Disentangling palaeodiversity signals from a biased sedimentary record: an example from the Early to Middle Miocene of Central Paratethys Sea

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Abstract: Changes in molluscan diversity across the 3rd order sequence boundary from the Lower to the Middle Miocene of the Paratethys were evaluated in the context of environmental bias. Taken at face value, quantitative data from nearshore and sublittoral shell beds suggest a transition from low-diversity Karpatian (Upper Burdigalian) to highly diverse Badenian (Langhian and Lower Serravallian) assemblages, but environmental affiliation of samples reveals a strong facies shift across the sequence boundary. Ordination methods show that benthic assemblages of the two stages, including 4 biozones and four 3rd order depositional sequences over less than four million years, are developed along the same depth-related environmental gradient. Almost all samples are from highstand systems tracts, but Karpatian faunas are mostly from nearshore settings, and Badenian faunas are strongly dominated by sublittoral assemblages. This study emphasizes the importance of highly resolved stratigraphic and palaeoenvironmental frameworks for deciphering palaeodiversity patterns at regional scales and highlights the effort required to reach the asymptote of the collector’s curve. Abundance data facilitate the recognition of ecological changes in regional biota and it is suggested that in second and higher order sequences the facies covered within systems tracts will drive observed diversity patterns.

The quality of the fossil record of biodiversity is strongly influenced by the rock record (Holland 2000; Smith 2007). The amount of sedimentary rock preserved has strongly fluctuated over time and is very similar to corresponding diversity patterns, suggesting that a major bias exists (Raup 1976; Miller & Foote 1996; Smith 2001; Peters & Foote 2001; Smith & McGowan 2007; Barrett et al. 2009). Alternatively, it suggests that both the rock record and diversity are driven by a common underlying factor, such as sea-level change (Peters 2005, 2006), a signal that can be regionally obscured at tectonically active margins (Crampton et al. 2003). The change in the proportion of onshore to offshore sediments preserved in the record, however, is probably as important as changes in the volume of rock preserved (Smith et al. 2001; Crampton et al. 2003, 2006). Although global datasets are comparatively robust to such biases (e.g. Marx & Uhen 2010), sequence stratigraphical architecture undoubtedly controls patterns of faunal change on a local and regional scale (Bulot 1993; Brett 1995, 1998; Patzkowsky & Holland 1999; Smith et al. 2001; Smith 2001). Specifically, most changes in first and last occurrences of species, and widespread changes in species abundance and biofacies, occur at sequence boundaries and at major transgressive surfaces (Holland 1995, 1999, 2000). It is therefore important to evaluate stage-level changes in taxonomic diversity, at the temporal scale of millions of years, in the context of rock volume- and environmental bias to ensure that these changes are not simply driven by sequence architecture (Smith 2001).

The present study focuses on diversities of two regional Miocene stages of the Paratethys, an epicontinental sea whose history is closely linked to the Alpine orogeny and that covered vast parts of Central and Eastern Europe (Rögl 1998, 1999) (Fig. 1). Standing diversity of the Central Paratethys indicates a strong increase in species richness at the boundary from the Karpatian (Upper Burdigalian) to the Badenian (Langhian and Lower Serravallian), which is interpreted as a major faunal turnover associated with the Langhian transgression (Harzhauser et al. 2003; Harzhauser & Piller 2007). Based on a comprehensive echinoderm dataset, however, it has been suggested that the low diversity of the Karpatian was rather caused by non-preservation of suitable habitats (Kroh 2007). In this study we use a species abundance dataset of benthic molluscs to evaluate the influence of environmental bias on the faunal change. Previous molluscan species lists from the area are not useful for

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this purpose because they are biased in favour of larger shells and biostratigraphically and palaeogeographically useful species, but stable temporal and spatial patterns of diversity can only be deciphered using large bulk samples from extensive field work (Koch 1978; Kosnik 2005).

