

TAPHONOMY AND PALEOECOLOGY OF THE LOWER BADENIAN (MIDDLE MIOCENE) MOLLUSCAN ASSEMBLAGES AT GRUND (LOWER AUSTRIA)

MARTIN ZUSCHIN¹, MATHIAS HARZHAUSER² and OLEG MANDIC¹

¹Department of Paleontology, University of Vienna, Althanstrasse 14, A-1090 Vienna, Austria; martin.zuschin@univie.ac.at;
oleg.mandic@univie.ac.at

²Museum of Natural History Vienna, Burgring 7, A-1014 Vienna, Austria; mathias.harzhauser@nhm-wien.ac.at

(Manuscript received June 5, 2003; accepted in revised form December 16, 2003)

Abstract: The typical sandy, shell-rich deposits of artificial outcrops in the Grund Formation were identified as distinctly allochthonous event beds with channel-structures, sharp erosional bases, and graded bedding. They are interpreted as proximal tempestites and contain a densely packed, polytaxic molluscan assemblage. The faunal composition and taphonomic features of shells indicate that transport occurred from wave- or current-agitated nearshore habitats into a dysaerobic, pelitic, inner shelf environment. This pelitic environment was colonized by a single molluscan species, the chemosymbiotic *Thyasira michelottii*, which occurs in life position, as confirmed by valve articulation and preservation of the inhalant tube and postero-ventral tunnel networks. In contrast to the depauperate autochthonous fauna, the skeletal concentrations contain a highly diverse molluscan fauna. We identified 130 species from more than 4200 individuals, but two bivalve species, *Timoclea marginata* and *Loripes dentatus*, strongly dominate each of the five samples from different shell beds. In contrast, the diversity (measured as species richness and heterogeneity diversity) and the frequency distribution of shell sizes differ strongly between the five shell beds. A regression analysis identifies the diversity of the shell beds as a function of shell sorting. Poorly sorted shell beds have higher species richness than well-sorted shell beds. The diversity in Grund is therefore taphonomically controlled, because sorting of the allochthonous shell beds is determined by their transport history.

Key words: Miocene, chemosymbiosis, diversity, paleoecology, taphonomy, shell beds, Mollusca.

Introduction

The taxonomic composition of the famous molluscan assemblages at the Lower Badenian (Middle Miocene) locality Grund

(Fig. 1) is very well known from numerous taxonomic investigations during the last 140 years (M. Hönes 1856; M. Hönes & Reuss 1859–1870; R. Hoernes & Auinger 1879–1882; Sieber 1947a,b, 1949). In contrast, due to very poor outcrop con-

