

Spatial variability within a single parautochthonous Paratethyan tidal flat deposit (Karpatian, Lower Miocene – Kleinebersdorf, Lower Austria)

With 11 figs, 1 tab.

Martin ZUSCHIN, Mathias HARZHAUSER & Oleg MANDIC

Abstract

Six samples from a single shell bed in two adjacent outcrops were studied at Kleinebersdorf (Lower Austria) to identify outcrop-scale variability in faunal composition, the nature of shell bed formation and the original environment of the molluscan fauna. Thirty-five taxa (32 species) were identified from 1581 individuals. A diversity analysis shows that the full range of species in the shell bed was not covered, but higher sampling intensity would only add more rare species without changing the rank order of the most abundant and middle ranked taxa. Diversity, estimated from the steepness of the species-individual curves and measured as heterogeneity diversity, differed consistently between the two outcrops. Patchiness in quantitative molluscan composition was best indicated by differences in the rank order of the most abundant species, but differences between outcrops were not statistically significant. The concentration process most likely responsible for the shell bed formation is gentle winnowing by currents, which were not strong enough to significantly transport or orient the shells. The rather low total diversity of this parautochthonous to slightly transported molluscan assemblage points to a physically controlled original environment. The cooccurrence of the most abundant bivalve species *Loripes dentatus*, *Dosinia lupinus* and *Diplodonta rotundata* points to a low-energy coastal setting with at least partly nutrient-rich sediment within the lower intertidal and/or upper subtidal, for example a sheltered embayment or semi-enclosed lagoon. The most abundant gastropod species, the batillariid *Granulolabium plicatum*, supports the interpretation of a parautochthonous to slightly transported tidal flat deposit.

Key words: tidal flat, diversity analysis, patchiness, Paratethys, Karpatian, molluscs

Zusammenfassung

In zwei benachbarten Aufschlüssen bei Kleinebersdorf (Niederösterreich) kann eine Molluskenschillage des Karpatium (Untermiozän) verfolgt werden. Innerhalb dieser Lage wurden 6 Proben genommen; diese enthielten insgesamt 1581 Individuen, die 35 Taxa (32 Arten) zugeordnet werden konnten. Untersucht wurden Unterschiede in der Molluskenzusammensetzung zwischen den beiden Aufschlüssen, die Genese des Molluskenschilles und das ursprüngliche Environment der Molluskenfauna. Die Diversitätsanalyse zeigt, dass das gesamte Artenspektrum durch die Proben nicht erfasst werden konnte. Eine höhere Beprobungsdichte würde jedoch lediglich einen Zuwachs innerhalb der Gruppe der selteneren Arten bewirken, während die Rangfolge der häufigsten Taxa unbeeinflusst bliebe. Diversität, ersichtlich vom Anstieg der Arten-Individuen Kurve und gemessen als Heterogenitätsdiversität ist deutlich unterschiedlich zwischen den 2 Aufschlüssen. Die Unterschiede in der quantitativen Molluskenzusammensetzung zwischen den beiden Aufschlüssen, welche am besten an der Rangordnung der quantitativ wichtigsten Arten zu erkennen sind, sind statistisch nicht signifikant. Die Schalenakkumulation entstand durch passive Anreicherung der Biogene infolge des Abtransportes des feineren Sedimentanteils durch schwache Strömungen. Das gemeinsame Vorkommen der häufigsten Bivalvenarten *Loripes dentatus*, *Dosinia lupinus* und *Diplodonta rotundata* zeigt ein eher niedrigerenergetisches Küstenenvironment mit stellenweise nährstoffreichem Sediment im niedrigen Intertidal oder höheren Subtidal einer geschützten Bucht oder teilweise abgeschnürten Lagune an. Der häufigste Gastropode *Granulolabium plicatum* deutet auf litorale Bedingungen eines Watts hin. Die hier herrschenden, restriktiven Umweltfaktoren erklären auch die relativ geringe Diversität der parautochthonen bis geringfügig transportierten Molluskenvergesellschaftung.

Schlüsselworte: Watt, Diversität, Paratethys, Patchiness, Karpatium, Mollusken

Introduction

Only few studies have dealt with spatial heterogeneity in fossil assemblages or modern death assemblages (e.g., CUMMINS et al. 1986, MILLER 1988, 1992, CoBABE & ALLMON 1994, BENNINGTON 2003) and apparently only one fossil study has examined outcrop-scale variability in faunal composition along individual bedding planes (MILLER 1997). The present contribution is part of a larger project that deals with Miocene molluscan associations in Austria and adjacent countries. This project investigated several localities, whose molluscan associations mainly occur in shell beds (e.g., HARZHAUSER and KOWALKE 2002, MANDIC et al. 2002, ZUSCHIN et al. submitted a, b). In most localities, however, the shell beds could not be traced laterally and therefore the spatial variability in their faunal composition remains unknown. In contrast, at the Karpatian locality Kleinebersdorf a single shell bed can be traced in two adjacent outcrops lying about 200 m apart (fig. 1). The 10 m difference in topographic level is most likely due to the presence of a small-scale post-sedimentary fault.

This site offers the opportunity to study the faunal composition along an individual bedding plane with special reference to differences between the two outcrops. The second aim of the study is to identify the mode of shell bed formation and to reconstruct the original environment of the molluscan fauna.

Geological setting and chronostratigraphy

The formation of the asymmetric Korneuburg Basin resulted from pull apart effects within the Alpine-Carpathian thrust belt during late Alpine movements (WESSELY 1998). The SSE-NNE elongated basin is about 20 km long and attains a maximum width of 7 km, but is strongly narrowed in its northern extension. A swell in the area of Obergänserndorf-Mollmannsdorf separates a southern part of the basin with a Neogene fill of about 650 m depth from a shallower northern one about 350 m deep. The basin margins are formed in the northern part by the Waschberg Zone and towards the south by the Flysch Zone. It subsided on its western border along the Schlieberg fault. The considerable increase of sediment thickness towards this western fault zone demonstrates the



Fig. 1: Geological map showing distribution of Neogene marine sediments in Austria and detailed topographic map (ÖK 1: 50.000) showing the study area at Kleinebersdorf. Arrows point to position of sampled outcrops (outcrop A: Lehner-Sandpit, outcrop B: Wohlmuth-Sandpit). Distance between outcrops is about 200 m.

TIME (Ma)	CHRONS	POLARITY	EPOCH	AGE	Planal Foram.	Nanno-Plankton	Mammals	CENTRAL PARATETHYS STAGES							
15.5	CSADn	0	MIOCENE	MIDDLE LANGHIAN	M7	NN5	MN6	BADENIAN							
15.5	CSADp	1			M6										
15.5	CSBn	1			M5										
16.5	CSBr	0			M5										
16.5	CSCn	1			M4										
17.5	CSCr	1		EARLY BURDIGALIAN	M3	NN4	MN4		16.4						
17.5	CSDn	0							KARPATIAN						
18.5	CSDr	0								OTTNANG.					
18.5	CSEn	0									EGGENBURGIAN				
19.5	CSEr	0										EGGERIAN			
20.5	C6n	0	MN3												
20.5	C6r	0						MN2							
21.5	C6An	1											MN1		
21.5	C6Ar	0												NN2	
22.5	C6AAr	1													M1
22.5	C6Bn	1		NN1											
23.5	C6Br	1			MN2										
23.5	C6Cr	1				NP25									
24.5	C6Cn	1					MP30								
24.5	C6Cr	0							P22						
			OLIG							LATE	CHAPTAN				

Fig. 2: Chronostratigraphic table and biostratigraphic zonation

synsedimentary tectonic activity during the Karpatian. In contrast, the eastern margin, which is also formed by the Flysch Zone, lacks any hints of major faults. Sedimentation started during the Eggenburgian (~ Early Burdigalian), but the main basin fill is represented by Karpatian deposits (~ Late Burdigalian) (fig. 2). Karpatian sediments are mainly represented by grey to yellow marly silt and fine to medium sand. Rarely, gravel and boulders may occur close to the Flysch Zone and ancillary diatomites occur in the northern part of the basin.

