horizons (foam sinter) in cave entrances. The *D. ruderatus*-fauna gradually declines and the continental steppe elements are replaced by thermophilous southern species, particularly by *Granaria frumentum* which dominates the karst steppes and sunny rocks. The foam sinter formation abruptly declines in the middle Atlantic, immediately before the Neolithic occupation. Since that time, the Bohemian Karst was continuously colonized and its plateaus with loess covers transformed into cultural landscape. The expansion of closed forest was hindered by grazing, which enabled a secondary expansion of open-country species and probably supported the immigration of *Capaea vindobonensis*, from the southeast.

- The later phase of the Climatic Optimum-the Epiatlantic is characterized by the culmination of demanding woodland malacocoenoses, as well as by the appearance of some thermophiles coming from the south, particularly *Truncatellina claustralis*. Nevertheless, karst steppes persist at many places, obviously due to pasture. Some anthropophobic forest snails, for instance *Bulgarica cana* occur throughout the Bo-hemian Karst. During the Climatic Optimum also the neoendemic microspecies *Bulgarica nitidosa* (of Balcan origin) appears.
- The Subboreal (sensu Jäger, 1969; 1400–700 BC): This predominantly dry phase is characterized by the expansion of the Knoviz Culture at the decline of the Bronze Age. The climate is unbalanced, which is reflected by the formation of coarse breakdown in cave entrances and formation of coarse screes poor in matrix. The tufa formation declines and rendsina soils develop on the deposits.
- The Subatlantic and historical times: sensitive forest species, such as *Bulgarica cana* decline, while *Alinda biplicata, Discus rotundatus* and *Helicodonta obvulata* culminate. Later, re-expansion of open-ground species and appearance of moder imigrants (*Cecilioides, Xerolenta* and even *Oxychilus cellarius*) take place.

Discussion and conclusions

The above developmental pattern is comparable with the results of pollen analyses (Firbas, 1949, 1952), but differs in a number of important details. This is due to environmental conditions in the area in question which are very different from those in regions where the Holocene paleoenvironmental history is based on pollen analyses. These are located in humid mountains or in marshy basins which are very poor in traces of prehistoric humans and are covered by mesic to marshy closed forests whereas the Bohemian Karst is a warm-dry area dominated by thermophilous, often semi-open woodland with numerous open patches affected by long-term human activities. The survival of xerothermic biocoenoses in the Bohemian Karst from the early Holocene was continuously supported by a dense prehistoric settlement that hindered the forest expansion during the moist phases of the Climatic Optimum. It should be also stressed that the reconstruction of Holocene paleoenvironments in the warm-dry areas of Czechlands is based not only on the succession of molluscan or vertebrate assemblages but also on the changes in sedimentation, soil formation and $CaCO_3$ metabolism in correlation with archaeological records, which provide a much broader evidence of particular events (standstill phases, erosion, scree accumulation, drying-up of tufa deposits, etc.) than the pollen analyses.

These results that coincide with observations from other xerothermic areas of Czechlands (e.g. Pálava, České Středohoří Mts.) suggest that the Postglacial in warm-dry lowlands and hill countries shows a development different from that in colder humid areas and thus represent a distinct facies characterized by specific faunal succession, soil and sediment development, which is in agreement with the proposal of K.-D. Jäger (1969) presented to the VII INQUA Congress.

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Glacial Cycles and Mammalian Biodiversity of Central Europe: Large Scale Migrations or Vicariance Dynamics?

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ABSTRACT The extensive fossil record was examined to reveal the geographic variation in patterns of the Pleistocene-Holocene faunal turnover. The considerable differences were found between the Mediterranean region (Balkans including) and central Europe. The response of individual species to the climatic fluctuations was not concerned, the central European interglacial communities did nowhere survived. The metapopulation dynamics, an essential factor of the response, has mostly operated rather on small than large geographic and time scales.

KEY WORDS: faunal turnover, Holocene, biogeography, mammals.