The Vienna Basin and adjacent basins have now been systematically studied for almost two centuries for molluscs and other invertebrates. Based on the publication of a visiting French geologist (Prevost 1820), these basins were key areas for the foundation of the concept of the Tertiary in the early 19th century (Rudwick 2005, pp. 546–549; Vávra 2010). The stratigraphy of the Central Paratethys is comparatively well studied (for review see Piller et al. 2007) and the taxonomic composition of the Central Paratethys molluscan fauna very well known (e.g. Schultz 2001, 2003, 2005). Compilations on the standing diversity of Neogene stages were published recently (Harzhauser et al. 2003, Harzhauser & Piller 2007). With respect to species-abundance patterns, it has been shown that at the scale of outcrops, shell beds, and samples most species are rare and diversity is patchy (Zuschin et al. 2004a, 2006), a pattern that is also evident for the total assemblage studied here. Diversity is influenced by taphonomic processes, for example by size sorting during tempestitic transport (Zuschin et al. 2005). Finally, it has been suggested that diversities of the marine Paratethys are lower than those of contemporary adjacent basins because diversity curves have rather gentle slopes when compared with such curves from the Miocene Boreal bioprovince (Kowalewski et al. 2002).

So far, however, studies dealing with potential biases of the raw diversities, including sampling efficiency, stage duration, fossil preservation or rock record bias, are scarce for the Paratethys (Kroh 2007). Studies on the quantitative composition of fossil molluscan lagerstätten have only been performed during the last few years (see references in Table 1). The present contribution is the first attempt to link this information to better understand one of the strongest diversity turnovers in the Central Paratethys, the transition from the Karpatian to the Badenian (Harzhauser et al. 2003; Harzhauser & Piller 2007).

**Geological setting**

The Paratethys was an epicontinental sea ranging from the French/Swiss border region in the west to the Transcaspian area (east of Lake Aral in
<table>
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<tr>
<th>Locality</th>
<th>Section</th>
<th>Stage</th>
<th>Stage</th>
<th>Biozone benthic foraminifers</th>
<th>Formation</th>
<th>Sequence stratigraphy (3rd order)</th>
<th>Systems tract</th>
<th>Age Geographical position</th>
<th>No. of shell beds</th>
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<td>Langhian</td>
<td>Upper Lagenida Zone</td>
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<td>TST</td>
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Table 1. Basic data of the studied assemblages
Kazakhstan) in the east. Its development started during the Late Eocene to Oligocene and was strongly linked to the alpine orogeny. It was separated from the Mediterranean by the newly formed land masses of the Alps, Dinarides, Hellenides, and the Anatolian Massif. Afterwards, it experienced a complex history of connection and disconnection with the Mediterranean Sea (Rögl 1998, 1999; Popov et al. 2004). The present study focuses on shell beds of the Vienna Basin and the North Alpine Foreland Basin; in terms of palaeogeography, they were part of the Central Paratethys, which ranged from southern Germany in the west to the Carpathian Foredeep, Ukraine in the east, and from Bulgaria in the south to Poland in the north (Fig. 1). Due to the complex geodynamic history, a regional chronostratigraphic stage system (Fig. 2) is used in the Central Paratethys. The two stages of interest here are the Karpatian and the Badenian. The Karpatian stage is characterized by a strong tectonic reorganization in the Central Paratethys area, leading to a change from west–east trending basins towards rift and intra-mountain basins (Rögl & Steininger 1983; Rögl 1998; Kováč et al. 2004b). Associated with this geodynamic impact is the abrupt, discordant progradation of upper Karpatian fossiliferous estuarine to shallow marine deposits over macrofossil-poor lower Karpatian offshore clays in the North Alpine Foreland Basin and in the Carpathian Foredeep (Adánek et al. 2003). The climate was subtropical with warm and wet summers and rather dry winters (Harzhauser et al. 2002; Kern et al. 2010). The early Middle Miocene is marked by a widespread marine transgression following a major drop in sea-level at the Burdigalian/Langhian transition (Haq et al. 1988; Hardenbol et al. 1998). The regression was intensified by regional tectonic movements, the so-called Styrian phase (Stille 1924; Rögl et al. 2006). Sediments of the Langhian transgression are commonly eroded or reduced in thickness at the basin borders, with continuous sedimentation occurring only in bathyal settings of the basin centres (Hohenegger et al. 2009). In shallow-marine environments of the Vienna Basin, erosion of up to 400 m took place between the youngest preserved Karpatian and the oldest preserved Badenian sediments (Strauss et al. 2006). Due to the tectonic reorganization, however, a broad connection opened between the Mediterranean Sea and the Paratethys during the Langhian transgression, through which free faunal exchange occurred (Rögl 1998; Studencka et al. 1998; Harzhauser et al. 2002; Harzhauser & Piller 2007). The rising