The Karpatian deposits of the Korneuburg Basin are dated into the latest Early Miocene. The correlation of the mammal fauna with paleomagnetic data allowed a dating into mammal zone MN 5, spanning a time of about 16.5–16.7 my (HARZHAUSER et al. 2002) (fig. 2). Magnetostratigraphic and palaeomagnetic data of SCHOLGER (1998) suggest that the basin rotated counter-clockwise by 20 degrees since the Karpatian. Additionally, a rather southern position of the Korneuburg Basin 16 my ago at 34 degrees palaeolatitude can be deduced (SCHOLGER 1998).

During the Karpatian, the basin was strongly cut off from the open Paratethys Sea. The adjacent Vienna Basin was largely covered by a huge fluvial-deltaic system which prograded from the south. A connection to the marine realm was indicated only along the northern tip, where the Paratethys Sea extended into the Alpine-Carpathian Foredeep. According to HARZHAUSER et al. (2002), the small, elongated satellite basin was divided into a southern, estuarine part and northern, predominately marine part. In the latter, shallow marine settings of 20–30 m water depth formed; here, scattered corals inhabited the silty to sandy bottom. The southern basin, separated from the marine northern basin by the Obergänserndorf-Mollmanssdorf swell, is characterised by estuarine settings. Tidal mudflats with extensive *Crassostrea* bioherms developed along large stretches of the coasts. A subtropical climate with a minimum mean annual temperature (MAT) of 17° C based on the requirements of crocodiles and cordylid lizards was proposed by BÖHME (2002). The winter months were frost-free; the minimal cold month temperature (CMT) ranged from at least 3° C to about 8° C.

The Korneuburg Basin yields one of the most diverse mollusc faunas known from the Karpatian of the Central

Paratethys. In total, 162 gastropod species and 65 bivalve species are reported by HARZHAUSER (2002), BINDER (2002) and CTYROKÝ (2002).

In total, 59 gastropod taxa have been described from the locality Kleinebersdorf (see Appendix) based on museum collections at the Natural History Museum of Vienna (HARZHAUSER 2002). The material “accumulated” during about 150 years of collecting and derived from at least 5 different outcrops. The list therefore reflects a rather overcomplete fauna – a fact also underlined by the specimen/species ratio. About 25% of the total gastropod fauna is documented by a mere 1–3 specimens despite the long period of collecting.

The bivalve record of Kleinebersdorf presented by CTYROKÝ (2002) comprises 15 species (see Appendix). Within the present study we identified 14 taxa from a single shell bed. The comparison between these two lists shows a congruence of only 3 species. Hence 11 species identified during the present investigation, were previously unknown from the locality. This is explained by the sampling strategies of the former (private) collectors, who were more attracted by gastropods than by bivalves. For more information on the gastropod and bivalve species of Kleinebersdorf, refer to the Appendix.

Material and Methods

The shell bed at the locality Kleinebersdorf in Lower Austria (figs 1, 3, 4) was described in the field in terms of geometry, biofabric, complexity and taxonomic composition. Non-standardized quantitative bulk samples (sediment weight: 2.1 kg to 4.6 kg, table 1) were taken from the shell bed at two adjacent outcrops. In each outcrop three samples were taken. In outcrop A (sandpit Lehner) the distance between the samples is about 3 m (between samples 7 and 8) and 10 m (between samples 5 and 7). In outcrop B (sandpit Wohlmuth) the distance between the samples is 1.5 m (between samples 1 and 2) and 9 m (between samples 2 and 9) (fig. 3). Each sample was divided into 4 splits, which were wet sieved through a 1 mm and 0.5 mm screen. The fraction 0.5–1 mm contained only unidentifiable shell hash. Therefore, only the material

Sample	Sediment weight (in g)	Number of individuals	Number of species	Shannon-Wiener index	Simpson index
1	3136	340	14	1,88	4,83
2	2691	216	16	1,85	4,57
5	2911	276	23	2,27	7,72
7	3971	98	13	2,05	6,32
8	4604	150	16	2,00	5,04
9	2113	501	23	1,88	4,49
Outcrop A	11486	524	28	2,23	6,98
Outcrop B	7940	1057	25	1,92	4,57
total	19426	1581	32	2,06	5,49

Table 1: Sediment weight, the number of individuals, the number of species, the values of the Shannon-Wiener index, and the values of the Simpson index for each sample, the assemblages of the two outcrops and the total assemblage.



Fig. 3: The two studied outcrops (above: Outcrop A, Lehner-Sandpit, below: Outcrop B, Wohlmuth-Sandpit). White circles mark position of samples.

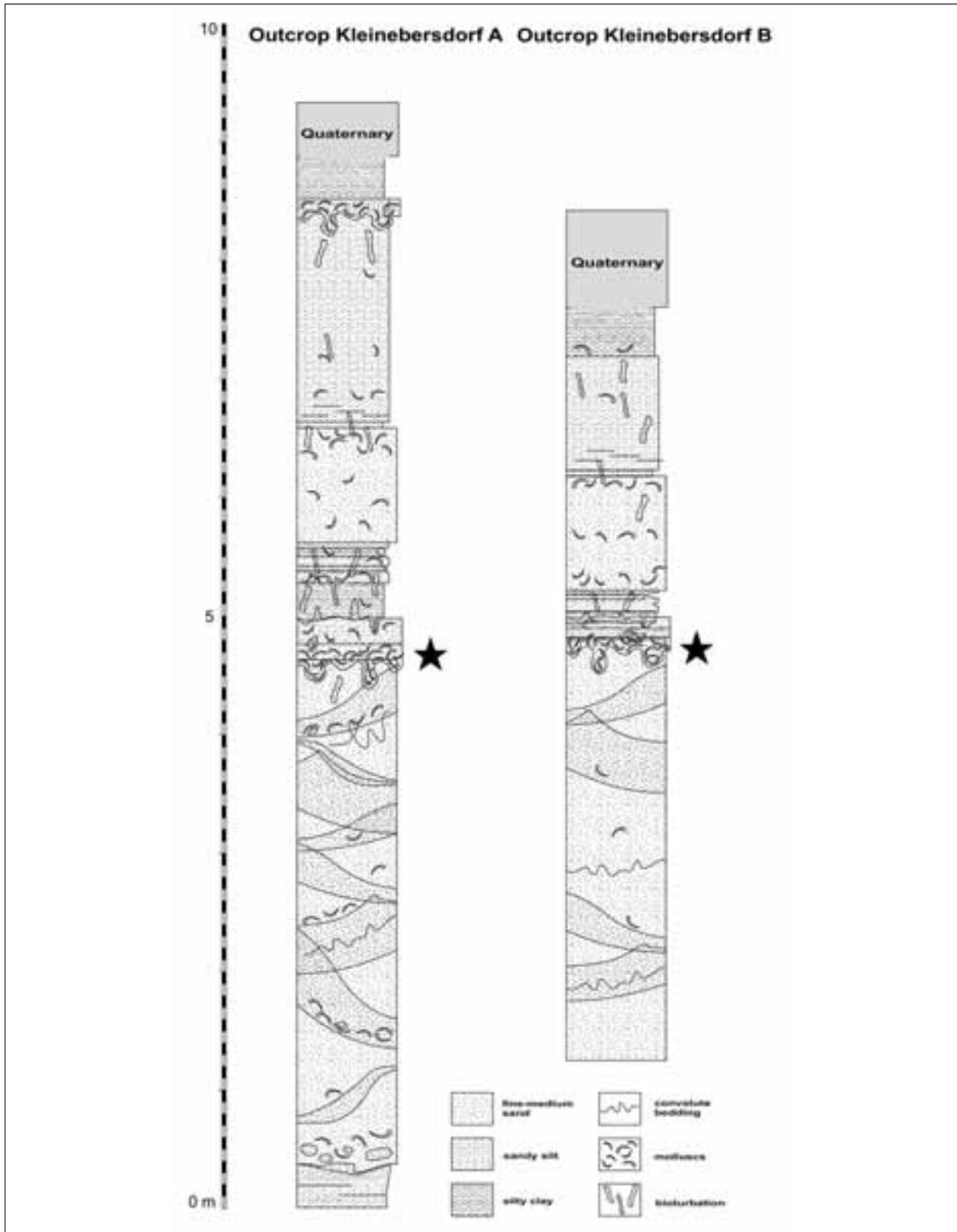


Fig. 4: The outcrops A and B at Kleinebersdorf show comparable successions. The lowermost silty and clayey unit, however, is only present in Outcrop A. Upsection follows a 4 m thick sandy unit with intensive cross-bedding. Its base bears clayey rip-up clasts. The overlying 20 to 30 cm thick coquina displays a wavy, warped lower boundary but is principally continuous. This texture is a secondary plastic deformation due to inhomogeneities within the water-saturated sediment and the load of the coquina onto the underlying sandy unit. This coquina represents the shell bed analysed here. The coquina is topped by interbedded clays, silts and sands and an additional small coquina in outcrop A. The two asterisks mark the studied shell bed in the two outcrops.

