Preliminary analysis of taxonomic diversity, turnover and provinciality in a subsample of large land mammals from the later Miocene of western Eurasia

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Abstract. We have recently reviewed the later Miocene (MN 6-13; ca 15-5 Ma ago) primates, hipparions, rhinocerotids, suoids and carnivores of Europe and the eastern Mediterranean. This work is still unpublished and analyses are underway, but a preliminary indication of some coarse patterns is given here for the sample consisting of the groups listed above: 1) There is a clear-cut difference between western and Central Europe on one hand and the eastern Mediterranean on the other. This is especially clear for species richness, which shows a rising trend throughout the Vallesian and earlier Turolian for the eastern regions and a falling trend for the western ones. 2) The major drops in species richness occurred between MN 6 and MN 7, between MN 9 and MN 10, and between MN 12 and MN 13. Of these, the "mid-Vallesian crisis" (MN 9-10) seems to have been entirely absent in the eastern Mediterranean, where species richness rose sharply during this interval. Correspondingly, the drop in MN 12-13, associated with the Messinian crisis, was predominantly an eastern phenomenon. 3) Taxon free analysis of body size and ecomorphology strongly supports the view that a diachronous opening up of the landscape from east to west took place in western Eurasia during the Astaracian and Vallesian. We postulate that the difference seen in faunal dynamics between east and west reflects habitat-related effects of this diachrony in response to the same global event of rapid physical change. 4) The early Turolian (MN 11) was characterized by high diversity and high faunal similarity, which both decreased during the later Turolian and ended with the Messinian crisis. 5) Despite highly uniform diversity and turnover patterns throughout the interval, western and Central Europe developed distinct ecological differences from about MN 10 onwards. These differences may have been associated with the persistence of closed habitats in Central Europe.

Key words: Species richness, faunal dynamics, faunal similarity, Europe, Neogene, Carnivora, Suoidea, Equidae, Rhinocerotidae, Primates

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I. INTRODUCTION

Quantitative analysis of change in Tertiary fossil land mammal faunas has so far been almost entirely restricted to North America, South America, and the Siwaliks (recent reviews by BARRY et al. 1990, MARSHALL & CIFELLI 1990, PASQUAL & ORTIZ 1990, STUCKY 1990, 1992, JANIS 1993). In particular, the European Neogene seems to have been practically ignored in this respect, except for local areas such as Spain (e. g., MOYÀ-SOLÀ & AGUSTÍ [1990], CERDEÑO [1992], DE BONIS et al. [1994]) or Greece (e. g., DE BONIS et al. [1992]). The main reasons are probably logistic complexity and stratigraphic uncertainty: The material is scattered over many museums in many countries, and the fossil localities are almost entirely isolated occurrences lacking lithostratigraphic ties, so that the stratigraphic correlations are considerably more uncertain than for regions with well-developed geochronologic frameworks based on superposition (LINDSAY 1990). Although these basic facts are unlikely to change, recent years have nevertheless seen considerable improvement in Eurasian Neogene correlations and chronology, especially in the progressive refinement of the MN-system (MEIN 1975, 1990, see also FAHLBUSCH 1991, DE BRUIJN et al. 1993). A big step forward was taken with the publication of the proceedings of the Schloss Reisensburg symposium on European Neogene Mammal Chronology (LINDSAY et al. 1990). Building on this basis, a second symposium, on the Evolution of Neogene continental biotopes in Central Europe and the Eastern Mediterranean (15-5 Ma), was arranged at Schloss Reisensburg in 1992 (see BERNOR et al. 1993). The present paper reports preliminary results obtained from a pooled sample of material revised for that meeting (ANDREWS et al. in press, BERNOR et al. in press, FORTELIUS et al. in press, HEISSIG in press, WERDELIN in press, WERDELIN & SOLOUNIAS in press).

