

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

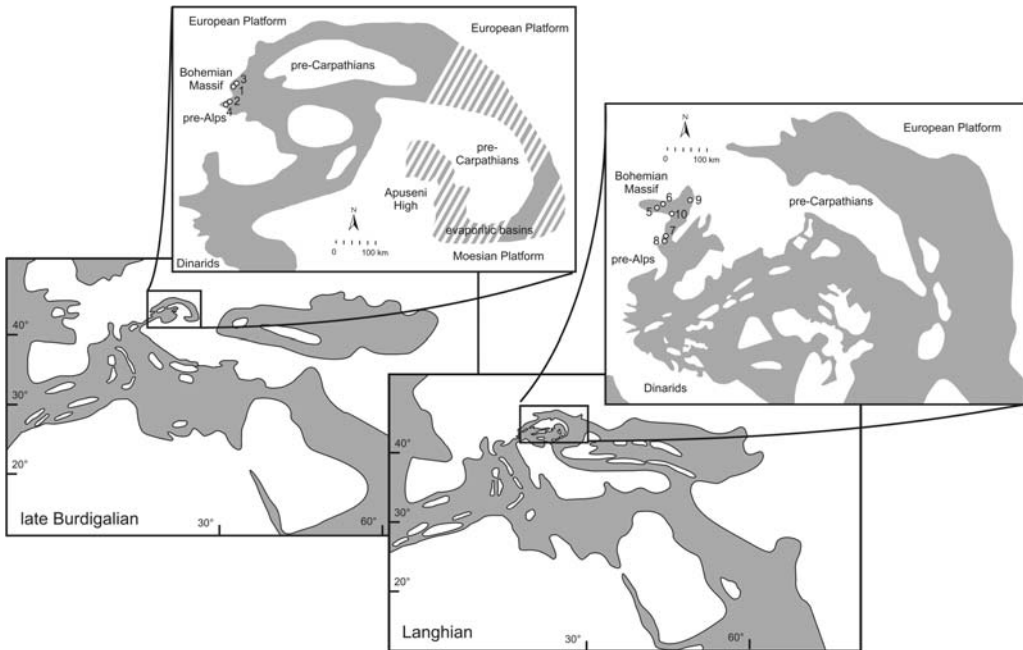


Fig. 1. Karpatian and Badenian palaeogeography of the Central Paratethys (modified after Rögl (1998) and Kováč *et al.* (2004a, 2007)) with approximate positions of studied localities. Karpatian (i.e. Upper Burdigalian) localities include: 1 = Laa a.d. Thaya; 2 = Kleinebersdorf; 3 = Neudorf bei Staatz; 4 = Korneuburg SPK. Badenian (i.e. Langhian and Lower Serravalian) localities include: 5 = Grund; 6 = Immendorf; 7 = Gainfarn; 8 = St. Veit; 9 = Borský Mikuláš, 10 = Niederleis.

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 (Prévost 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 1. Basic data of the studied assemblages