Introduction

The large scale migrations and extinctions events are traditionally looked upon as the major way in which the vertebrates responded the climatic and environmental fluctuations of the Quaternary past. The traditional paradigmatic concept further explains that (a) individual species as well as entire communities contributing the respective zonobiomes shifted southwardly in time of glacials, by which (b) those of the central Europe survived in the Mediterranean refugia, and (c) they started the postglacial recolonizations of their recent ranges just from there. This type of faunal dynamics can be in short characterized as a periodic alternation of two chorologic units (respective either to glacial or interglacial communities) which differ almost completely: in their core species, energetic structure and even in the satellite species contributing them. Despite of general support from the actual fossil record to this view there are more reasons for which the above concept should not be considered universally valid in all its details. Thus, the recent data from molecular phylogeographies demonstrated quite convincingly that there is little congruence in dispersal history among individual species contributing the recent communities and that the Mediterranean seems to be rather an area of paleoendemism than a source for northwards postglacial colonization (Bilton et al., 1998). Moreover, as demonstrated elsewhere (Horáček and Ložek, 1988; Horáček, 1991) the patterns of the faunal response to climatic fluctuations was, at least in certain groups, apparently different in the Early Pleistocene of central Europe as both the glacial and interglacial assemblages were rather uniform not only in their species composition but also in core elements and their overall dominance patterns.

The present paper is intended to survey briefly some further discrepance as reveal of the geographic variations in patterns of faunal turnover over the recent cycle (Vistulian and Holocene).

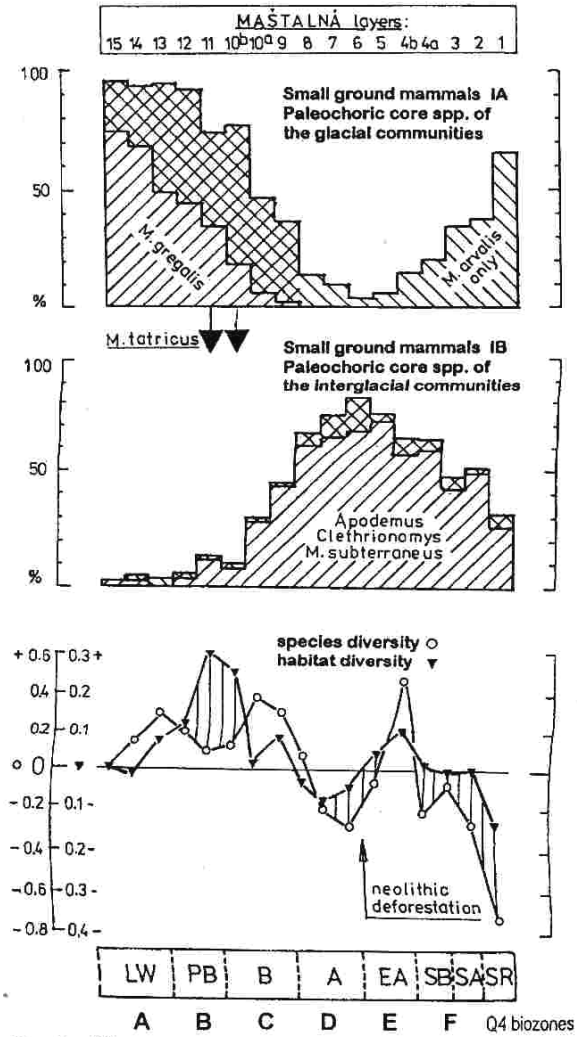

Fig. 1. The percentages of the IA and IB core species in faunal sequence of Maštalná (southeastern Slovakia, MNI = 1851, span of record: ca 30 ka) and the respective sequential changes in species and habitat diversity. Note FAD of the Carpathian neoendemite *Microtus tatricus* in time of the Early Holocene ecological release.

Methods and material studied

The paper is primarily based on the extensive record of small mammals obtained for the recent glacial cycle (Vistulian-Holocene) in the Czech and Slovak Republic. It covers more that 700 community samples yielding altogether a minimum of 29,000 individuals and 4300 distributional records. Most of them come from the continuous sedimentary series at which the observed sequences of faunal events are fixed by direct superposition. The material has been supplemented with corresponding data from neighbouring countries (mostly Hungary and Germany - Kordos, 1982; Storch, 1995; etc.) and analysed with aid of several quantitative techniques. The resulting picture was compared with the record available from the Balkans and Asia Minor (e.g. Popov, 1994; Storch 1988; own material) - in total about 200 community samples have been taken in account.