We are well aware of the multitude of potential and actual biases that plague analyses of this kind (e. g., VAN VALEN 1984, 1985a, b; VAN VALEN & MAIORANA 1985; STUCKY 1990; MCKINNEY 1990a, b; VAN VALKENBURGH & JANIS 1993), and present our crude results without any claims to finality. Instead, we hope that the surprisingly clear patterns which appear to emerge will be critically examined and discussed, so that more satisfactory analyses can eventually be performed, and, hopefully, more durable conclusions reached. We do not wish to appear overly apologetic, however. Even crude quantitative estimates seem to us vastly superior to no quantitative estimates at all.

II. MATERIAL AND METHODS

The database for this study is almost entirely derived from manuscripts prepared for the 1992 Schloss Reisensburg symposium, as detailed in the Introduction. For the analysis of diversity, turnover and faunal similarity, the sole source is the range charts provided in these manuscripts. Taxon-free (ecomorphological) analyses and analyses of body mass patterns are based on the

NOW-database in Helsinki, a local clone of the ETE-database (DAMUTH 1993). The contents of the NOW database are mostly derived from the same manuscripts, augmented by locality information from the published literature. Spanish suoids were taken from VAN DER MADE (1992) and Spanish rhinoceroses from CERDEÑO (1989). The version of NOW used for this study included 329 localities and 381 taxa, with a total of 1215 species/locality occurrences.

The study area consists of Europe and Southwestern Asia, as far as the Caucasus and Iran. It was divided into four regions, following instructions for the 1992 Reisensburg symposium: Western Europe (France, Spain, Portugal), Central Europe (Germany, Switzerland, Austria, Poland, the Czech and Slowak Republics, Hungary), Southeastern Europe (Romania, Bulgaria, the former Yugoslavia, Greece, European Turkey), and Southwestern Asia (Anatolia, including islands close to the coast [Samos!], the Caucasus, Iran). We have departed from the original instructions by including northern Italy in Central Europe, and by placing the Caucasus in Southwestern Asia rather than in Southeastern Europe. These regions clearly are not biogeographically defined provinces, but the differences between them do have biogeographic meaning.

Locality ages follow STEININGER et al. (1990) and MEIN (1990) as far as possible, and otherwise whatever information has been available to the individual authors. All ages were interpreted and analyzed in terms of MN units. We have not incorporated any chronological updates resulting from the second Reisensburg symposium in this paper. The ranges of taxa are taken as the interval from the first appearance to the last. In case of endpoints of uncertain age, the age limit giving the smallest range was used (see FORTELIUS et al. in press). Taxa were counted as present in an interval even if not recorded, if present before and after it. In some cases this means that taxa are counted as present in an area and interval for which no actual fossil localities are known (e. g., MN 7/8 of Southeastern Europe).

Diversity was analyzed in the sense of species richness only, for the whole area and for each of the four regions separately. Absolute turnover was calculated as the number of entries and exits in one MN unit, relative turnover as this number divided by diversity of the same interval. No attempt was made to distinguish between immigration and evolution of new taxa in situ. Probability of extinction was calculated as the number of exits divided by diversity (a simplified version based on VAN VALEN [1984]). Faunal similarity between the four regions defined above was analyzed by means of the Simpson Index (SIMPSON 1947). For discussion and justification of these procedures see FORTELIUS et al. (in press), WERDELIN (in press), WERDELIN & SOLOUNIAS (in press).

The body mass estimates are derived from several sources: FLEAGLE (1988) for primates, FORTELIUS et al. (in press) for suoids, and unpublished analyses by FORTELIUS, VIRANTA & WERDELIN for horses, rhinoceroses and carnivores. These analyses are based mainly on regression equations given in LEGENDRE & ROTH (1988), DAMUTH & MACFADDEN (1990), ANYONGE (1993) and FORTELIUS & KAPPELMAN (1993). Body masses were analyzed only in terms of group means, with groups defined variously in terms of time, region, taxonomy and/or ecomorphology.