![Fig. 2. Stratigraphic details for the studied sections and standing diversity of Karpatian and Badenian gastropods compiled from regional species lists and monographs (after Harzhauser & Piller 2007). The sections belong to six formations and four 3rd order sequence stratigraphic cycles and are all, except Gainfarn 2, from early or late HSTs (cf. Table 1). EBBE = Early Badenian Build-up Event.](image-url)
sea-level and the Middle Miocene climatic optimum potentially strongly influenced marine life in the Central Paratethys (Harzhauser et al. 2003). In contrast to the Karpatian, the Badenian stage is characterized by highly fossiliferous offshore sands and pelites, and by carbonate platforms (corallineacean limestones and coral carpets). Several fossil groups increase strongly in diversity at the onset of the Badenian (Fig. 2). This event has been explicitly worked out for gastropods, with 505 taxa having their first occurrences (FOs), and for foraminifers, with FOs of 82 taxa (Harzhauser & Piller 2007). These authors dubbed this event as ‘Early Badenian Build-up Event’ (EBBE).

**Material and methods**

We studied benthic molluscs from 10 localities from the Karpatian (Upper Burdigalian) to the Badenian (Langhian and Lower Serravallian), covering all available fossil lagerstätten in the Vienna Basin and the North Alpine Foreland Basin that were amenable to bulk sampling (Fig. 3, Table 1). All samples are from siliciclastic pelitic, sandy and gravelly sediments, are characterized by aragonite and calcite preservation and were sieved through a 1 mm mesh. Detailed palaeoecological and taphonomical studies have been published on some of the sections (see references in Table 1). The shell beds of the respective localities were deposited between 16.5 and 12.7 Ma and belong to six formations, four 3rd order sequence stratigraphic cycles (Tb.2.2 to Tb.2.5 of Hardenbol et al. 1998), and are mostly part of highstand systems tracts (HST); only one section belongs to a transgressive systems tract (TST) (Strauss et al. 2006). All fossiliferous Karpatian assemblages belong to a single regional benthic foraminifera biozone, and the studied Badenian assemblages to three such biozones (Table 1) (Uvigerina graciliformis zone, Lower and Upper Lagenidae zones and Bolivina/ Bulimina zone; Grill 1943; Steininger et al. 1978). The faunal transition from the Karpatian to the Badenian is studied at the level of stages and biozones. For the purpose of this study, samples are environmentally assigned to the intertidal to very shallow sublittoral (<1 m water depth), termed as nearshore for the rest of the paper, and to the deeper sublittoral (few metres to several tens of metres of water depth). Palaeoenvironmental designations of samples were based on palaeogeographical positions of localities and actualistic environmental requirements of dominant molluscan taxa. Independent data from foraminifera confirm our assignments and suggest a total range of depositional water depths from intertidal to several tens of metres (pers. comm. Holger Gebhart, Patrick Grunert, Johann Hohenegger & Fred Rögl, 2009). Logarithmic scale rank abundance plots of family level data were used to compare community organization between stages and the data were fit to geometric series, log-series, broken stick and log-normal abundance models using the program PAST (Hammer et al. 2001). Species accumulation curves were computed to compare species richness between stages, biozones and environments using the program Estimates with 50 sample order
randomizations without replacement. (Colwell 2009). Diversity was measured as species richness and as evenness, which is based on the proportional abundance of species (for a review see Magurran 2004). To compensate for sampling effects in species richness we used Margalef’s diversity index. The Simpson index, which is affected by the 2–3 most abundant species, and the Shannon index, which is more strongly affected by species in the middle of the rank sequence of species, were used as measures of evenness (see Gray 2000 for discussion). All indices were calculated using the program PAST (Hammer et al. 2001). The Margalef index was calculated with the equation

