turolian (MN13) large mammal record of both studied sectors prohibits accurate comparison. Nevertheless, after 6.5 My the Southern Balkan small and large mammal fauna show high endemicity and strong northern influences (Schmidt-Kittler et al., 1995; Vasileiadou et al., 2003; Bouvrain and Bonis de, 2007). At the same time a trend towards more forested and humid conditions occurs
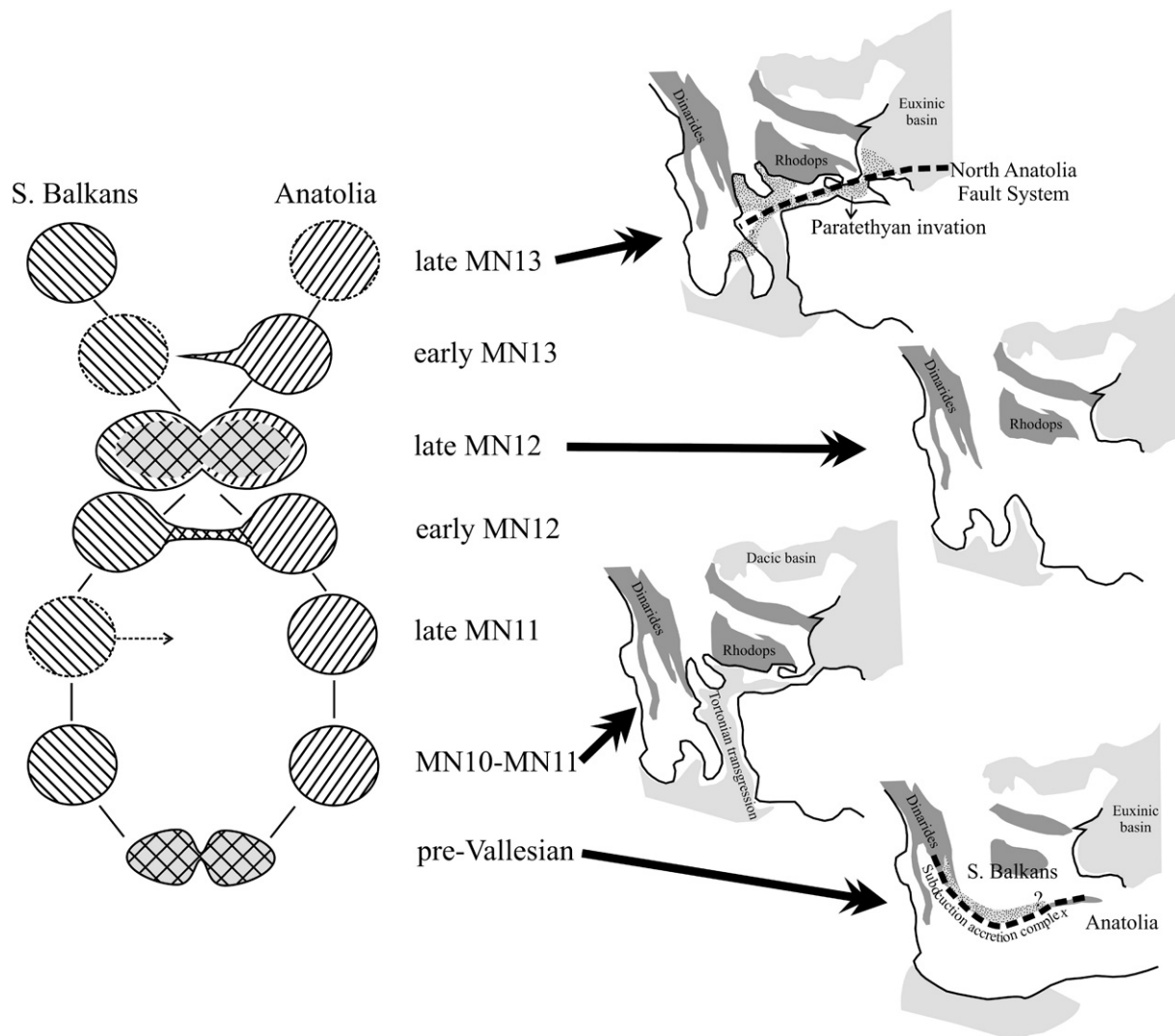
Fig. 9. Schematic model of biogeographic relations through time between Southern Balkans and Anatolian chronofaunas and palaeogeographic reconstruction of the Aegean region during the Turolian (combined from Kojumdgieva, 1987; Mercier et al., 1989; Rögl, 1999; Çağatay et al., 2006; Popov et al., 2006). Light grey: marine environment; spotted light grey: shallow marine environment; dark grey: mountainous environment; white: continental environment; dashed lines: main tectonic/orogenic lines.