Biostratigraphic dating was applied, as a rule, mostly with aid of the criteria and stages proposed by Horáček and Ložek (1988).

Survey of results

1. The occurence patterns within the total sample group the included species into three distinct chorologic units: IA Palaeochoric elements of glacial communities, IB Paleochoric elements of interglacial communities and II Apochoric elements of the Holocene interglacial, mostly appearing first in the postneolithic time. Thanks to specificities of the Holocene faunal development, the recent fauna of central Europe is extensively contributed from all three units.
2. An overall diversity (expressed as amount of interregional differences in structure of supposedly synchronous assemblages) is relatively low over whole central Europe during the Late Vistulian and Preboreal while it considerably increased during the Boreal and Atlantic and decreased again in the post-neolithic period.
3. The replacement of the two above mentined chorologic units (IA, IB) at the Pleistocene-Holocene boundary was relativelly sharp in the western part of central Europe, especially in Germany and Bohemia while in the Carpathians (Fig. 1), it was rather prolonged and associated with a considerable stage of ecological release.
4. Considerable geographic differences occurred in survival of individual glacial elements as well as in course of appearance of the interglacial elements (Fig. 2). While the glacial

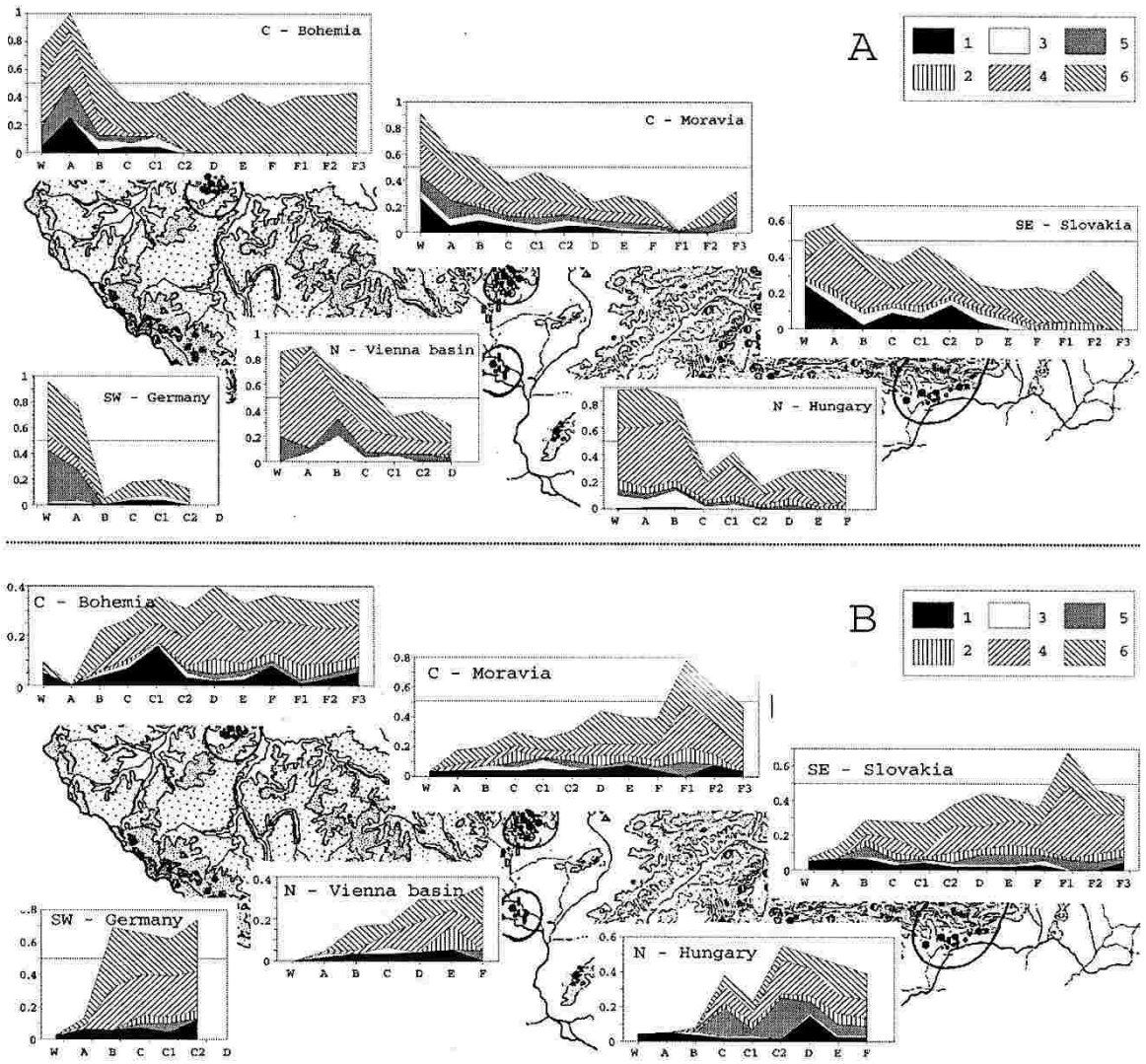

Fig. 2. Late Pleistocene and Holocene changes in mean percentages of some core species of the glacial - IA (A) and interglacial - IB (B) small ground mammals communities in six regions of central Europe over last 30 ka period (W, A - Late Glacial; B - Preboreal; C - Preboreal/Boreal; C1 - Boreal; C2 - Boreal/Atlantic; D - Atlantic; E - Epiatlantic; F - Epiatlantic/Subboreal; F1 - Subboreal/Subatlantic; F2 – Subatlantic/Subrecent; F3 - Subrecent). (A) 1 - *M.nivalis*, 2 - *Ochotona*, 3 - *M.oeconomus*, 4 - *M.gregalis*, 5 - *Dicrostonyx*, 6 - *M.arvalis*. (B) 1 - *S.araneus*, 2 - *M.subterraneus*, 3 - *Sicista*, 4 - *Apodemus*, 5 - *G.glis*, 6 - *C.glareolus*.

elements disappeared rapidly in the southern Germany or in Bohemia, in the Carpathian region, *Ochotona* or *Microtus gregalis* survived to the middle Holocene, *M.nivalis* or *M.oeconomus* even to the recent time. *Dicrostonyx* dissappeared from the Carpathian region already prior to the beginning of Holocene while it survived until Boreal in Moravia and even to the Late Holocene in Poland. The woodland and demanding interglacial elements (such as *Clethrionomys*, *Sylvaemus*, *Glis*) regularly appear in the Carpathian basin and in southern Germany even prior the beginning of Holocene while in the Bohemian massif their appearance is rather delayed.

5. Anyhow, despite all local specificities, the major pattern of the faunal development - the alternation of two chorologic units - is more or less clearly marked in every series.
6. Although the corresponding record from southeastern Europe and/or Asia Minor is still too scarce to allow a detailed comparison, the picture it reveals is clearly quite a different. The major difference from the central Europe is here, in short, that in no one series and no one record there we meet any trace of a well pronounced alternation in species composition or essential shifts in community structure. There is no considerable increase in the central European interglacial elements, though the Early Holocene records, especially from

the Pontic region, suggest a regular appearance of *Clethrionomys*, *M.subterraneus fingeri* or even *Sicista* sp. which, similarly as *Ochotona*, also recorded here, nowdays absent in Turkey at all.