$$D_{Mg} = (S - 1)/\ln N$$

where $S = \text{the total number of species}$ and $N = \text{the total number of individuals}$. The Simpson index is expressed as $1 - D$ and was calculated with the equation

$$D = \sum_{i=1}^{S} \frac{n_i(n_i - 1)}{N(N - 1)}$$

where $S = \text{the total number of species}$, $n_i = \text{the number of individuals in the } i^{th} \text{ species}$ and $N = \text{the total number of individuals}$. The Shannon index was calculated with the equation

$$H = -\sum_{i=1}^{S} p_i \ln p_i$$

where $S = \text{the total number of species}$, and $p_i = \text{the proportion of individuals found in the } i^{th} \text{ species}$. Species richness, the Simpson index and the Shannon index were chosen because they are the most commonly employed measures of diversity (Lande 1996). It should be mentioned, however, that the underlying statistical distribution of a sample will generally influence the constancy of evenness measures and that the Shannon index is particularly sensitive to sample size (Lande 1996; Magurran 2004; Buzas & Hayek 2005). Non-metric multidimensional scaling (NMDS, Kruskal 1964) was used as an ordination method to evaluate the presence of environmental gradients in the dataset and was performed using the software package PRIMER (Clarke & Warwick 1994). Surface outcrop areas and their environmental affiliation of the Karpatian and Badenian in Austria are adapted from Kroh (2007) and were calculated from digital 1:200 000 scale map series of the Geological Survey of Austria for the Burgenland (Pascher et al. 2000) and Lower Austria and Vienna (Schnabel 2002).

**Results**

Sampling intensity was very high (213 samples, yielding 494 species from >49 000 shells), but the species accumulation curve for the total assemblage does not level off (Fig. 4). The number of families, genera and species, however, is significantly higher for Badenian than for the Karpatian assemblages (Fig. 5a). While in the Karpatian sampling intensity was sufficient to cover diversity at all hierarchical levels, for the Badenian the diversity of species and genera do not show a tendency to level off (Fig. 5b).

Strong differences in the abundances of dominant families and in the shape of the rank abundance plot of family level data indicate environmental

![Fig. 4. Species accumulation curve of the total assemblage with 95% confidence intervals. Inset: number of samples per environment and stage. Sampling intensity was very high but the species accumulation curve does not level off.](image-url)
differences between shelly assemblages of the two stages (Fig. 6). Karpatian molluscan assemblages are dominated by neritid and potamid–batillariid gastropods, which indicate the prevalence of tidal flat deposits, whereas the Badenian molluscan assemblages are dominated by corbulid and venerid bivalves and rissoid gastropods, which all indicate the preponderance of sublittoral conditions (Fig. 6a). In accordance rank abundance plots suggest higher evenness for the total Badenian assemblage (Fig. 6b) and diversity indices are significantly higher for sublittoral than for nearshore samples in our dataset (Fig. 7). An environmental bias may therefore explain the apparent faunal turnover. In fact, in the Karpatian more samples derive from nearshore environments, whereas the Badenian is strongly dominated by sublittoral samples. This difference is even more pronounced when considering biozones. In the Lower Lagenidae zone, samples are exclusively from the sublittoral; nearshore samples of the Badenian only occur in the Upper Lagenidae zone and in the Bolivina/Bulimina zone (Fig. 8).