Locality	Section	Stage international	Stage regional	Biozone benthic foraminifers	Formation	Sequence stratigraphy (3rd order)	Systems tract	Age	Geographical position		No. of shell beds	No. of samples	References
									Latitude	Longitude			
Laa a.d. Thaya	Wienerberger AG	Burdigalian	Karpatian	Uvigerina graciliformis	Novy Prerov Fm	Tb.2.2	Late HST	16.5	48°43'07"	16°24'57"	1	4	Unpublished data
Kleinebersdorf	Kleinebersdorf Sandpit Lehner	Burdigalian	Karpatian	Uvigerina graciliformis	Korneuburg Fm	Tb.2.2	Late HST	16.5	48°29'37"	16°23'44"	1	3	Zuschin <i>et al.</i> 2004a
	Kleinebersdorf Sandpit Wohlmuth	Burdigalian	Karpatian	Uvigerina graciliformis	Korneuburg Fm	Tb.2.2	Late HST	16.5	48°29'42"	16°23'48"	1	3	Zuschin <i>et al.</i> 2004a
Korneuburg	Korneuburg SPK	Burdigalian	Karpatian	Uvigerina graciliformis	Korneuburg Fm	Tb.2.2	Late HST	16.5	48°21'28"	16°23'14"	96	110	Unpublished data
Neudorf bei Staatz		Burdigalian	Karpatian	Uvigerina graciliformis	Novy Prerov Fm	Tb.2.2	Late HST	16.5	48°43'07"	16°30'14"	1	6	Unpublished data
Grund		Langhian	Badenian	Lower Lagenidae Zone	Grund Fm	Tb.2.3	Early HST	15	48°38'18"	16°03'48"	5	5	Zuschin <i>et al.</i> 2004b, 2005
Immendorf		Langhian	Badenian	Lower Lagenidae Zone	Grund Fm	Tb.2.3	Early HST	15	48°39'00"	16°07'49"	5	25	Zuschin <i>et al.</i> 2006
Niederleis	Niederleis Buschberg	Langhian	Badenian	Lower Lagenidae Zone	Lanzhot Fm	Tb.2.3	Early HST	15	48°33'48"	16°24'17"	4	4	Mandic <i>et al.</i> 2002
	Niederleis Bahnhof	Langhian	Badenian	Lower Lagenidae Zone	Lanzhot Fm	Tb.2.3	Early HST	15	48°32'25"	16°24'39"	5	5	Mandic <i>et al.</i> 2002
St. Veit a.d. Triesting		Langhian	Badenian	Upper Lagenidae Zone	Lanzhot Fm	Tb.2.3	Late HST	14.5	47°55'55"	16°08'53"	9	9	Unpublished data
Gainfarn	Gainfarn 1	Langhian	Badenian	Upper Lagenidae Zone	Lanzhot Fm	Tb.2.3	Late HST	14.5	47°56'45"	16°10'59"	7	8	Zuschin <i>et al.</i> 2007
	Gainfarn 2	Langhian	Badenian	Upper Lagenidae Zone	Jakubov Fm	Tb.2.4	TST	14	47°56'40"	16°10'57"	14	14	Zuschin <i>et al.</i> 2007
Borsky Mikulas		Serravallian	Badenian	Bolivina/Bulimina Zone	Studienka Fm	Tb.2.5	Early HST	13	48°36'20"	17°11'57"	3	17	Švagróvský 1981; Unpublished data

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; Kovác *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 (Adámek *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

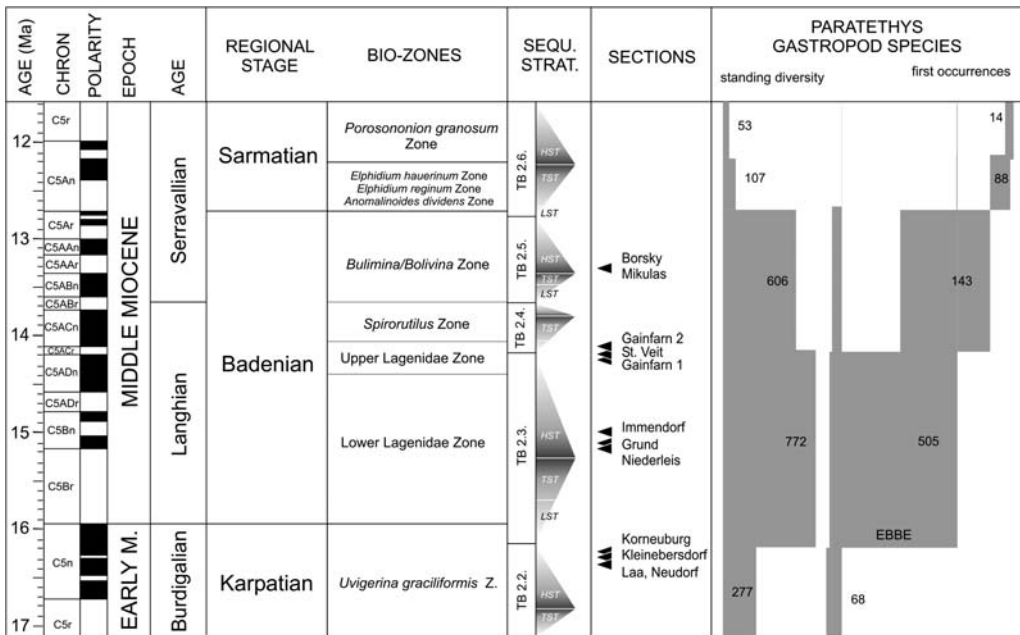


Fig. 2. Stratigraphic details for the studied sections and standing diversity of Karpatian and Badenian gastropods compiled from regional species lists and monographs (after Harzhauser & Piller 2007). The sections belong to six formations and four 3rd order sequence stratigraphic cycles and are all, except Gainfarn 2, from early or late HSTs (cf. Table 1). EBBE = Early Badenian Build-up Event.