>1 mm of the four splits was quantitatively picked for all biogenic components under a binocular microscope.

Wherever possible, whole shells were sorted into species. A whole shell is defined as any shell having > 90 % of the original form for which an anterior-posterior length in bivalves or a long-axis length in gastropods (usually the apex-base length) can be measured (DAVIES et al. 1990, for review see ZUSCHIN et al. 2003). Each piece of shell not matching that definition is a fragment and was not included in our quantitative analysis because most fragments could not be identified to the species level and taphonomic features of fragments usually differ from those of whole individuals (DAVIES et al. 1989, STAFF & POWELL 1990). Each disarticulated valve was counted as a unique individual because the samples are small compared to the sampling domain (GILINSKY & BENNINGTON 1994).

We distinguished 35 taxa (14 bivalves and 21 gastropods) from 1581 whole shells. The shelly material, however, is taphonomically strongly altered by dissolution. We therefore slightly simplified the data matrix for the quantitative and diversity analysis. The five individuals of Naticidae indet. (non *Polinices pseudoredemptus*) were added to *Natica* cf. *tigrina*. The two individuals of *Cyllenina* sp. were added to *Cyllenina ternodosa*. The 24 individuals of Nassariidae indet. were added to *Nassarius edlaueri*.

Diversity was measured as species richness and as heterogeneity diversity (*sensu* PEET 1974), which is based on the proportional abundance of species and considers species dominance and evenness (for a review see MAGURRAN 1988). The Simpson index, which is affected by the 2-3 most abundant species, was used to calculate species dominance. The Shannon-Wiener index, which is more strongly affected by species in the middle of the rank sequence of species, was used to calculate evenness (GRAY 2000).

Diversity curves (species-individual curves) were computed for each sample, the two outcrops and the total assemblage using the program EstimateS, with 50 sample order randomizations without replacement (COLWELL 1997). In order to test the significance of taxonomic differences between the two quarries, an analysis of similarity (ANOSIM, CLARKE & WARWICK 1994) based on the Bray-Curtis similarity coefficient (BRAY & CURTIS 1957) was applied to the complete data set including all taxa. Because of different volumes of sediment sampled, percentage abundances were used (CLARKE & WARWICK 1994) and subjected to a square-root transformation in order to reduce the influence of occasional large abundance values for some taxa (FIELD et al. 1982). Non-metric multidimensional scaling (MDS, KRUSKAL 1964) was used as an ordination method to provide a visual comparison of the pattern of Bray-Curtis values among the 6 samples. The stress value in this analysis indicates how faithfully the high-dimensional relationships among the samples are represented in the 2-dimensional ordination plot. Potentially useful 2-d plots should have a stress value < 0.2 and this value should be attained from several restarts of

the analysis (CLARKE & WARWICK 1994). In this study, the minimum stress value of 0.06 was attained eleven times from 30 random starting configurations. The frequent recurrence of this very low value therefore indicates that the high dimensional relationships among the samples are represented faithfully in the 2-d ordination plot (CLARKE & WARWICK 1994).

Results

The studied shell bed is 30–50 cm thick (figs 3, 4, 5) and consists of a densely packed, polytaxic skeletal concentration (terminology after KIDWELL et al. 1986, KIDWELL & HOLLAND 1991). Along both outcrops the basal contact of the shell bed is sharp and also very wavy and irregular because of abundant loading structures (figs 4, 5). The shells in the coquina parallel this postdepositional irregular surface but do not secondarily accumulate in the topographic lows. The top of the shell bed varies laterally from sharp to rather transitional into sand. The shells are only weakly oriented and are taphonomically strongly altered by dissolution.

The six most abundant taxa (*Granulolabium plicatum*, *Agapilia pachii*, *Loripes* (*Microloripes*) *dentatus*, *Nassarius edlaueri*, *Dosinia* (*Asa*) *lupinus* and *Polinices pseudoredemptus*) make up 88.1% of the shells in the total assemblage, 86.5% in the assemblage of outcrop A, 89.8% in the assemblage of outcrop B; in each of the five samples they contribute between 82.3% and 89.9%. In the total assemblage and in the assemblages of two outcrops, most species (22, 19, 19 respectively) contribute less than 1% each to the faunal composition. In most individual samples (except samples 7 and 9), however, the majority of species contributes more than 1% to the faunal composition (fig 6, fig. 7).

The ANOSIM test shows no significant differences in molluscan composition between the two outcrops (R-stat = 0.37, p = 0.1). This lack of differences is also demonstrated by the lack of separation between sample groups in the multidimensional scaling (fig. 8).

Diversity was evaluated for the total fauna and for each sample of the shell bed. Although the number of counted individuals is relatively high, species richness does not level off for the total assemblage, the two outcrops or individual samples (table 1, figs 9, 10). In contrast to species richness, heterogeneity diversity is very stable within samples, for the two outcrops and for the total assemblage: the Shannon-Wiener index and the Simpson index do not increase with sample size (figs 9, 10).

Huge differences are evident between the total number of species present (32), the number of species in the two outcrops (outcrop A: 28, outcrop B: 25) and the number of species in individual samples, which range from 13 to 23 (tab. 1). The slopes of the diversity curves (species-individual curves) differ strongly between samples (fig. 9) and are much steeper for outcrop A than for outcrop B (fig. 11). The Simpson index (5.49 for the total assem-