At the level of stages and biozones the environmental affiliations of samples correlate with diversities, which are high wherever assemblages are dominated by samples from the sublittoral (Fig. 9). An exception is the Bolivina/Bulimina zone, but there the sampling intensity was by far the lowest (Table 1). Species accumulation curves of environments within stages and biozones are always steeper for sublittoral than for nearshore assemblages. Differences between environments within time slices are significant except for the Karpatian (i.e. the Uvigerina graciliformis zone) as indicated by overlapping confidence intervals (Fig. 10). Strong
diversity differences between sublittoral assemblages at the level of stages and biozones indicate habitat differences, most notably between the well-sampled *Uvigerina graciliformis* zone of the Karpatian and the Lower and Upper Lagenidae zones of the Badenian (Fig. 10b). In fact, an ordination of family-level data suggests the presence of a distinct water depth gradient (Fig. 11). Sublittoral
samples from the *Uvigerina graciliformis* zone of the Karpatian represent shallower environments than those from the Lower and Upper Lagenidae zones. Differences between the latter can be explained by substrate differences. Assemblages from the Lower Lagenidae zone tend to be from sandy environments and are therefore more diverse than those from the Upper Lagenidae zone, which are rather from pelitic environments. Environmental affiliation of Karpatian and Badenian outcrops in eastern Austria support this finding. In the Karpatian the importance of terrestrial, fluvial, fluvio-marine and limnic environments suggests that most fossiliferous marine outcrops are from nearshore environments. In the Badenian, in contrast, most outcrops preserve fully marine environments (Fig. 12) (compare also Kroh 2007).

**Discussion**

**The importance of local and regional studies**

The present study demonstrates that the quantitative evaluation of bulk samples significantly improves the understanding of regional diversity changes at temporal scales ranging from tens of thousands to a few million years and thereby confirms
previous authors who emphasized the importance of rigorous, extensive sampling combined within a highly resolved stratigraphic and palaeoenvironmental framework for deciphering palaeodiversity patterns (e.g. Koch 1978; Jackson et al. 1999; Kosnik 2005). Several lines of evidence suggest great importance of regional and local studies for the understanding of global diversity patterns. Biodiversity can be studied at a series of hierarchical scales which all contribute to an understanding of its distribution in time and space (Willis & Whittaker 2002). Diversity is, however, biologically meaningful at local scales, where ecological processes operate and at regional scales because local communities receive species from a biogeographically delimited metacommunity (Hubbell 2001). Long-term diversity trends actually differ significantly among major regions of the world (e.g. Miller 1997; Jablonski 1998). With respect to the rock record there is a global diversity signature that relates to supercontinent cycles, but on shorter time-scales regional processes are more important and, due to heavy sampling bias, the European and North American data sets drive these patterns (McGowan & Smith 2008). Correspondingly, fossil first and last occurrences are dominated by records from these two continents (Kidwell & Holland 2002) and the Cenozoic tropics are undersampled because Europe and North America had largely moved out of the tropics by Cenozoic time (Jackson & Johnson 2001). McGowan & Smith (2008) therefore suggest focusing on the construction of regional data sets within tectonically and sedimentologically meaningful frameworks. Such regional diversity studies can typically be performed at low taxonomic