III. RESULTS

About 2/3 of the taxa included in this sample are carnivore species, and carnivores consequently dominate the overall picture to some extent. Since carnivores and non-carnivores tend to show somewhat different patterns they have been separated in many of the analyses that follow.

S p e c i e s   r i c h n e s s . For the non-carnivores, the species richness curves are either ascending or descending, depending on region (Fig. 1a). The western regions (Western Europe, WE, and Central Europe, CE) display high richness in the Astaracian, with a distinct drop

through the Vallesian and low richness throughout the Turolian. The eastern regions (Southeastern Europe, SEE and Southwestern Asia, SWA) show an almost exactly opposite trend, with richness rising through the Vallesian to a peak in the early Turolian. There is no evidence in the west of the marked drop in richness from MN 12 to MN 13 seen in the east. The low (later) Astaracian species richness for SWA probably reflects the scarcity of localities, but this explanation is not applicable to the late Miocene differences.

The carnivore pattern is less distinct but roughly similar (Fig. 1b). The diversity curves for WE and SEE and SWA are quite similar to the corresponding curves for non-carnivores, with early and late maxima, respectively. Central European carnivore diversity falls during the Astaracian, as in the eastern regions, but unlike them does not recover in the Turolian. An interesting though possibly spurious detail is that both carnivore and non-carnivore patterns agree on a western European diversity peak in MN 8 and a Central European one in MN 9.
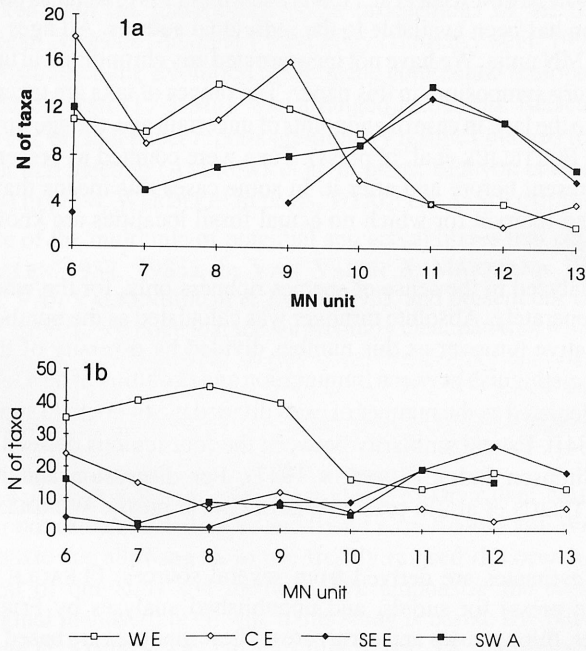

Fig. 1. Species richness by region of Middle and Late Miocene European and southwest Asian mammals. 1a: Non-carnivores (primates, suoids, hipparions and rhinoceroses). 1b: Carnivores.

T u r n o v e r . Absolute turnover (the summed entries and exits for each interval and region) largely reflect diversity, and roughly the same patterns are seen. The relative contributions of entries and exits to absolute turnover are similar, but the exit pattern is more distinct (analyzed separately only for non-carnivores -- for carnivores, see WERDELIN [in press]). The non-carnivore entry pattern shows high values in MN 6 for all regions with good data, then low values in the later Astaracian, rising through the Vallesian to a maximum in MN 10, then descending through the Turolian (Fig. 2a). Central Europe shows a high value for MN 9 and zero for MN 10, but this may