7. Nearly the same holds for the situation in Balkans (perhaps best demonstrated on a sequence in Temnata dupka cave in Bulgaria by Popov, 1998). In accord with further data it demonstrates that the situation in Balkans reminded rather that in Asia Minor than in central Europe. Except for invasion of *L.lagurus* (accompanied by Eolagurus luteus and Allactaga) characteristic of the Balkan glacial assemblages, no essential faunal turnover can be observed as well in species composition as in community structure. The index core species of the central European glacial communities do here absent (except for *M.arvalis*) and neither the central European interglacial taxa exhibit here any marked increase - they appeared rather irregularly and rare.
8. In short, all this means that the traditional idea on a southward shift in faunal zonality during the glacials by which the community patterns of central European interglacial was retained, can be rejected for sure. The pattern of the central European interglacial communities disappeared at all during the glacial without producing any effect upon the faunal situation in the expected refugia, at least in the southeastern Mediterranean and Balkans. No support is available either for the idea that these regions were directly invaded by the northern populations or that the central European interglacial taxa colonised here the continuos ranges during the glacial time. A lack of any essential changes in their occurrence pattern or abundance around the Pleistocene/Holocene (which, for the source area of a massive migration wave, one certainly would expect), is also worth of mentioning.
9. Already a rough account of records (Fig. 3) demonstrates that even from Czech and Slovak Republic, the interglacial elements such as *Clethrionomys*, *Sylvaemus* or *Sicista* have repeatedly been recorded in context of the glacial assemblages, quite regularly especially in the Carpathian region. Frequency of these taxa in glacial assemblages is a very low, of course - about 0.1 to 0.8 percent only. Such records as well as the numerous records of glacial elements in the interglacial assemblages, suggest that in more taxa the local exctinction over whole central Europe was perhaps not completed even during the recent glacial cycle.
10. Being whole the region of central Europe looked upon as a single unit (Fig. 4), yet its overall faunal development is smooth and reminds just the situation in the Mediterranean.

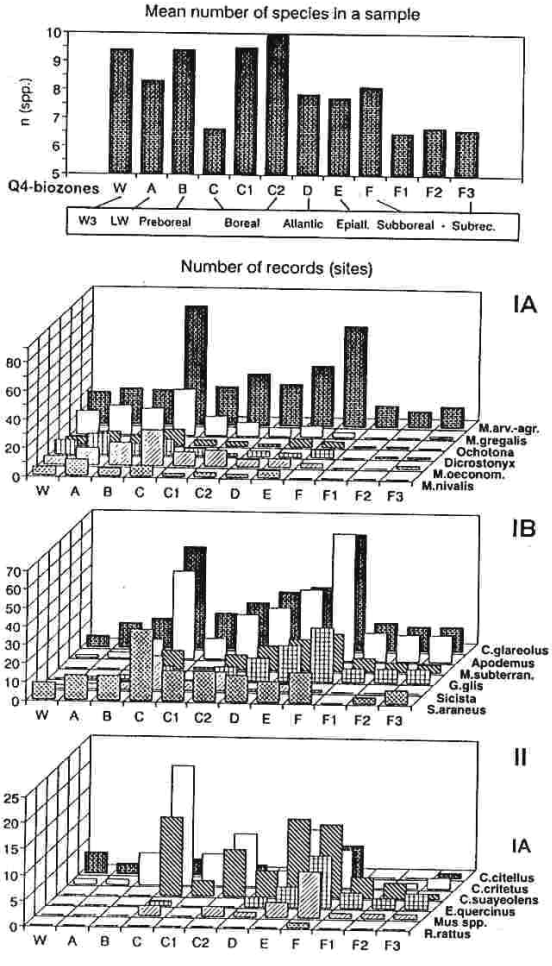

Fig. 3. A general survey of the Late Pleistocene and Holocene record of several index species from Czech and Slovak Republics: numbers of sites which reveal their presence in the respective stratigraphic horizons (expressed in terms of the Holocene biozones sensu Horáček and Ložek, 1988).