Fig. 10. Species accumulation curves with 95% confidence intervals of environments in stages (a) and biozones (b). Sublittoral environments are always more diverse than nearshore environments but for the Karpatian (i.e. the Uvigerina graciliformis zone) the differences are not significant as indicated by overlapping confidence intervals. Strong diversity differences between sublittoral assemblages at the level of stages and biozones are evident, most notably between the well-sampled Uvigerina graciliformis zone of the Karpatian and the Lower and Upper Lagenidae zones of the Badenian and point to habitat differences of the respective assemblages. K ns = Karpatian nearshore; B ns = Badenian nearshore; K sl = Karpatian sublittoral; B sl = Badenian sublittoral; LLZ ns = Lower Lagenidae zone nearshore; LLZ sl = Lower Lagenidae zone sublittoral; ULZ ns = Upper Lagenidae zone nearshore; ULZ sl = Upper Lagenidae zone sublittoral; BBZ ns = Bolivina/Bulimina zone nearshore; BBZ sl = Bolivina/Bulimina zone sublittoral; UgZ ns = Uvigerina graciliformis zone nearshore; UgZ sl = Uvigerina graciliformis zone sublittoral.

Fig. 11. Non-metric multidimensional scaling (nMDS) of family level data of the studied assemblages suggests the presence of a distinct water depth gradient along axis 1. Samples from nearshore environments of all biozones cluster at the left. Sublittoral samples from the Uvigerina graciliformis zone of the Karpatian represent shallower environments than those from the Lower and Upper Lagenidae zones. Differences between the latter are tentatively explained by substrate differences (samples from the Lower Lagenidae zone tend to be from sandy environments, samples Upper Lagenidae zone are rather from pelitic environments). LLZ = Lower Lagenidae zone; ULZ = Upper Lagenidae zone; BBZ = Bolivina/Bulimina zone; UgZ = Uvigerina graciliformis zone. Numbers 1–8 in the plot refer to some outliers. 1–4 are characterized by high abundances of otherwise rare taxa. In 5–7 the number of specimens is relatively low, taxonomic composition heterogeneous and environmental affiliation therefore not straightforward. 8 is a sample with very high number of shells, which are strongly dominated by one taxon.
levels with highly resolved stratigraphic control (e.g. Johnson & Curry 2001; Hendy et al. 2009). Knowledge of local abundances of organisms enables determination of sampling completeness (Koch 1987) and to recognize ecological reorganization of regional biota, which can be independent from standing diversity (Jackson et al. 1999; Todd et al. 2002). In line with these evidences, this paper highlights the sheer sampling effort that is required to reach the asymptote of the collector’s curve (Figs 4, 5, 9 & 10), a feature that is well known from modern and fossil molluscan assemblages (e.g. Jackson et al. 1999; Bouchet et al. 2002; Zuschin & Oliver 2005) and which suggests that most fossiliferous marine outcrops in this stage are from nearshore environments.

Environmental bias in stages and biozones

This study demonstrates strong differences in quantitative molluscan composition between two succeeding stages (Fig. 6), but it also underlines a predominance of nearshore and shallow sublittoral habitats in the studied Karpatian versus a predominance of somewhat deeper environments in the studied Badenian outcrops. Since shelf environments have a higher diversity than the physically stressed nearshore environments, the diversity increase from the Karpatian to the Badenian in our dataset can be largely related to an environmental shift. When considering biozones, this environmental shift is especially pronounced at the 3rd order sequence boundary between the Karpatian Uvigerina graciliformis and the Badenian Lower Lagenidae zones. This pattern amplifies the impression of a diversity increase due to the Langhian transgression from a literal reading of the fossil record (Fig. 8). Following Jablonski (1980), it is therefore important to sample a single habitat or across a suite of habitats when evaluating diversity changes through time.

Although our data are from a relatively small subset of the Central Paratethys, they are considered as representative because a study on echinoderms from the whole Central Paratethys also showed that comparable habitats of the Karpatian and Badenian stages had very similar faunas and diversities (Kroh 2007). This author specifically stressed that the non-presence of Karpatian shallow-water carbonates in the rock record explains much of the lower echinoderm diversity compared to the Badenian. Our study adds a new aspect in demonstrating that also among siliciclastic sediments a facies shift from nearshore and shallow sublittoral habitats in the Karpatian to somewhat deeper environments in the Badenian is responsible for diversity differences.