be artificial, due to scarcity of MN 10 localities. As was the case for diversity, the eastern regions show low values in the Astaracian and high values in the Turolian, while the opposite is true of the western ones. This is even more clear for the extinctions (Fig. 2b). It is also clear that the extinction-driven turnover event in MN 9 is a phenomenon restricted to the western regions. Another interesting feature is that (except for the doubtful case of CE), the extinction peak occurs in MN 9 and is followed by an entry peak in MN 10 (MN 11 for SWA).
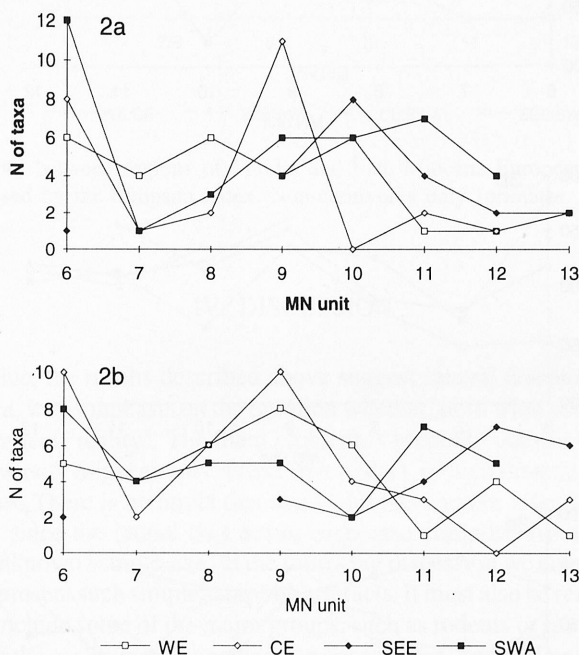

Fig. 2. Number of entries (2a) and extinctions (2b) by region of Middle and Late Miocene European and southwest Asian non-carnivore mammals (primates, suoids, hipparions and rhinoceroses).

Relative turnover (absolute turnover divided by diversity for the same region and interval) shows a distinct peak at MN 9 for most combinations of taxa and regions, but the details are not easy to interpret. Western and Central European carnivores show very regular relative turnover curves, low in the Astaracian, rising to a peak at MN 9, and then staying high until the end of the Miocene (as far as the data allow calculation) (Fig. 3a). The general trend, for non-carnivores and for all taxa combined, is a drop from MN 6 to MN 7/8, a rise to a peak in MN 9, and a subsequent decline to a somewhat lower Turolian level (Fig. 3b).

The probability of extinction (relative turnover ignoring entries) shows a somewhat irregular pattern for non-carnivores (Fig. 3c) and carnivores alike. For the non-carnivores there is a distinct difference between east and west in that eastern levels are high in the Astaracian (MN 6 for SEE), sink in the Vallesian and rise again through the Turolian. The western pattern is considerably less dynamic, but largely the opposite, with relatively high values in the Vallesian. For both western regions the values stay high from MN 9 to MN 10, but then the curves split. This Turolian departure of CE from the western pattern is seen very clearly in the taxon-free analyses described below.
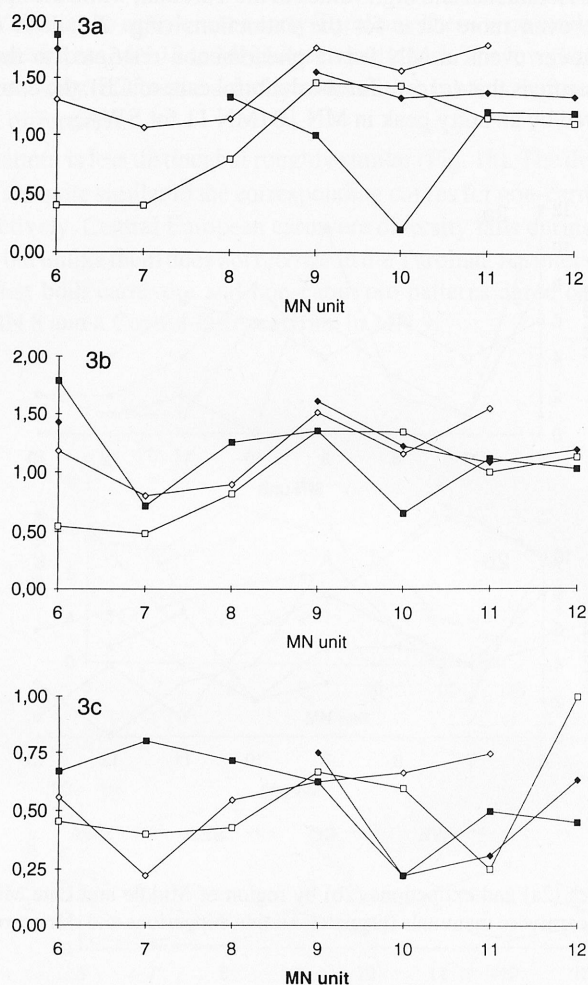
Fig. 3. Relative turnover by region of Middle and Late Miocene European and southwest Asian mammals. 3a: Carnivores. 3b: All taxa. 3c: Non-carnivores (primates, suoids, hipparions and rhinoceroses).