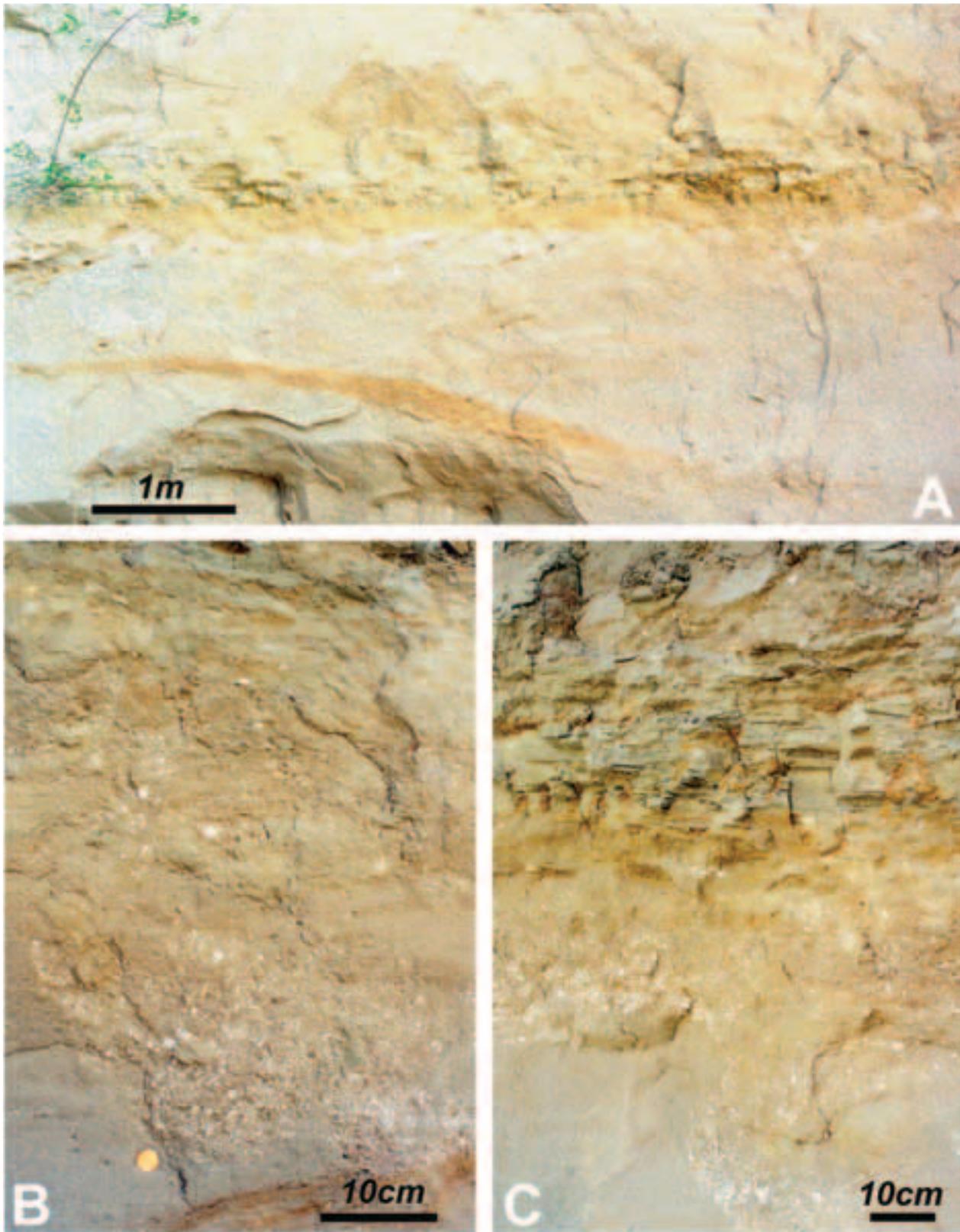


Fig. 5: The investigated shell bed in the Lehner-Sandpit (outcrop A). 5A. General appearance of Lehner-Sandpit shell bed (outcrop A). 5B. and 5C. Loading of the coquina portions into the underlying, cross-bedded sands.

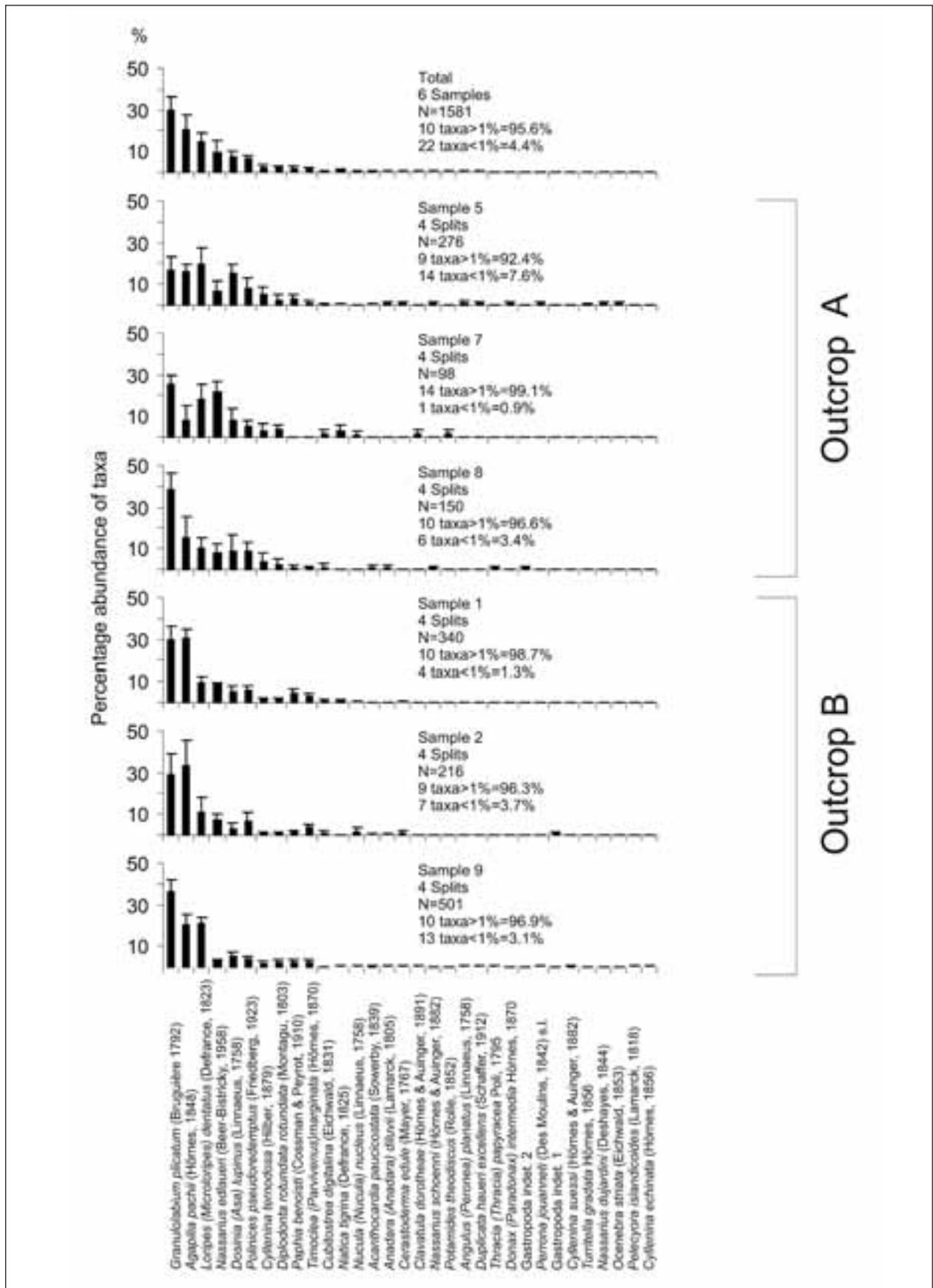


Fig. 6: Taxonomic composition and percentage abundance with 95% confidence intervals of the quantitatively important taxa in individual samples of the shell bed and of the total assemblage.

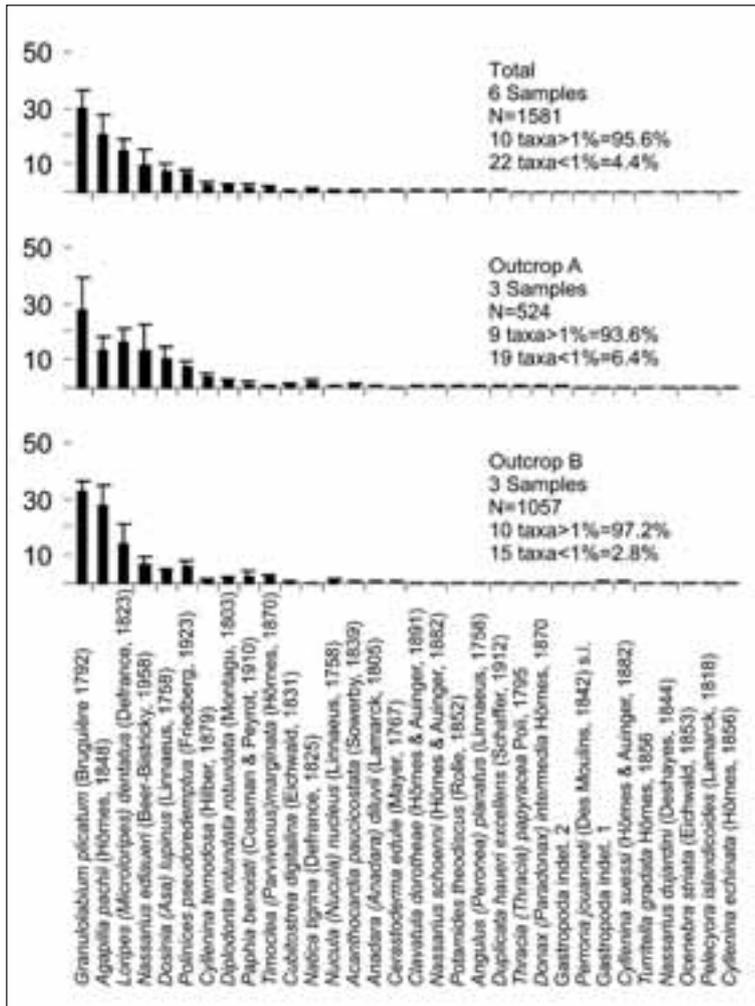


Fig. 7: Taxonomic composition and percentage abundance with 95% confidence intervals of the quantitatively important taxa in the two outcrops and in the total assemblage.

blage) scatters widely between samples but is much higher in outcrop A (6.98, range 5.04 to 7.72) than in outcrop B (4.57, range 4.49 to 4.83) (tab. 1). Similarly, the Shannon-Wiener index (2.06 for the total assemblage) scatters widely among individual samples but is consistently higher in outcrop A (2.23, range 2.00 to 2.27) than in outcrop B (1.92, range 1.85 to 1.88) (tab. 1).