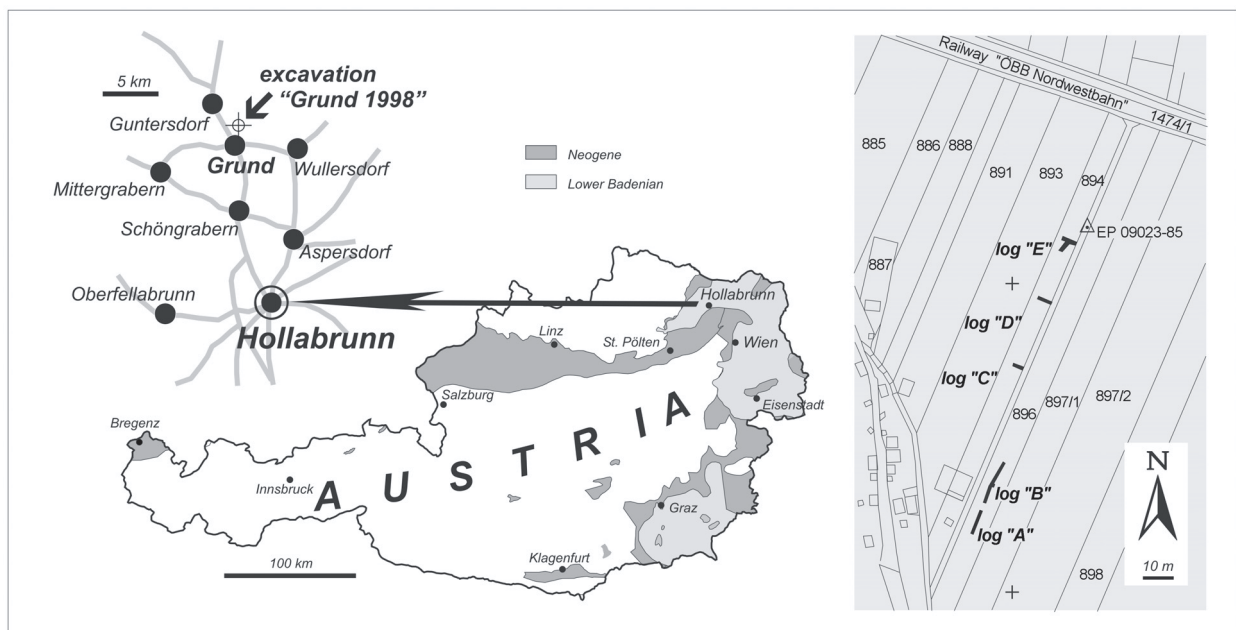


Fig. 1. Study area and sample location.

ditions, virtually nothing was known about the taphonomic character of the shelly assemblages, and so far no data on relative abundances of the respective species are available.

Most paleontologists working in the region subliminally anticipated that the assemblage was parautochthonous (e.g. Sieber 1937 when discussing variations in sculpture of gastropods from Grund) and recently the locality Grund was included in a study comparing Miocene alpha diversities between the Paratethys and the European Boreal bioprovince (Kowalewski et al. 2002).

Here, we examine the artificial outcrops which were recently used to clarify the stratigraphy, sedimentology and taphonomy of the locality Grund (Ćorić et al. 2004; Roetzel et al. 1999; Roetzel & Pervesler 2004; Zuschin et al. 2001; Zuschin et al. submitted). Based on the new data from this extensive field work, we will show that most shells at Grund were deposited in allochthonous, most likely tempestitic, shell beds. The shells were transported from shallow water into a somewhat deeper environment with autochthonous, monospecific *Thyasira* in life position (Zuschin et al. 2001). We present abundance data on the fauna preserved in the shell beds and reconstruct the probable original habitats of the transported shells. Finally, we estimate the diversity at Grund, compare diversities between shell beds and evaluate the influence of transport on species richness.

Material and methods

Standardized quantitative bulk samples were taken from five Middle Miocene shell beds at the locality Grund in Lower Austria (Fig. 1, Fig. 2). Each sample was divided into 16 subsamples and four randomly chosen splits were wet sieved through a 1 mm screen. The material >1 mm of the four splits was quantitatively picked for all biogenic components under a binocular microscope.

We counted 4215 whole shells; wherever possible, these were sorted into species. We distinguished 130 species (61 bivalves, 68 gastropods, 1 scaphopod) from 4105 whole shells (see Appendix for a complete list of species). The data matrix was slightly simplified into 125 species: Seven species were summarized in the rissoid gastropod genera *Alvania* (5) and *Turboella* (2) because they could not be consistently distinguished. An