in Northern Greece (Karistineos and Ioakim, 1989; Kovar-Eder, 2003; Merceron et al., 2005). This could be the effect of the Paratethyan invasion into the North Aegean realm, resulting from the westward propagation of the North Anatolian fault system (Kojumdgieva, 1987; Mercier et al., 1989; Popov and Nevesskaya, 2000; Sylvestrou, 2000; Syrides, 2000; Çağatay et al., 2006; Snel et al., 2006; Tranos, pers. com.). The Southern Balkans lose again full communication with Anatolia (Fig. 9), while in the East, the relicts of the middle Turolian fauna are shifted to the south (Eronen et al., 2008).

5. Conclusions

The analysis of the Turolian large mammal community at the western domain of the Greco-Iranian province shows that the large mammal assemblages from Southern Balkans and Anatolia shared a very short part of their latest Miocene history in common, living under differentiated environmental conditions. As the temporal shift in adaptive features (such as hypsodonty), driven by overall environmental trends, does not presuppose the time and spatial continuum of phylogenetic lineages and, therefore, ecosystems, the Pikermian Biome sensu Solounias et al. (1999) looks like a large scale over-simplification; the present study failed to support the presence of a uniform large mammal community established during Turolian in the western part of Eastern Mediterranean. Instead, the analysis clearly demonstrates that the emergence, acme and fall of the middle Turolian "Pikermian" fauna was highly controlled by overall climatic and regional physio-geographic factors, having all the typical characters of a mammalian event, similar to those recorded at the same time in western Europe and Asia (van Dam and Weltje, 1999; Barry et al., 2002; Agusti et al., 2006). For most of the Turolian, the large mammal fauna of Southern Balkans appears to have been isolated from that of Anatolia, representing a quite distinct biogeographic region, which explains its high degree of endemicity, as well as, several morphoecological differences between analogous taxa from the two geographic sectors. During the period 7.3–7.1 My, the Southern Balkans were temporarily part of the sub-Paratethyan bioprovince, allowing the emergence and expansion of the "Pikermian" large mammal fauna, which drastically declined after 7.0 My.

Acknowledgements

Appendix A. Range chart of SE European Turolian large mammals

SPECIES	Species code
Mesopithecus delsoni	2
Mesopithecus pentelicus	3
Adcrocuta eximia	7
Chasmaporthetes bonisi	8
Felis attica	9
Hyaenictitherium wongii	11
Ictitherium viverrinum	13
Belbus beaumonti	15
Machairodus aphanistus	18
Machairodus giganteus	19
Metailurus major	22
Metailurus parvulus	23
Paramachairodus orientalis	24
Plesiogulo crassa	26
Plioviverrops orbignyi	28
Promeles palaeattica	29
Promephitis lartetii	31
Protictitherium crassum	32
Simocyon primigenius	33
Thalassictis robusta	36
Ursavus depereti	37
Coerolophodon anatolicus	40
Choerolophodon pentelici	41
Deinotherium giganteum	42
Tetralophodon atticus	43
Zygolophodon turicensis	45
Ancylotherium pentelicum	47
Chalicotherium goldfussi	48
Macrotherium macedonicum	49
Acerorhinus ex gr. zernowi	51
Diceros neumayri	52
Chilotherium samium	53
Chilotherium schlosseri	54
Chilotherium kowalevskii	55
Chilotherium ex. gr. habereri	56
Dihoplus pikermiensis	57
Hipparion brachypus	58
Hipparion dietrichi	59
Hipparion"dietrichi"	60
Hipparion matthewi/macedonicum	61
Hipparion mediterraneum	63
Hipparion proboscideum	65
Hipparion prostylum	66
Hipparion forstenae	67
Hipparion sp.	68
Pliohyrax graecus	69
Pliohyrax kruppii	70
Orycteropus gaudryi	72
Hystrix primigenia	73
Microstonyx major	74