Discussion

The shell bed is interpreted as a parautochthonous or slightly transported tidal flat deposit whose fine-grained sedimentary components have largely been winnowed by currents that were not strong enough to significantly transport the shells (FÜRSICH & OSCHMANN 1993, FÜRSICH 1995). The weak orientation of the shells, the absence of size-sorting and the lack of any sedimentary structures point to gentle winnowing as the most likely concentration process. The rather low total diversity of 32 species points to a physically controlled original environment, and the composition of the molluscan fauna, with the ba-

tillariid gastropod *Granuloblabium plicatum* as the most abundant species, supports the interpretation of a tidal flat deposit. Additionally, the presence of large *Crassostrea gryphoides* shells, observed in the coquina exposed at outcrop B, points to a nutrient-rich lower intertidal to uppermost subtidal environment. For example, *Crassostrea gryphoides* and *Crenomytilus aquitanicus* bistroemes were recorded in the southern Korneuburg Basin and flourished there as result of nutrient input within a small estuary (HARZHAUSER et al. 2002).

The most important bivalve contributors to the studied shell bed are (in hierarchical order) *Loripes (Microloripes) dentatus*, *Dosinia (Asa) lupinus* and *Diplodonta rotundata*. The Recent *Loripes* and *Diplodonta* are burrowers, being common in calm water regimes of the lower intertidal to upper subtidal zone (STANLEY 1970, MILISIC 1991). *Diplodonta* bears chemosymbiotic bacteria in its gill tissues and is well adapted to nutrient-rich, oxygen-depleted sediments (TAYLOR & GLOVER 2000). The extant *Dosinia* is a fast and deep burrower common on moderately exposed sand flats; it avoids wave-ridden sandy beaches (STANLEY 1970). Such a combination of actualistic data points to a



Fig. 8: Ordination of samples of the two outcrops using Multidimensional scaling (MDS). Points close to one another represent samples that are more similar in taxonomic composition than points farther away from one another. The molluscan composition in outcrop A is more heterogeneous than in outcrop B, but differences between the two outcrops are not statistically significant.

low-energy coastal setting with at least partly nutrient-rich sediment within the lower intertidal and/or upper subtidal. A sheltered embayment or lagoon with a partially restricted circulation pattern adjacent to an estuary as proposed by HARZHAUSER et al. (2002) is most likely.

Our diversity analysis shows that the full range of species in the shell bed was not covered, but in contrast to species richness, heterogeneity diversity (measured with the Shannon-Wiener index and with the Simpson index) does not increase with increasing sample size for the total assemblage, the two outcrops or for individual samples (figs 9, 10, 11). Incorporating more samples or more individuals per sample would therefore simply add more rare species, but would not change the rank order of the most abundant and the middle-ranked species. Although rare species can be very important for palaeoecological and palaeoenvironmental interpretations, in quantitative studies using abundance data they do not change the position of a sample in ordination space (cf. OLSZEWSKI & WEST 1997).

The molluscan composition in outcrop A is more heterogeneous than in outcrop B. The six most abundant species are the same in all samples, but their rank order differs between samples and between outcrops (figs 6, 7). Additionally, most rare species occur in one or two samples only (fig. 6). Therefore, the samples of outcrop A show a much wider scatter than those of outcrop B in the multidimensional scaling (fig. 8). These differences between outcrops, however, are not statistically significant. Some patchiness is indicated for diversities: The slope of the species-individual curve is much steeper for outcrop A than for outcrop B (fig. 11). Moreover, the Simpson index and the Shannon-Wiener index are also consistently higher in samples from outcrop A (table 1).

This study shows that the extensive list of mollusc species reported by HARZHAUSER (2002) and CTYROKÝ (2002) from Kleinebersdorf contrasts with the low diversity of our quantitative analysis. This discrepancy between the collection-based faunal list and the quantitative point-diversities is a good example for the importance and

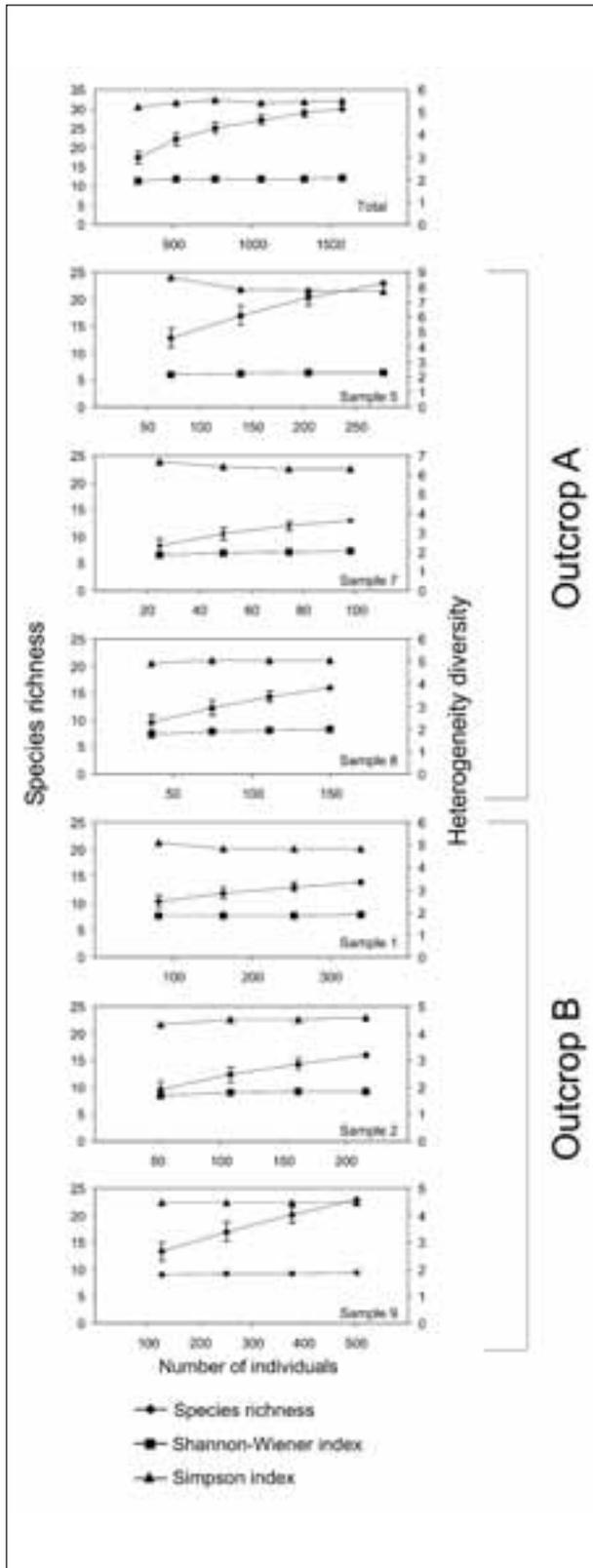


Fig. 9: Species richness and heterogeneity diversity (measured with the Shannon-Wiener index and the Simpson index) for the total fauna and for the samples of the two outcrops. Within samples and for the total assemblage, species richness does not level off, but heterogeneity diversity is very stable. The slopes of the species-individual curves differ strongly between samples.

limitations of unsystematic and non-quantitative, but long-lasting collecting activity: it provides information on the presence of those rare species that would not be covered by a feasible quantitative sampling program. On the other hand, however, it overemphasizes the proportion of the rarest species.