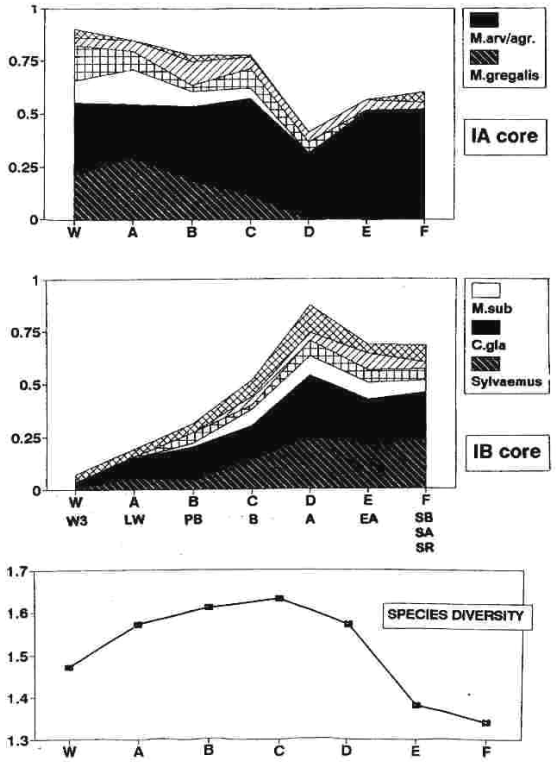

Fig. 4. The percentages of the IA and IB core species and the corresponding values of species diversity over the last 30 ka: mean values in the total sample, i.e. those for whole central Europe. Comp. Fig. 1 for differences of the large scale pattern from the situation in a sole site.

Apparently it is due to extensive local variation in course of faunogenetic events, short-term vicariance dynamic, irregularities in time and spatial distribution of the respective vicariance events and considerable effect of faunal provincionalism (which was particularly pronounced during the early Holocene when the total sample species diversity reaches its peak).

Discussion

The above discussed data suggest for more species multiple survival in small local isolates. The question open to discussion is whether such a possibility can be considered realistic in respect to actual adaptive limits of the respective taxa. The nowdays distributional situation with the species like *Microtus agrestis*, *Sicista* spp., *Microtus oeconomus*, *Microtus subterraneus*, *M.nivalis*, *Arvicola terrestris*, *Sorex alpinus*, *Neomys anomalus*, *Cricetus cricetus*, *Spermophilus citellus* can serve as a model. Indeed, all these taxa are apparently capable to survive long in mutually isolated micropopulations often under condition of extreme rarity as well as, on the other hand, to respond breaks of ecological release with a rapid abundance increase. In all these species, a massive spread and continuous distribution has been limited just only to a certain shorter periods within a glacial cycle, specific for each of them. Except for these breaks their distribution is discontinuos, characterized by a greatly pronounced patchiness and exhibiting a variegated vicariance patterns.

In other words, just such a fine scale metapopulation dynamics is to be expected as a key factor which mediated distributional fluidity of the inhabitants of periglacial zone over the climatic fluctuations and disposed them to a rapid responsal to breaks of climatic amelioration and/or ecological release as it is well evidenced in the fossil record (e.g. at time of the Neolithic deforestation). It seems neccessary to expect that in more species such rapid recolonisation events proceed rather from multiple local sources than from distant major refugia via large scale migrations. Anyhow, for the period under study, the distant migrations are to be expected particularly in those taxa which spread was considerably delayed - e.g. in dormice or in more elements of the glacial communities - such as in lemmings or *M.gregalis*, which invasion into central Europe did not proceeded simultaneously and it was far of being episodical, of course (cf. e.g. Horáček and Sánchez, 1984).

In respect to biodiversity history of central Europe, it is important to remind that (a) there were local differences in timing of range regression or range expansion in individual species, in actual impact of these events upon resident local communities as well as in the observed or expected vicariance events in different regions, (b) in most species can be well expected a pronounced capability to undergo conditions of a rarity dynamics, (c) the region of central Europe provides greatly variegated landscape patterns which continuously could promote its considerable patchiness both in climatic and habitat respects (cf. also Storch, 1992). It is just the whole of all these factors which is to be considered the most important incipient sources of the natural biodiversity of the region.

Conclusions

(1) There have been considerable differences in patterns of the Pleistocene faunal turnover between the Mediterranean region (including Balkans, at least south of the Carpathians) and the more northern situated regions. (2) In both the regions, local vicariance and rarity dynamics has been apparently quite a frequent in most faunal elements and contributed to the overall picture of the large scale faunal processes much more than commonly believed. (3) Even from the actual fossil record there is more support for the above statements of molecular phylogeographies than for a textbook-like version of traditional paradigm. (4) In accord to the traditional scenarios, the essential factor explaining the past story of the mammalian faunal tunover is the metapopulation dynamic. Nevertheless, it seems more probable that its major components - extinctions and migrations - have operated rather on relatively small geographic and time scales, while the continental or global scales came here in actual play in a lesser extent. (5) Just the combination of all these factor with a greatly variegated environmental pattern of central Europe has permanently been the most importance source factor of its mammalian biodiversity.

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