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 (coralline 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 Serravalian), 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



Fig. 3. Map of sample localities in Austria and Slovakia. Karpatian (i.e. Upper Burdigalian) localities include: 1 = Laa a.d. Thaya; 2 = Kleinebersdorf; 3 = Neudorf bei Staatz; 4 = Korneuburg SPK. Badenian (i.e. Langhian and Lower Serravalian) localities include: 5 = Grund; 6 = Immendorf; 7 = Gainfarn; 8 = St. Veit; 9 = Borský Mikuláš, 10 = Niederleis (modified after Sawyer & Zuschin 2011).

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

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

where S = the total number of species, n_i = the number of individuals in the i th species and N = 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 = the total number of species, and p_i = the proportion of individuals found in the i th 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

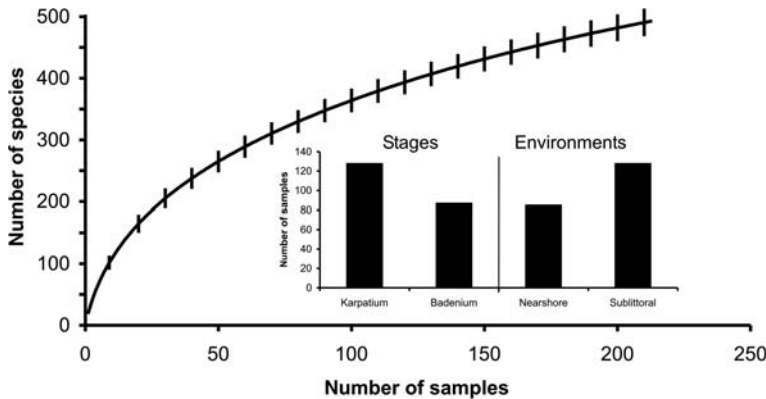


Fig. 4. Species accumulation curve of the total assemblage with 95% confidence intervals. Inset: number of samples per environment and stage. Sampling intensity was very high but the species accumulation curve does not level off.