Faunal similarity . Plotting the value of SIMPSON indices for selected pairwise comparisons of regions also reveals meaningful patterns (Fig. 4). This is mainly the case for non-carnivores, however. For unknown (probably mainly taphonomic) reasons the carnivore pattern is rather irregular, and is ignored here. For the non-carnivores it is very clear that all west-west and all east-east comparisons throughout the interval give higher values than any east-west comparisons. It is also clear that the similarity between SWA and the two western regions increased after MN 6, and then decreased to a very low value in MN 10, only to rise sharply to a peak similarity in MN 11. An interesting feature is seen during the middle and late Turolian, where WE returns to low similarity with SWA, but CE continues to increase its similarity to that region.
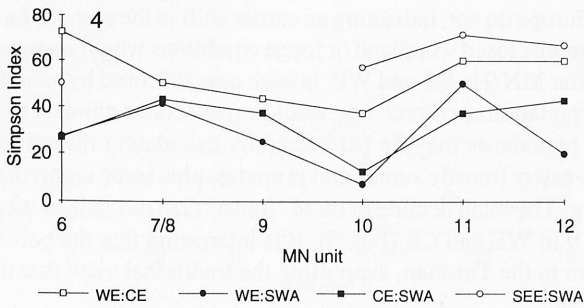
Fig. 4. Faunal similarity between regions of Middle and Late Miocene European and southwest Asian mammals as expressed by the Simpson index. Non-carnivores only (primates, suoids, hipparions and rhinoceroses).

IV. DISCUSSION

Taken at face value, the results described above suggest several reasonable conclusions. We will review them here, with emphasis on the question whether, or to what extent, the patterns seen can be expected to reflect "reality". The main problem is probably uneven coverage of intervals and regions – low diversity might simply reflect lack of data, or high diversity the presence of one or more rich localities. There is no doubt that this factor has a major effect, but it is not a simple matter to deal with, since the faunal lists are in each case compiled from several localities of different and often unknown sample size. In the following discussion we emphasize aspects which appear unlikely to represent such simple sampling artefacts. It must also be remembered, of course, that our data do not include some of the major groups, such as rodents or ruminants. Adding more taxa will serve to test the preliminary hypotheses proposed here, and will undoubtedly change the patterns to some extent.

In the presently available material, there appears to be a good deal of consistency in the way the study area is split into eastern and western parts, with two regions representing each. The high western and Central European non-carnivore diversity and its rapid decline in the later Vallesian and early Turolian is in sharp contrast to the rapid diversity increase seen in SEE and SWA during the same interval (Fig. 1a). The low Astaracian (especially MN 7/8) diversity in the eastern regions is undoubtedly an artifact due to lack or scarcity of localities, but the rise through the Astaracian cannot be explained in this way, and neither can the low Turolian diversity for the western regions. The same contrast is seen in the carnivore material, although less dramatically, and with the difference that the eastern diversity increase begins after MN 10 rather than MN 9 (Fig. 1b). The Western and Central European "mid-Vallesian crisis" is one of the most robust features of the diversity and turnover patterns of both carnivores and non-carnivores, and is entirely lacking in the eastern regions. As noted above, this event is the only one clearly associated with peak absolute extinction levels (probability of extinction for the western regions stays high into MN 10, so from the point of view of the surviving taxa the "crisis" continued, although its effect on diversity was less dramatic). These results support the conclusion that the early/late Vallesian transition in Western (and, apparently, Central) Europe is distinguished from other turnover events by high extinction values (MOYÀ-SOLÀ & AGUSTÍ 1990).