Appendix A (continued)

SPECIES	Species code	WESTERN LFAs											EASTERN LFAs																			
		NIK	RZO	PXM	VATH	HDJ	PER	HAL	PIK	KER	KAL2-4	DYTI	Loc34	COY	Loc63/69	Loc26/27/70	KAVAK	KAYA	Qx	KTD	Q2/MLN	Q6	GARK	MYT	KTA/B	Q4	Loc45	Q1/MTL	KINIK	MAHM	AKKAS	Q5	COBAN
Dorcatherium sp.	78																																
Lucentia sp.	79																																
Pliocervus sp.	80																																
Bohlinia attica	82																																
Helladotherium duvernoyi	83																																
Palaeotragus ex. gr. *coelophrys*	84																																
Palaeotragus rouenii	85																																
Samotherium boissieri	86																																
Samotherium major	87																																
Criotherium argalioides	88																																
Gazella capricornis	90																																
Gazella mytilinii	92																																
Gazella pilgrimi	93																																
Gazella cf. *ancyrensis*	94a																																
Gazella sp.	95																																
Miotragocerus vallencienesi	97																																
Majoreas woodwardi	99																																
Nisidorcas planicornis	100																																
Oioceros rothi	101																																
Oioceros wegneri	102																																
Tragoreas oryxoides	103																																
Skoufotragus zemalisorum	104																																
Skoufotragus laticeps	105																																
Skoufotragus schlosseri	106																																
Palaeoreas lindermayeri	107																																
Palaeoryx majori	109																																
Palaeoryx pallasi	110																																
Prostrepsiceros fraasi/ rotundicornis	113																																
Prostrepsiceros zitteli	114																																
Prostrepsiceros axiosi	115																																
Protoryx capricornis	116																																
Protoryx carolinae	117																																
Protragelaphus skouzesi	118																																
Sporadotragus parvidens	120																																
Tragoportax amalthea	121																																
Tragoportax punjabicus	122																																
Tragoportax rugosifrons	123																																
Plesiaddax ssp.	124																																

Excluding single occurrences: 1. *Ouranopithecus turcae* (COY), 4. *Mesopithecus monspessulanus* (DYTI), 5. ? *Enhydriodon laticeps* (PIK), 6. *Dinocrocuta senyureki* (KAY), 10. *Hyaenictis graeca* (PIK), 12. *Ictitherium intuberculatum* (COB), 14. *Ictitherium pannonicum* (KER), 16. *Indarctos atticus* (PIK), 17. *Lycyaena chaeretis* (PIK), 20. *Martes woodwardi* (PIK), 21. *Pseudailurus lorteti* (Loc 34), 25. *Parataxidea maraghana* (Q1/MTLA), 27. *Plioviverrops guerini* (VATH), 30. *Promephitis hootoni* (AKK), 34. *Sinictis pentelici* (PIK), 35. *Thalassictis hyaenoides* (PIK), 38. *Ursavus ehrenbergi* (HAL), 39. *Agriotherium* ssp. (KAY), 44. *Tetralophodon longirostris* (KER), 46. *Mammut borsoni* (HDJ), 50. *Aceratherium* sp. (PIK), 62. *Hipparion nikosi* (Q5), 64. *Hipparion moldavicum* (AKK), 71. *Tapirus jeanpiveteaui* (HDJ), 75. *Propotamochoerus* n. sp. (RZO), 76. *Propotamochoerus provincialis* (DYTI), 77. *Paracamelus aguirei* (COB), 81. *Procapreolus* sp. (DYTI), 89. *Dytikodorcas longicornis* (DYTI), 91. *Gazella deperdita* (DYTI), 94b. *Gazella schlosseri* (DYTI), 96. *Hispanodorcas orientalis* (DYTI), 98. *Miotragoceros macedoniensis* (DYTI), 108. *Palaeoreas zouavei* (RZO), 111. *Urmiatherium rugosifrons* (Q1/MTLA), 112. *Pheraios chryssomallos* (PER), 119. *Protragelaphus theodori* (DYTI). Data from Bernor et al. (1996), Bouvrain and Bonis de (2007), Fortelius et al. (2003), Geraads et al. (2003), Giaourtsakis et al. (2006), Güleç et al. (2007), Hristova et al. (2002), Koufos (2006), Koufos et al. (2006a,b), Koufos et al. (in press), Sen (2005), Sen et al. (1994), Spassov (2002), Theodorou et al. (2003). Taxa marked with light gray: pre-Turolian First Occurrence Datum; black squares: certain occurrences; gray squares: not recorded but considered present; question marks: uncertain occurrences. Abbreviations as in Fig. 1.