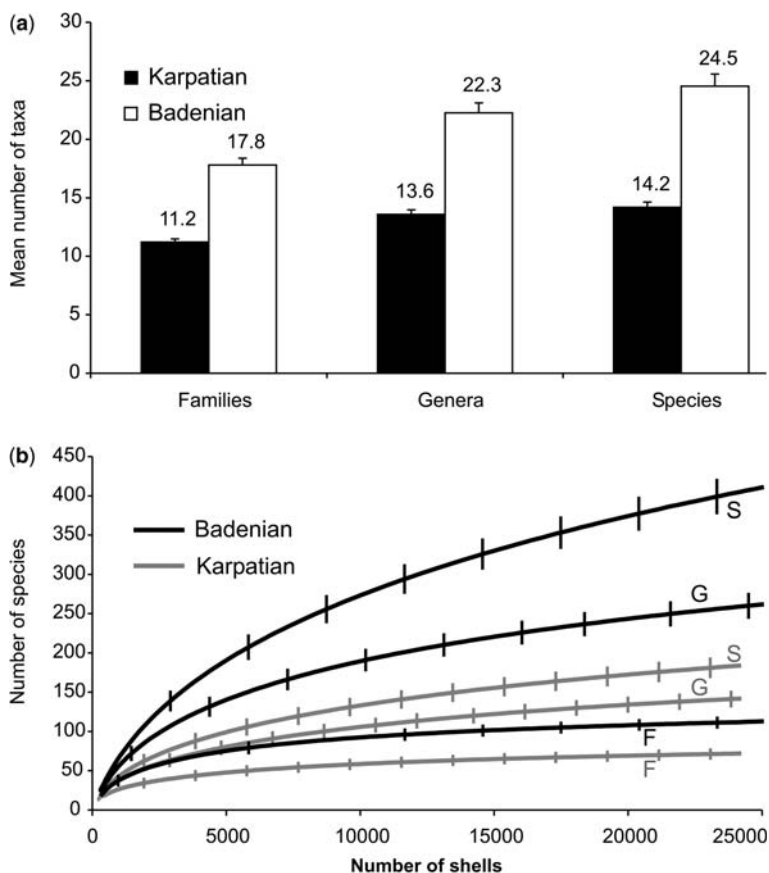


Fig. 5. Diversities in stages. (a) Average number of families, genera and species in samples with 95% confidence intervals. (b) Taxa accumulation curves for families, genera and species of the total assemblages with 95% confidence intervals. At all three taxonomic levels diversities differ significantly between the Karpatian and Badenian. For the Badenian the species- and genus accumulation curves do not show a tendency to level off, although sampling intensity was very high. F = families; G = genera; S = species.

differences between shelly assemblages of the two stages (Fig. 6). Karpatian molluscan assemblages are dominated by neritid and potamidid–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 *Bolimina/Bolimina* 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 *Bolimina/Bolimina* 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

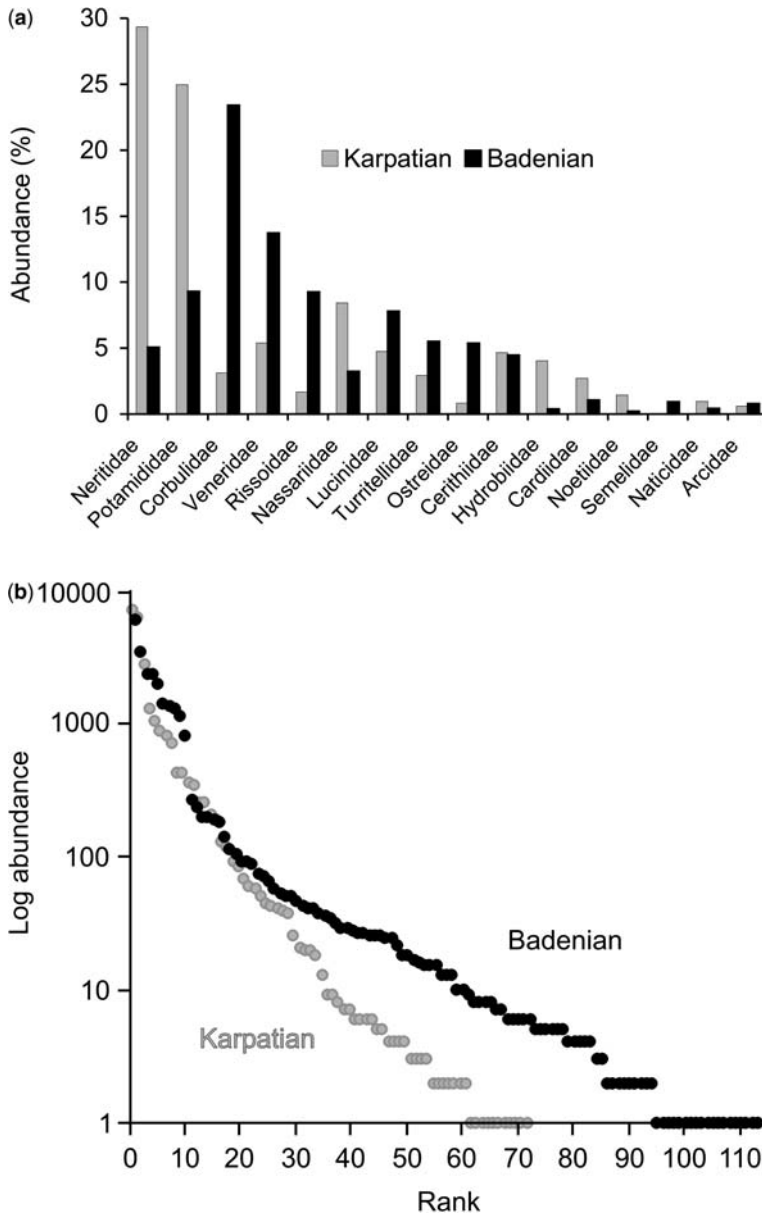


Fig. 6. Abundances of family level data for stages. (a) Percentage abundance of most important families. Karpatian assemblages are dominated by families indicative of tidal flat deposits and Badenian assemblage are dominated by families indicative of sublittoral conditions. (b) Rank abundances of families suggest higher evenness in Badenian assemblages. The log normal abundance model best describes the data in both stages (Karpatian: Chi-square = 5.265, $p = 0.7289$, Badenian: Chi-square = 11.73, $p = 0.2287$); the other three tested models have very low p -values, which implies bad fits.