Conclusion

This case study is one of the few attempts to trace diversities and faunal composition of a discrete shell bed in two adjacent outcrops. The studied shell accumulation developed during the Late Karpatian along the shores of the Korneuburg Basin, which was part of the Paratethys bioprovince. Its lithology, faunal composition and the paleogeographic situation indicate a tidal flat setting inhabited mainly by the herbivorous batillariid gastropod *Granulolabium plicatum*, and the neritid gastropod *Agapillia pachii*. The bivalves *Loripes dentatus*, *Dosinia lupinus* and *Diplodonta rotundata* flourished under the quiet water conditions within the lower intertidal to upper subtidal zone, where they lived as deeply burrowing suspension feeders. The spectrum of the most important species of the tidal flat is completed with scavenging nassariid gastropods and the predatory *Polinices pseudoredeemptus*.

The data indicate that the fauna of that Karpatian tidal flat was dominated by very few species occurring in large quantities. The full range of species in the shell bed was not covered by our sampling strategy, but heterogeneity diversity measures show that the rank order of the most abundant and the middle-ranked species is very stable. Diversity, estimated from the steepness of the species-individual-curves and measured as heterogeneity diversity, differs consistently between the two outcrops. Additional patchiness in quantitative molluscan composition was best indicated by differences in the rank order of the most abundant species, but differences between outcrops were not statistically significant.

Acknowledgements

This study was supported by Project 13745-Bio of the Austrian Science Fund. We thank Franz TOPKA for help during the fieldwork, Hubert DOMANSKI for assistance with sample preparation and Michael STACHOWITSCH for stimulating discussions. The detailed comments of journal reviewers Ronald JANSSEN, Richard MEYRICK and Werner E. PILLER improved the manuscript and are gratefully acknowledged.

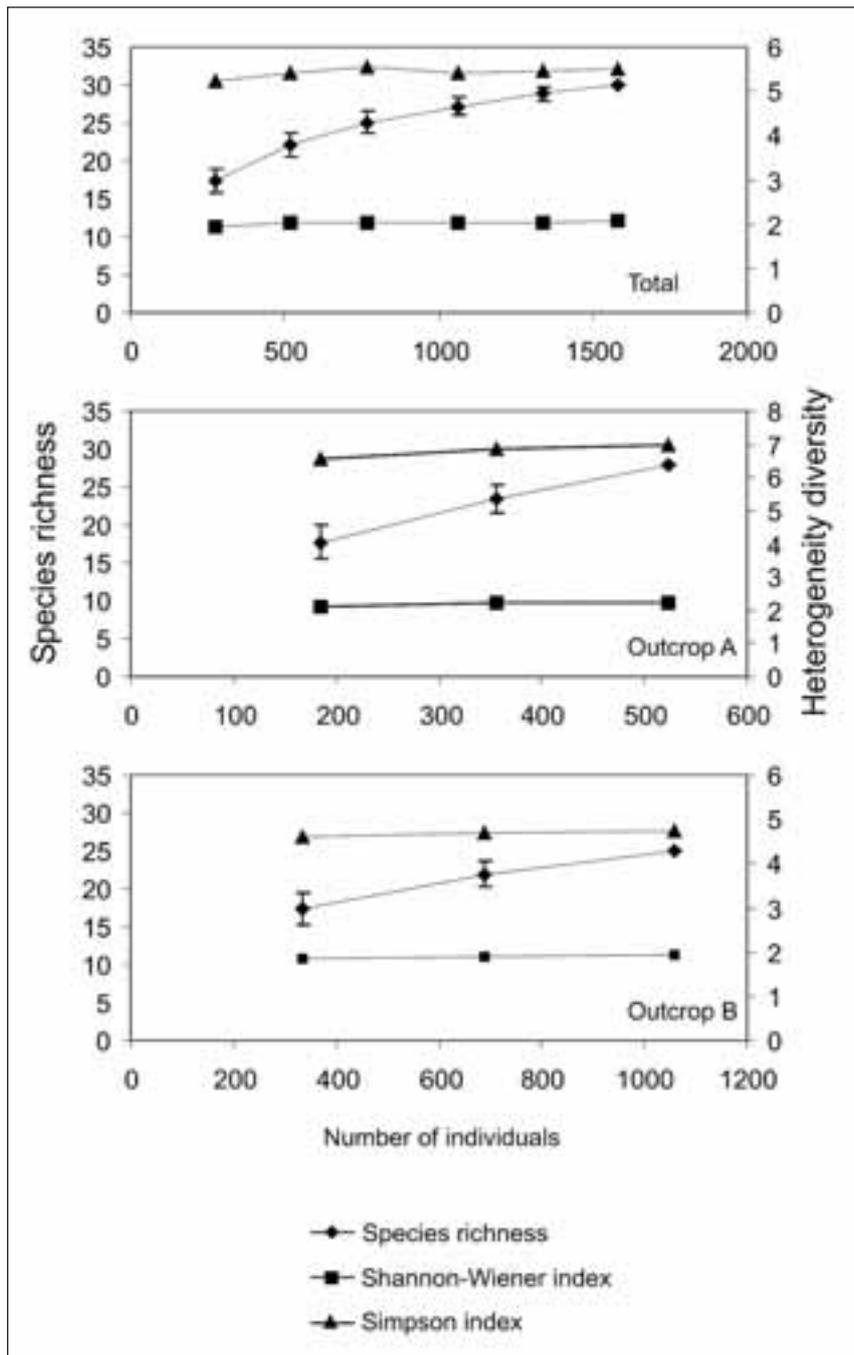


Fig. 10: Species richness and heterogeneity diversity (measured with the Shannon-Wiener index and the Simpson index) for the total fauna and for the two outcrops. For the total assemblage and for the two outcrops, species richness does not level off, but heterogeneity diversity is very stable.

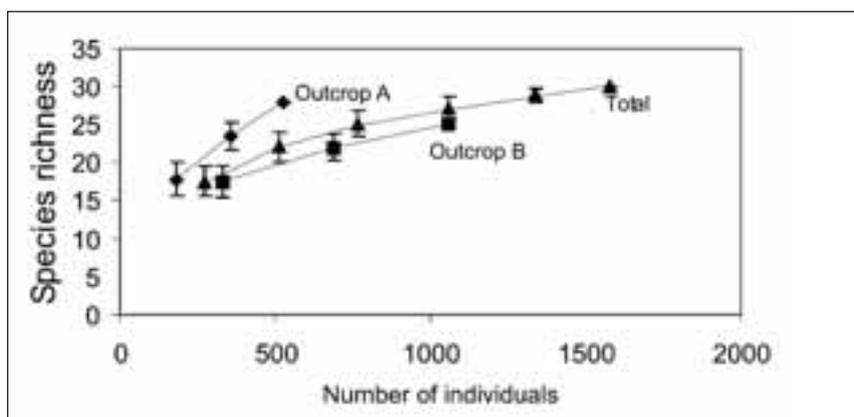


Fig. 11: Species-individual curves for the total fauna and for the fauna in the two outcrops. Generally, species richness does not level off, but the slopes of the species-individual curves differ strongly between outcrops.