This pattern is easily related to the concept of a time-transgressive east-to-west spread of the "Pontian" open woodland chronofauna, as previously recognized on qualitative evidence (BERNOR

et al. 1979, BERNOR 1983, 1984). DE BONIS et al. (1994) recently used correpondence analysis to show that the Vallesian faunas of western Europe cluster together with Middle Miocene faunas, but those of eastern Europe do not, indicating an earlier shift in the east. As far as the present results go, the change from more closed woodland or forest conditions would seem to have happened after MN 6 in SWA and after MN 9 in CE and WE, in each case followed by an initial decline in species richness. If this interpretation is correct, one would expect forest animals to be the most affected. A crude test of this hypothesis may be performed by calculating the percentage of brachydont omnivores and plant-eaters (mostly suoids and primates, plus some carnivores) in the faunas. The result is quite striking: The main decline in these "forest" taxa did indeed take place after MN 6 in SWA and after MN 9 in WE and CE (Fig. 5). It is interesting that the percentage of brachydont taxa in CE rises again in the Turolian, supporting the traditional view that open woodlands were never established there.
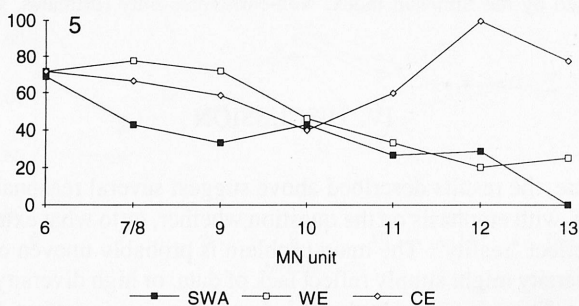

Fig. 5. Proportion of brachydont herbivores and omnivores in the mammalian faunas of Western Europe, Central Europe and Southwestern Asia.

Another interesting (and, perhaps, reassuring) aspect of these changes is seen in the body size patterns, especially when broken down by ecomorphology as above. The brachydont herbivores and omnivores are again the most revealing, and contrast sharply with mesodont and hypsodont herbivores. For the brachydont taxa (Fig. 6a) the general trend is quite similar in all regions, with an initial rise, followed by a plateau or a decline. The differences in level and timing are quite suggestive, however: From MN 6 to MN 9, the curve for SWA lies above the others, and also rises more rapidly. From MN 9 to MN 10 the curves for two western regions rise sharply, almost to the level of the eastern one, as small species become extinct. In the Turolian the two western curves depart, with mean body size continuing to increase in WE, where the contribution of this group to the whole fauna was by then low, and falling in CE where brachydonts were relatively more important. A slight decline from MN 10 to MN 12 is also seen in SWA, but the situation there was static compared to the other regions.