Palaeogeography and palaeoclimatic

It may be possible that for palaeogeographical reasons the non-preserved deeper shelf assemblages of the Karpatian were less diverse than their preserved Badenian counterparts. During the Karpatian a marine connection of the Central Paratethys existed only with the Mediterranean Basin, via the Slovenian ‘Trans-Tethyan Trench corridor’ (Bistrusic & Jenko 1985). In the Badenian, open connections with the Eastern Paratethys may also have existed, although the timing of the connections is highly controversial (Rögl 1998; Studencka et al. 1998; Steininger & Wessely 2000; Popov et al. 2004). In both time slices, however, the Mediterranean Basin was at least temporarily connected to the Indo-Pacific, enabling water circulation between both oceans, although faunas differed considerably (Harzhauser et al. 2007). A palaeogeographical scenario for the observed diversity differences is therefore rather speculative and not supported by hard data. From a palaeoclimatological perspective the differences between the time slices are rather small. This is because the Karpatian and Lower to Middle Badenian were characterized by subtropical temperatures of the Middle Miocene climate optimum (Bohme 2003; Latal et al. 2006; Bruch et al. 2007; Kern et al. 2010), which enabled the presence of thermophilic molluscs at

Fig. 12. Area and environments of Karpatian and Badenian outcrops in Eastern Austria (modified after Kroh 2007). Badenian outcrops mostly preserve fully marine environments. Karpatian terrestrial, fluvial, fluvo-marine and limnic environments are very prominent, suggesting that most fossiliferous marine outcrops in this stage are from nearshore environments.
that time in the Paratethyan Basins (Harzhauser et al. 2003). In fact, nearshore assemblages, which are available from both time slices, do not support the scenario of higher Badenian diversities (Fig. 10a).

The sequence stratigraphic framework

In our study on 3rd order cycles from the Central Paratethys, most outcrops are from highstand systems tracts (Fig. 2, Table 1). These are internally characterized by relatively gradual biofacies replacements with major faunal turnovers occurring at sequence boundaries (Zuschin et al. 2007), a pattern that corresponds to sequence stratigraphic expectations (e.g. Brett 1995, 1998; Holland 2000). The dominance of HSTs corresponds well to the fact that the thickest parts of the sedimentary record were built at times of progradation and that the transgressive phases are only represented by thin levels (e.g. Jablonski 1980; Fürsich et al. 1991; Clifton 2006).

Among the studied sequences, however, diversities clearly depend on facies (Figs 9 & 10), which differ in a systematic way due to a biased sedimentary record. Karpatian shell beds are mostly preserved from nearshore and shallow sublittoral environments, which discordantly overlay macrofossil-poor Karpatian offshore clays, whereas from the Badenian mostly somewhat deeper shelf assemblages are recorded. This is most evident in the Lower Lagenidae zone, which completely lacks nearshore assemblages (Figs 8, 10 & 11).

But also later in the Badenian, nearshore assemblages are strikingly underrepresented when compared to the Karpatian (Fig. 8). Sequence stratigraphic models predict that nearshore sediments of the HST will be eroded during subsequent 3rd order sea-level drops. This would explain the paucity of nearshore sediments in the three Badenian 3rd order cycles. This interpretation is supported by 3-D seismic reflection data, which reveal significant drops of relative sea-level (90–120 m) between the cycles (Strauss et al. 2006). The dominance of such environments and corresponding lack of somewhat deeper water shelf assemblages in the Karpatian is counterintuitive, however, and is probably related to the strong tectonic reorganization of the Central Paratethys at the Karpatian/Badenian boundary (Adánek et al. 2003). One explanation for the scarcceness of shelf environments is the uplift of the North Alpine Foreland Basin and the subsequent retreat of the sea. Deeper marine environments became established only in the Carpathian Foredeep (Rögl 1998). In contrast, the new tectonic regime initiated rapid subsidence in small satellite basins of the Vienna Basin, where such littoral deposits escaped erosion (Wessely 1998; Kern et al. 2010).