References

- BENNINGTON, J.B. (2003): Transcending patchiness in the comparative analysis of palaeocommunities: a test case from the Upper Cretaceous of New Jersey. – *Palaios*, **18**: 22-33.
- BINDER, H. (2002): Die Land- und Süßwasserschnecken aus dem Karpat des Korneuburger Beckens. – *Beiträge zur Paläontologie*, **27**: 161-203.
- BÖHME, M. (2002): Lower Vertebrates (Teleostei, Amphibia, Sauria) from the Karpatian of the Korneuburg Basin – palaeoecological, environmental and palaeoclimatical implications. – *Beiträge zur Paläontologie*, **27**: 339-353.
- BRAY, J. R. & CURTIS, J. T. (1957): An ordination of the upland forest communities of southern Wisconsin. – *Ecological Monographs*, **27**: 325-349.
- CLARKE, K. R. & WARWICK, R. M. (1994): Changes in marine communities: An approach to statistical analysis and interpretation. – 1-144; Plymouth (Plymouth Marine Laboratory).
- COBABB, E. A. & ALLMON, W. D. (1994): Effects of sampling on paleoecologic and taphonomic analyses in high-diversity fossil accumulations: an example from the Eocene Gosport Sand, Alabama. – *Lethaia*, **27**: 167-178.
- COLWELL, R. K. (1997): EstimateS: Statistical estimation of species richness and shared species from samples. Version 5 users guide and application. – published at <http://viceroy.eeb.uconn.edu/estimates>.
- CTYROKY, P. (2002): Marine und brachyhaline Bivalven aus dem Karpatium des Korneuburger Beckens (Österreich, Untermiozän). – *Beiträge zur Paläontologie*, **27**: 215-258.
- CUMMINS, H., POWELL, E. N., STANTON, R. J. JR., & STAFF, G. (1986a): Assessing transport by the covariance of species with comments on contagious and random distributions. – *Lethaia*, **19**: 1-22.
- DAVIES, D. J., POWELL, E. N., STANTON, R. J. JR., (1989): Taphonomic signature as a function of environmental process: shells and shell beds in a hurricane-influenced inlet on the Texas coast. – *Palaeogeography, Palaeoclimatology, Palaeoecology*, **72**: 317-356.
- DAVIES, D. J., STAFF, G. M., CALLENDER, W. R., POWELL, E. N. (1990): Description of a quantitative approach to taphonomy and taphofacies analysis: all dead things are not created equal. – In: Miller, W. (Ed.), *Paleocommunity temporal dynamics: The long-term development of multispecies assemblages*. – *The Paleontological Society Special Publication* **5**, 328-350; Knoxville (The University of Tennessee).
- FIELD, J. G., CLARKE, K. R. & WARWICK, R. M. (1982): A practical strategy for analysing multispecies distribution patterns. – *Marine Ecology Progress Series*, **8**: 37-52.
- FÜRSICH, F. T. (1995): Shell concentrations. – *Eclogae Geologicae Helveticae*, **88**: 643-655.
- FÜRSICH, F. T. & OSCHMANN, W. (1993): Shell beds as tools in basin analysis: the Jurassic of Kachchh, western India. – *Journal of the Geological Society, London*, **150**: 169-185.
- GILINSKY, N. L. & BENNINGTON, J. B. (1994): Estimating numbers of whole individuals from collections of body parts: a taphonomic limitation of the paleontological record. – *Paleobiology*, **20**: 245-258.
- GRAY, J.S. (2000): The measurement of marine species diversity with an application to the benthic fauna of the Norwegian continental shelf. – *Journal of Experimental Marine Biology and Ecology*, **250**: 23-49.
- HARZHAUSER, M. (2002): Marine und brachyhaline Gastropoden aus dem Karpatium des Korneuburger Beckens und der Kreuzstettener Bucht (Österreich, Untermiozän). – *Beiträge zur Paläontologie*, **27**: 61-159.
- HARZHAUSER, M. & KOWALKE, T. (2002): Sarmatian (Late Middle Miocene) Gastropod Assemblages of the Central Paratethys. – *Facies*, **46**: 57-82.
- HARZHAUSER, M., BÖHME, M., MANDIC, O. & HOFMANN, CH.-CH. (2002): The Karpatian (Late Burdigalian) of the Korneuburg Basin – A Palaeoecological and Biostratigraphical Synthesis. – *Beiträge zur Paläontologie*, **27**: 441-456.
- HÖRNES, M. (1856): Die fossilen Mollusken des Tertiär-Beckens von Wien. I. Band. Univalven. – *Abhandlungen der Geologischen Reichsanstalt*, **3** (1870): 1-404.
- KIDWELL, S. M., FÜRSICH, F. T., & AIGNER, T. (1986): Conceptual framework for the analysis and classification of fossil concentrations. – *Palaios*, **1**: 228-238.
- KIDWELL, S. M. & HOLLAND, S. M. (1991): Field description of coarse bioclastic fabrics. – *Palaios*, **6**: 426-434.
- KRUSKAL, J. B. (1964): Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. – *Psychometrika*, **29**: 1-27.
- LOZOUET, S. (1986): Redéfinition des Genres *Potamides* et *Pirenella* (Gastropoda, Prosobranchia) à partir des espèces actuelles et fossiles: Implications phylétiques et biogéographiques. – *Annales de Paléontologie*, **72** (3): 163-210.
- MAGURRAN, A. E. (1988): *Ecological diversity and its measurement*. – 1-179; Princeton, New Jersey (Princeton University Press).
- MANDIC, O., HARZHAUSER, M., SPEZZAFERRI, S. & ZUSCHIN, M. (2002): The paleoenvironment of an early Middle Miocene Paratethys sequence in NE Austria with special emphasis on paleoecology of mollusks and foraminifera. – *Geobios*, **24**: 193-206.
- MILISIC, N. (1991): Skoljke i puzevi Jadrana. – 1-302; Split (Logos).
- MILLER, A. I. (1988): Spatial resolution in subfossil molluscan remains: implications for paleobiological analyses. – *Paleobiology*, **14**: 91-103.
- MILLER, A. I., PARSONS, K. M., CUMMINS, H., BOARDMAN, M. R., GREENSTEIN, B. J. & JACOBS, D. K. (1992): Effect of Hurricane Hugo on molluscan skeletal distributions, Salt River Bay, St. Croix, U.S. Virgin Islands. – *Geology*, **20**: 23-26.
- MILLER, A. I. (1997): Counting fossils in a Cincinnatian storm bed: Spatial resolution in the fossil record. – In: BRETT, C. E. & BAIRD, G. C. (Eds): *Paleontological events. Stratigraphic, ecological, and evolutionary implications*. – 57-72; New York (Columbia University Press).
- OLSZEWSKI, T. & WEST, R. R. (1997): Influence of transportation and time-averaging in fossil assemblages from the Pennsylvanian of Oklahoma. – *Lethaia*, **30**: 315-329.
- PEET, R. K. (1974): The measurement of species diversity. – *Annual Reviews of Ecology and Systematics*, **5**: 285-307.
- SCHOLGER, R. (1998): Magnetostratigraphic and palaeomagnetic analysis from the Early Miocene (Karpatian) deposits Teiritzberg and Obergänserndorf (Korneuburg Basin, Lower Austria). – *Beiträge zur Paläontologie*, **23**: 25-26.
- STAFF, G. M., POWELL, E. N., 1990. Local variability of taphonomic attributes in a parautochthonous assemblage: can taphonomic signature distinguish a heterogeneous environment? – *Journal of Paleontology*, **64**, 648-658.
- STANLEY, S. M. (1970): Relation of Shell Form to Life of the Bivalvia (Mollusca). – *Memoir GSA*, **125**: 1-296.
- TAYLOR, J. D. & GLOVER, E. (2000): Functional anatomy, chemosymbiosis and evolution of the Lucinidae. – In: HARPER, E. M., TAYLOR, J. D. & CRAME, J. A. (Eds): *The evolutionary biology of the Bivalvia*. – *Geological Society Special Publications*, **177**: 207-225; London (Geological Society of London).
- WESSELY, G. (1998): Geologie des Korneuburger Beckens. – *Beiträge zur Paläontologie*, **23**: 9-23.
- ZUSCHIN, M., STACHOWITSCH, M. & STANTON, R. J., JR. (2003): Patterns and processes of shell fragmentation in modern and ancient marine environments. – *Earth-Science Reviews*, **63**: 33-82.
- ZUSCHIN, M., HARZHAUSER, M. & MANDIC, O. (submitted a): Influence of Size-sorting on diversity estimates from tempestitic shell beds. – *Palaios*.
- ZUSCHIN, M., HARZHAUSER, M. & MANDIC, O. (in press): Taphonomy and Palaeoecology of the Lower Badenian (Middle Miocene) molluscan assemblages at Grund (Lower Austria). – *Geologica Carpathica*, 55.

Manuskript submitted 2003 – 06 – 24

Manuskript accepted 2003 – 10 – 01

Appendix caption

The complete lists of molluscs described from the locality Kleinebersdorf. The gastropod data are from HARZHAUSER (2002). The bivalve record was published by CTYROKÝ (2002) but is here revised on generic and on (sub)species level. Note that of 15 species identified from samples investigated within the present study, only 3 (*Timoclea (Parvivenus) marginata marginata* (HÖRNES), *Cubitostrea digitalina* (EICHWALD) and *Pelecypora (Cordiopsis) islandicoides* (LAMARCK)) were previously known from Kleinebersdorf. Moreover, whereas *Loripes (Microloripes) dentatus* (DEFRANCE) could be identical with *Loripes (Loripes) dujardini* of CTYROKÝ (2002), the other most frequent taxa characterizing the studied shell bed such as *Diplodonta (Diplodonta) rotundata rotundata* (MONTAGU) or *Dosinia (Asa) lupinus* (LINNAEUS) were not recorded in previous studies.