Appendix B. Character matrix

Characters	Out	Weet	Eeet	Elet	Wemt	Eemt	Wlmt	Elmt	Eelt	Characters	Out	Weet	Eeet	Elet	Wemt	Eemt	Wlmt	Elmt	Eelt
Max age	9.0	8.7	8.7	8.0	7.5	7.5	7.3	7.3	7.0										
Min age	8.7	8.0	8.0	7.5	7.3	7.3	7.0	7.0	6.7										
1	1	0	1	0	0	0	0	0	0	61	1	1	0	1	1	1	0	1	0
2–3	0	1	0	0	1	0	2	0	0	62	0	0	0	0	0	0	0	0	1
4	0	0	0	0	0	0	0	0	0	63	0	0	0	0	1	0	1	0	0
5	0	0	0	0	0	0	1	0	0	64	0	0	0	0	0	0	0	0	1
6	1	0	1	0	0	0	0	0	0	65	0	1	0	1	0	1	0	1	0
7	1	1	0	0	1	1	1	1	1	66	0	0	0	1	0	1	0	1	0
8	0	1	0	0	0	0	0	0	0	67	0	0	0	0	0	1	0	1	1
9	0	0	0	0	0	0	1	1	1	69–70	0	0	0	1	0	2	2	2	0
10	0	0	0	0	0	0	1	0	0	71	0	0	0	0	1	0	0	0	0
11	0	1	0	1	1	1	1	1	1	72	0	0	0	0	0	0	1	1	1
12	1	0	0	0	0	0	0	0	1	73	0	0	0	0	0	1	1	0	1
13	0	1	0	0	1	0	1	1	1	74	0	1	1	0	1	1	1	1	1
14	0	0	0	0	0	0	1	0	0	75	0	1	0	0	0	0	0	0	0
15	0	0	0	0	0	0	0	1	1	76	0	0	0	0	0	0	0	0	1
16	0	0	0	0	0	0	1	0	0	77	0	0	0	0	0	0	0	0	1
17	0	0	0	0	0	0	1	0	0	78	1	0	0	0	1	0	1	1	0
18	1	0	0	1	0	0	0	1	0	79	0	0	0	0	1	1	1	0	0
19	0	1	0	0	1	1	1	1	0	80	0	0	0	0	0	0	1	0	1
20	0	0	0	0	0	0	1	0	0	81	0	0	0	0	0	0	0	0	0
21	1	0	1	0	0	0	0	0	0	82	1	0	1	0	1	0	1	0	0
22	0	0	0	0	1	0	1	0	1	83	0	1	1	0	1	0	1	1	1
23	0	0	0	0	0	0	1	1	1	84	1	0	1	1	0	1	1	1	0
24	0	0	0	0	1	0	1	0	0	85	1	1	1	1	1	1	1	1	1
25	0	0	0	0	0	0	0	1	0	86–87	0	0	1	1	2	2	2	2	2
26	0	0	0	0	1	0	1	0	0	88	0	0	1	1	0	1	0	0	0
27	0	0	0	0	1	0	0	0	0	89	0	0	0	0	0	0	0	0	0
28	0	1	0	0	1	0	1	1	0	90	0	0	0	0	1	1	1	1	1
29	0	0	0	0	1	0	1	1	0	91	0	0	0	0	0	0	0	0	0
30	0	0	0	0	0	0	0	0	1	92	0	0	0	0	0	1	0	1	1
31	0	0	0	1	1	0	1	0	0	93	0	1	0	1	1	1	0	1	1
32	1	0	0	1	0	0	0	1	0	94a	1	0	1	1	0	1	0	0	0