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

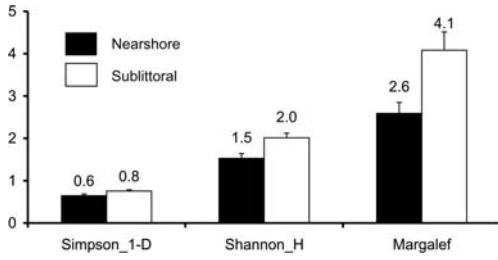


Fig. 7. Diversity indices of samples tallied based on environments. Diversity indices are significantly higher for sublittoral than for nearshore samples in our dataset and an environmental bias may therefore explain the apparent faunal turnover from the Karpatian to the Badenian.

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

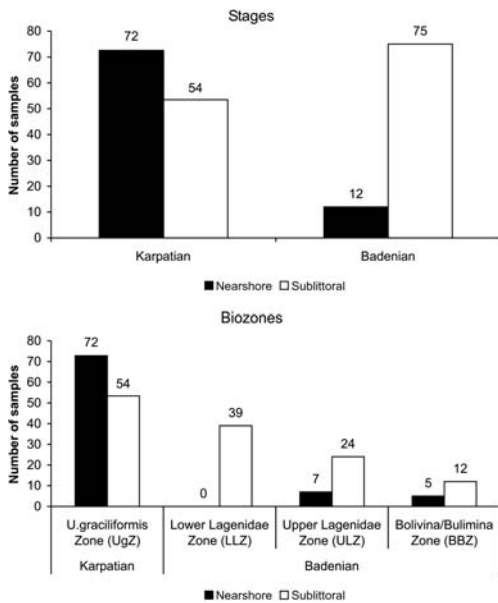


Fig. 8. Number of nearshore and sublittoral samples in stages and biozones. More Karpatian samples derive from nearshore environments, but the Badenian is strongly dominated by sublittoral samples. This environmental shift is especially pronounced at the 3rd order sequence boundary between the Karpatian *Uvigerina graciliformis* and the Badenian Lower Lagenidae zones and amplifies the impression of a diversity increase due to the Langhian transgression from a literal reading of the fossil record.

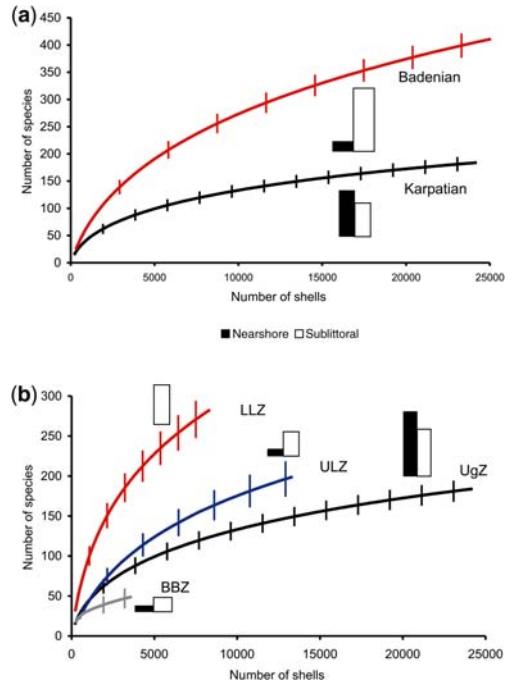


Fig. 9. Species accumulation curves with 95% confidence intervals in relation to sampled environments for stages (a) and biozones (b). Diversities are high wherever assemblages are dominated by samples from the sublittoral. An exception is BBZ, where sampling intensity was by far the lowest. LLZ = Lower Lagenidae zone; ULZ = Upper Lagenidae zone; BBZ = *Bolivina/Bulimina* zone; UgZ = *Uvigerina graciliformis* zone.