As already demonstrated by LOZOUET (1986), *Granulolabium bicinctum* (BROCCHI) is a descendant of *Granulolabium plicatum* (BRUGUIÈRE). During the late Early Miocene, this species group shows an extreme morphological plasticity, which is reflected in the description of numerous “species”, “subspecies” and “varieties” in the older literature. LOZOUET (1986) synonymized most of those taxa and tried to overcome that problem by using the term *Grabulolabium plicatum bicinctum*. In this study we prefer *Granulolabium plicatum*, including morphologies described by HÖRNES (1856) as “*Cerithium moravicum*” and “*Melanopsis tabulata*”. Similarly, the *Granulolabium bicinctum* sensu HARZHAUSER (2002) has to be included in this complex.

Taxa	Ctyroký 2002	this study
<i>Nucula (Nucula) nucleus</i> (Linnaeus, 1758)		x
<i>Anadara (Anadara) diluvii</i> (Lamarck, 1805)		x
<i>Anadara (Anadara) turonica</i> (Dujardin in Hörnes, 1870)	x	
<i>Glycymeris (Glycymeris) deshayesi</i> (Mayer, 1868)	x	
<i>Crenomytilus? aquitanicus</i> (Mayer-Eymar, 1858)	x	
<i>Pecten subarcuatus styriacus</i> (Hilber, 1879)	x	
<i>Aequipecten scabrellus hungaricus</i> (Csepregy-Meznerics, 1960)	x	
<i>Crassadoma multistriata</i> (Poli, 1795)	x	
<i>Manupecten cf. fasciculatus</i> (Millet, 1854)	x	
<i>Macrochlamis tournali</i> (de Serres, 1829)	x	
<i>Anomia (A.) ephippium</i> Linnaeus, 1758	x	
<i>Crassostrea gryphoides</i> (Schlotheim, 1813)	x	
<i>Cubitostrea digitalina</i> (Eichwald, 1831)	x	x
<i>Chama (Psolopus) gryphina</i> (Lamarck, 1819)	x	
<i>Loripes (Microloripes) dentatus</i> (Defrance, 1823)		x
<i>Loripes (Loripes) dujardini</i> (Deshayes, 1850)	x	
<i>Diplodonta (Diplodonta) rotundata rotundata</i> (Montagu, 1803)		x
<i>Cerastoderma edule</i> (Mayer, 1767)		x
<i>Acanthocardia (Acanthocardia) paucicostata</i> (Sowerby, 1839)		x
<i>Angulus (Peronea) planatus</i> (Linnaeus, 1758)		x
<i>Donax (Paradonax) intermedia</i> Hörnes, 1870		x
<i>Pelecypora (Cordiopsis) islandicoides</i> (Lamarck, 1818)	x	x
<i>Timoclea (Parvivenus) marginata</i> (Hörnes, 1870)	x	x
<i>Paphia (Callistotapes) benoisti</i> (Cossmann & Peyrot, 1910)		x
<i>Dosinia (Asa) lupinus</i> (Linnaeus, 1758)		x
<i>Thracia (Thracia) papyracea papyracea</i> Poli, 1795		x

	Harzhauser 2002	this study
<i>Agapilia pachii</i> (Hörnes, 1848)	x	x
<i>Paroxystele amedei</i> (Brongniart, 1823)	x	
<i>Granulolabium bicinctum</i> (Brocchi, 1814)	x	x
<i>Granulolabium plicatum</i> (Bruguière, 1792)	x	x
<i>Potamides theodiscus</i> (Rolle, 1852)		x
<i>Tympanotonos cinctus</i> (Basterot, 1825)	x	
<i>Terebralia bidentata</i> (Defrance in Grateloup, 1840)	x	
<i>Cerithium turonicum</i> (Mayer, 1878)	x	
<i>Cerithium vulgatum europaeum</i> (Mayer, 1878)	x	
<i>Protoma cathedralis paucicincta</i> Sacco, 1895	x	
<i>Turritella (Turritella) gradata</i> Menke in Hörnes, 1856	x	x
<i>Turritella (Turritella) bellardii</i> Mayer, 1866	x	
<i>Turritella (Archimediella) erronea</i> (Cossmann, 1914)	x	
<i>Turritella (Eichwaldiella) bicarinata</i> (Eichwald, 1830)	x	
<i>Rissoina podolica</i> Cossmann, 1921	x	
<i>Calyptraea (Calyptraea) depressa</i> Lamarck, 1822	x	
<i>Aporrhais pespelecani</i> (Linné, 1766)	x	
<i>Eratopsis subcypraeola</i> (d'Orbigny, 1852)	x	
<i>Zonaria dertamygdaloides</i> (Sacco, 1894)	x	
<i>Polinices pseudoredemptus</i> (Friedberg, 1923)	x	x
<i>Polinices redemptus</i> (Michelotti, 1847)	x	
<i>Euspira helicina</i> (Brocchi, 1814)	x	
<i>Neverita josephina</i> (Risso, 1826)	x	
<i>Natica tigrina</i> Defrance, 1825	x	x
<i>Triphora</i> sp.	x	
<i>Ocenebra crassilabiata</i> (Hilber, 1879)	x	
<i>Ocenebra striata</i> (Eichwald, 1853)	x	x
<i>Purpura vindobonensis</i> (Hörnes, 1856)	x	
<i>Pyrene (Alia) polonica</i> (Pusch, 1837)	x	
<i>Mitrella fallax</i> (Hörnes & Auinger, 1880)	x	
<i>Anachis haueri</i> (Hörnes & Auinger, 1880)	x	
<i>Euthria (Euthria) puschi</i> (Andrezejowski, 1830)	x	
<i>Babylonia eburnoides</i> (Matheron, 1842)	x	
<i>Fusinus hoessi</i> (Partsch in Hauer, 1837)	x	
<i>Euthriofusus burdigalensis</i> (Defrance, 1820)	x	
<i>Nassarius dujardini</i> (Deshayes, 1844)		x
<i>Nassarius schoenni</i> (Hörnes & Auinger, 1882)	x	x
<i>Nassarius edlaueri</i> (Beer-Bistricky, 1958)	x	x
<i>Nassarius subprismaticus</i> (Hörnes & Auinger, 1882)	x	
<i>Nassarius sturi</i> (Hörnes & Auinger, 1882)	x	
<i>Nassarius cerithiformis</i> (Auinger in Hilber, 1879)	x	
<i>Cyllenina echinata</i> (Hörnes, 1856)	x	x
<i>Cyllenina ternodosa</i> (Hilber, 1879)	x	x
<i>Cyllenina suessi</i> (Hörnes & Auinger, 1882)	x	x

<i>Duplicata haueri excellens</i> (Schaffer, 1912)	x	x
<i>Tudicla rusticula</i> (Basterot, 1825)	x	
<i>Narona (Aneurystoma) austropolonica</i> Baluk, 1997	x	
<i>Narona (Tribia) partschi</i> (Hörnes, 1856)	x	
<i>Trigonostoma (Trigonostoma) imbricatum</i> (Hörnes, 1856)	x	
<i>Trigonostoma (Ventrilia) exwestiana</i> (sacco, 1894)	x	
<i>Conus (Conolithus) dujardini</i> Deshayes, 1845	x	
<i>Conus (Conolithus) sp.</i>	x	
<i>Conus (Chelyconus) ponderosus</i> (Brocchi, 1814)	x	
<i>Clavatula dorotheae</i> (Hörnes & Auinger, 1891)	x	x
<i>Clavatula barbarae</i> (Hörnes & Auinger, 1891)	x	
<i>Clavatula asperulata</i> (Lamarck, 1822)	x	
<i>Clavatula laevigata</i> (Eichwald, 1830)	x	
<i>Perrona louisae</i> (Hörnes & Auinger, 1891)	x	
<i>Perrona jouanneti</i> (Des Moulins, 1842) s. l.	x	x
<i>Architectonica (Architectonica) simplex</i> (Bronn, 1831)	x	
<i>Acteocina lajonkaireana</i> Basterot, 1825	x	