The body size history of mesodont and hypsodont herbivores is quite different (Fig. 6b). Apart from MN 9, WE and SWA show virtually identical curves, with slow increase in the Astaracian and a decline after MN 10. The difference seen in MN 9 is that the curve for WE drops to a minimum there, whereas it rises to a maximum in SWA. As before, the sharpest rise happens first in the east (MN 7/8 to MN 9) and later in the west (MN 9 to MN 10). Central Europe shows an entirely different curve, with a high plateau from MN 6 to MN 9, and a sharp decline from MN 9 to MN 10, followed by a low plateau (as far as data allow). For the animal-eaters the pattern is again different, and largely similar for all regions: A low plateau from MN 6 to MN 10, a steep rise from MN 10 to MN 11, and a decline through the Turolian.
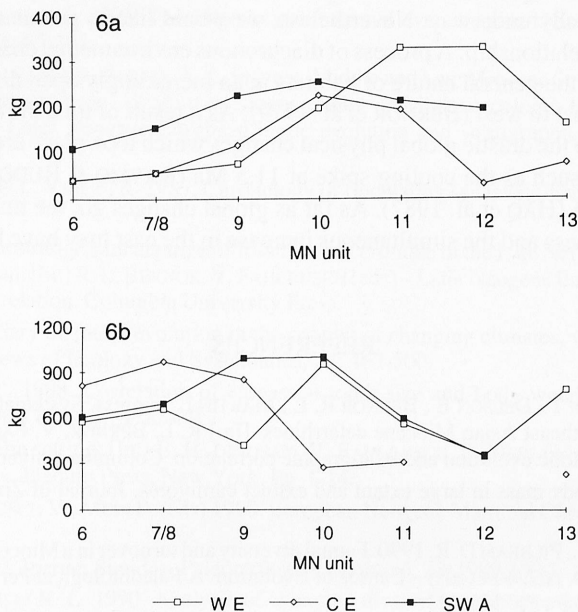
Fig. 6. Mean estimated body mass of ecomorphological groups of Middle and Late Miocene European and southwest Asian mammals. 6a: Brachydont herbivores and omnivores. 6b: Mesodont and hypsodont herbivores.

It would be premature to base detailed conclusions on these patterns, but it is certainly suggestive that the timing of the change is earlier in the east than in the west, that it is more dramatic in the west, and that there appears to be a strong positive correlation between mean body size of "forest" forms and the degree of openness of the habitat, as derived from independent evidence. It is also remarkable that these ecomorphological changes are so different between Western and Central Europe, especially since their species richness and turnover curves are so similar. This is especially the case for the Turolian, when maximum environmental dissimilarity is expected.

Finally, the development of faunal similarity fits the general picture quite well (Fig. 4). From MN 6 to MN 9, east-west similarity was moderate, then dropped to a minimum at MN 10, only to rise again to a maximum in MN 11. As seen before, western and Central Europe part their ways after MN 11, with WE returning to low similarity values and CE gradually becoming increasingly similar to SWA. To some extent this may reflect scarcity of data for CE, but it should be noted that the pattern appears several times in technically independent results presented above.

To summarize, the quantitatively most important changes recorded for the study area and interval occurred between the mid-Vallesian and early Turolian. In terms of species richness and turnover, the effects were largely opposite between western and Central Europe on the one hand and southeastern Europe and southwestern Asia on the other. In the west, diversity crashed at and after the "mid-Vallesian crisis", whereas it rose sharply in the east during the same interval. It appears likely that the main ecological aspect of these changes was the time-transgressive transition from closed to open woodland first suggested by BERNOR et al. (1979). In terms of faunal similarity

between east and west, these changes first resulted in low similarity in MN 10, immediately followed by high similarity in MN 11, when eastern immigrants established themselves in the west.

Serious attempts at explanation of these patterns must await the compilation and analysis of more data that is already underway. Nevertheless, we would like to postulate, in a general way, the following causal relationship: A process of diachronous environmental change was taking place in the area, changing the general nature of habitats in an increasingly open direction, more or less progressively from east to west (BERNOR et al. 1979). As a result of this, the eastern taxa were, in a sense, preadapted to the drastic global physical changes which took place around the Astaracian-Vallesian transition, such as the cooling spike at 11.5 Ma (RAYMO & RUDDIMAN 1992) and the regression at 10.5 Ma (HAQ et al. 1987). As far as global changes go, the mid-Vallesian crash in western species richness and the simultaneous increase in the east may have had identical causes.

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