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

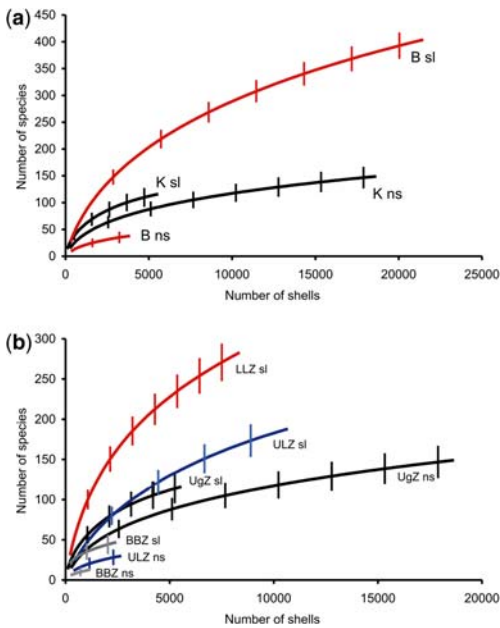


Fig. 10. Species accumulation curves with 95% confidence intervals of environments in stages (a) and biozones (b). Sublittoral environments are always more diverse than nearshore environments but for the Karpatian (i.e. the *Uvigerina graciliformis* zone) the differences are not significant as indicated 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 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.

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

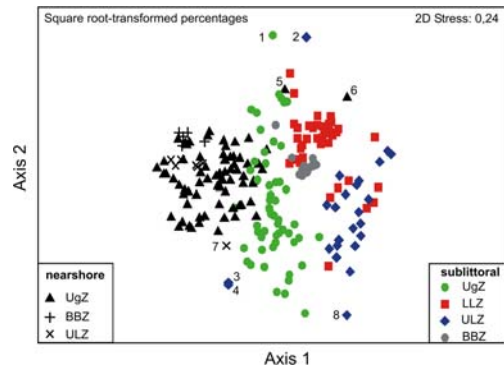


Fig. 11. Non-metric multidimensional scaling (nMDS) of family level data of the studied assemblages suggests the presence of a distinct water depth gradient along axis 1. Samples from nearshore environments of all biozones cluster at the left. Sublittoral samples from the *Uvigerina graciliformis* zone 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 straight forward. 8 is a sample with very high number of shells, which are strongly dominated by one taxon.

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

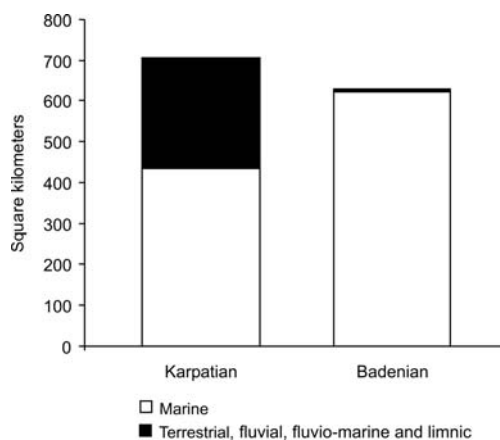


Fig. 12. Area and environments of Karpatian and Badenian outcrops in Eastern Austria (modified after Kroh 2007). Badenian outcrops mostly preserve fully marine environments. Karpatian terrestrial, fluvial, fluvio-marine and limnic environments are very prominent, suggesting that most fossiliferous marine outcrops in this stage are from nearshore environments.

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 species are rare (Gaston 1994; Harnik 2009). The use of abundance data allowed the recognition of ecological changes across a stage boundary, which drive the observed diversity increase and which can be explained by a strong environmental shift.

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 palaeoclimate

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' (Bis-tricic & 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 (Böhme 2003; Latal *et al.* 2006; Bruch *et al.* 2007; Kern *et al.* 2010), which enabled the presence of thermophilic molluscs at

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 well 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 (Adámek *et al.* 2003). One explanation for the scarceness 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; Tomašových & 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 mid-cycle 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 through 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.

We thank S. Ćorić, P. Pervesler, R. Roetzel and numerous students for help with sampling; S. Dominici, J. Hohenegger, A. Kroh, F. Rögl, J. Sawyer and A. J. Tomašových for discussions; A. Kroh and J. Reischer for providing the data for Figure 12; A. Smith and A. J. McGowan for letting us present this work at the Lyell symposium 2010; A. J. McGowan and J. Nebelsick for a stimulating review of the manuscript. This study was supported by project P19013-B17 of the Austrian Science Fund (FWF).

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