Tectonics therefore affected sequence architecture in this particular setting by controlling subsidence and sedimentary input, highlighting the problem that sequence stratigraphic models were conceived for passive margin and only poorly predict sediment accumulation in tectonically active settings.

Comparison with other studies

Many studies have treated the distribution and preservation of shell beds in relation to flooding surfaces and sequence boundaries (e.g. Kidwell 1988, 1989, 1991; Banarjee & Kidwell 1991; Abbott & Carter 1997; Kondo et al. 1998; Fürsich & Pandey 2003). A series of others have examined palaeocommunity dynamics at local to regional scales in relation to the rock record (e.g. Patzkowsky & Holland 1999; Goldman et al. 1999; Olszewski & Patzkowsky 2003; Olszewski & Erwin 2004; Scarponi & Kowalewski 2004; Hendy & Kamp 2004; Dominici & Kowalke 2007; Zuschin et al. 2007; Tomasových & Siblík 2007). Only few studies, however, have dealt with diversity changes as related to depositional sequences. The results depend on scale, tectonic setting and environments preserved (or available to sample). Diversity seems largely to be decoupled from 1st order cycles because stage-level post-Palaeozoic marine standing diversity of western Europe increases although marine sediment outcrop area decreases (Smith 2001; see also Smith & McGowan 2007). A strong relation, however, has been proposed for 2nd order sequence stratigraphic cycles (Smith 2001). Two case studies suggest highest diversity or sampling probability at midcycle position at the top of transgressive systems tract intervals (Smith et al. 2001; Crampton et al. 2006), but the causes seem to differ somewhat between tectonic settings (see discussion in Crampton et al. 2006). At the active margin of New Zealand, for example, the best preservation of molluscan faunas is at mid-cycle position at the top of transgressive systems tracts, and poorest preservation towards the end of highstand systems tracts. This is related to continuous subsidence and creation of accommodation space (Crampton et al. 2006). At the passive margin of western Europe, due to minimum accommodation space, shallow-water deposition is displaced onto the cratonic interiors, where erosive loss during subsequent lowstands is most pervasive (Smith et al. 2001). In both areas, however, long-term diversity trends are related to distinct facies biases. In the Cenomanian/Turonian of western Europe a distinct diversity decrease can be related to an increase of offshore at the expense of onshore sedimentary facies in the course of platform drowning due to sea-level rise (Smith et al. 2001). In the Neogene of New Zealand an apparent decline in species
diversity reflects erosion of shallow-water deposits and a relative increase of bathyal at the cost of shelf facies (Crampton et al. 2003). The importance of environments covered within systems tracts is finally also stressed in a study on late Quaternary 4th order sequences deposited on the Po Plain (Italy). There, transgressive systems tract samples displayed the highest, and the highstand systems tract samples the lowest diversity. At the same time, turnover across sequences is negligible and major diversity shifts across systems tracts are mostly driven by Waltherian-type environmental shifts (Scarponi & Kowalewski 2007).

Conclusions

The diversity increase between two regional stages of the Central Paratethys is largely due to an environmental shift, which is related to selective preservation and erosion of environments due to tectonics and sea-level drops. Although most samples analysed in this study stem from highstand systems tracts, diversity differences between stages and biozones are significant. Pure standing diversity estimates will reveal biogeographical relations and might capture faunal migrations aside from reflecting palaeoecological and palaeoclimatic benchmarks. They will not, however, reliably mirror biodiversity. This study therefore strongly supports the importance of environmental bias when considering faunal changes though time and suggests that in second and higher order sequences the facies covered within systems tracts will drive diversity patterns. The importance of rigorous, extensive sampling within a highly resolved stratigraphic and palaeoenvironmental framework for deciphering palaeodiversity patterns at regional scales is emphasized. The sheer sampling effort that is required to reach the asymptote of the collector’s curve is highlighted and it is strongly recommended to use abundance data, which enable the recognition of ecological changes in regional biota.

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