33	0	0	0	0	0	0	1	0	0	94b	0	0	0	0	0	0	0	0	0
34	0	0	0	0	0	0	1	0	0	96	0	0	0	0	0	0	0	0	0
35	0	0	0	0	0	0	1	0	0	97	0	0	1	1	1	1	1	1	1
36	0	0	0	0	1	0	1	0	1	99	0	0	1	1	0	1	0	0	0
37	0	0	0	0	1	0	0	1	0	100	0	1	1	0	1	0	0	0	1
38	0	0	0	0	0	0	1	0	0	101	0	0	1	0	1	0	1	0	0
39	0	0	1	0	0	0	0	0	0	102	0	0	0	0	0	1	0	1	0
40	1	0	1	1	0	1	0	0	0	103	0	0	0	1	0	1	0	0	0
41	1	1	0	0	1	1	1	1	1	104–5–6	0	0	0	1	2	2	0	3	3
42	1	0	1	0	1	0	1	0	0	107	0	0	0	1	1	0	1	0	0
43	0	0	0	0	0	0	1	0	1	108	0	1	0	0	0	0	0	0	0
44	1	0	0	0	0	0	1	0	0	109	0	0	0	0	0	0	1	1	1
45	1	1	0	0	0	0	1	1	0	110	0	0	1	1	1	1	1	1	1
46	0	0	0	0	1	0	0	0	0	111	0	0	0	0	0	0	0	1	0
47	0	0	0	0	1	1	1	1	1	112	0	0	0	0	1	0	0	0	0
48	1	0	0	0	1	0	0	0	0	113	0	1	1	0	1	1	1	0	1
49	0	0	0	0	1	0	0	0	0	115	0	1	0	0	1	0	0	0	0
50	1	0	0	0	0	0	1	0	0	116	0	0	0	1	0	1	0	0	0
51	0	0	1	0	0	0	0	0	1	117	0	0	0	0	1	0	1	0	0
52	1	1	1	1	1	1	1	1	1	118	0	0	0	0	0	0	1	0	0
53–54	1	0	1	1	0	0	0	2	0	119	0	0	0	0	0	0	0	0	0
55	1	0	1	0	0	1	0	0	0	120	0	0	0	1	0	1	1	1	1
56	0	0	1	1	0	1	0	0	1	121	0	0	0	0	0	0	1	1	1
57	0	0	1	1	1	1	1	1	1	122	0	0	0	0	0	0	0	0	1
58	0	0	0	0	1	0	1	1	1	123	0	1	0	1	1	1	0	1	0
59	0	0	0	0	0	0	0	1	1	124	0	0	1	0	0	1	0	0	0
60	0	1	0	0	1	0	0	0	0										

Character numbers correspond to the species of Appendix A. Multiple state characters: 2–3: *Mesopithecus delsoni–M. pentelicus*; 53–54: *Chilotherium samium–Ch. schlosseri*; 69–70: *Pliohyrax kruppii–Pliohyrax graecus*; 86–87: *Samotherium boissieri–S. major*; 104–105–106: *Skoufotragus zemalisorum–Sk. laticeps–Sk. schlosseri*.

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