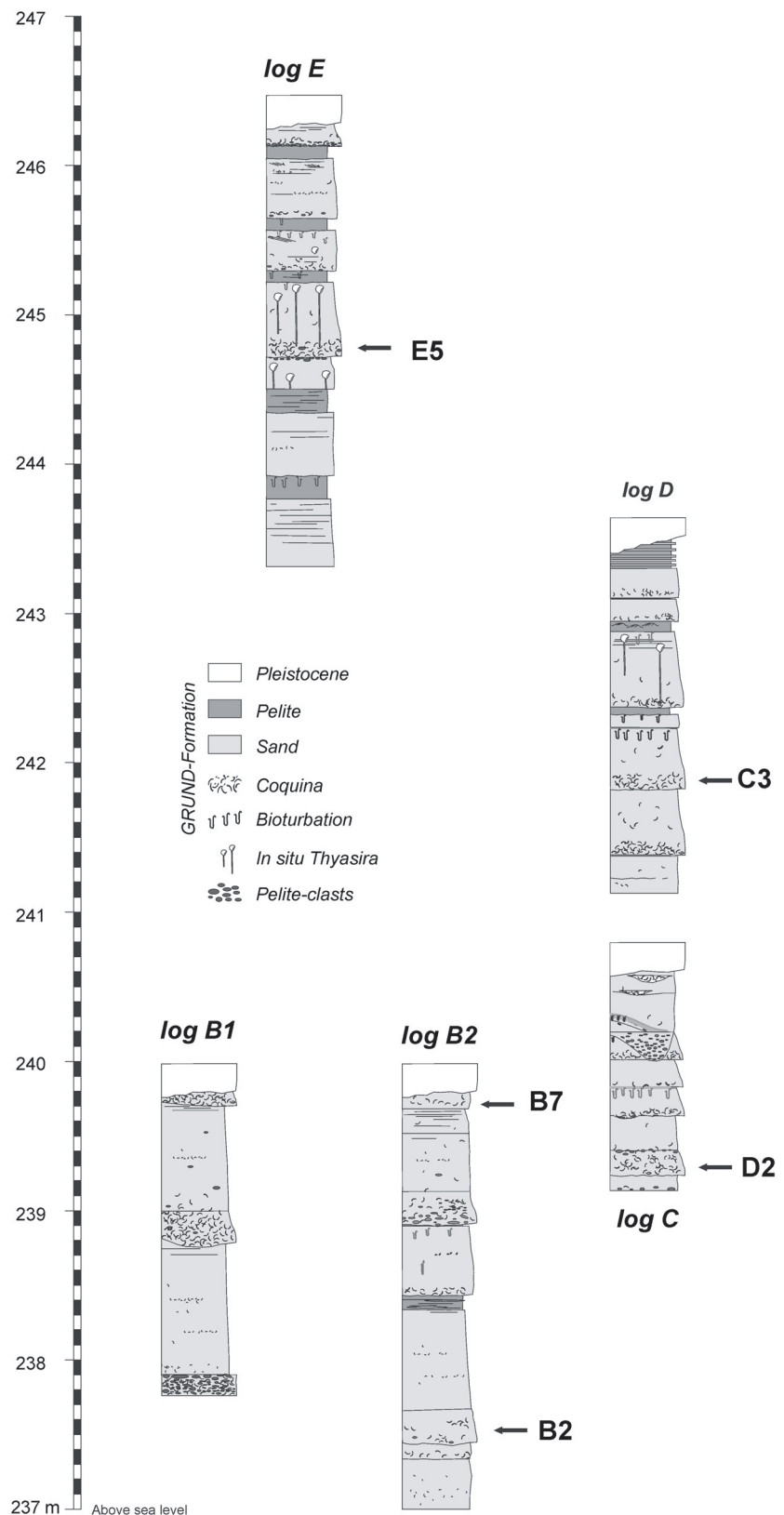


Fig. 2. The five studied logs are characterized by a rapid change of allochthonous psammitic and autochthonous pelitic sedimentation. The sandy layers contain thick polytaxic skeletal concentrations. Many double-valved shells of *Thyasira michelottii* occur in sandy sediments in an anterior up position approximately 5–10 cm below a pelitic bed. Arrows indicate the positions of the quantitative bulk samples.

additional 110 poorly preserved gastropods were summarized into 11 taxa at the genus and family levels because the shelly material was taphonomically strongly altered by abrasion (*Granulolabium?* sp. (2 individuals), Potamididae indet. (11), *Turritella* sp. (4), *Calyptrea* sp. (1), Naticidae indet. juv. (15), Nassariidae indet. juv. (61), *Perrona* sp. (1), Turridae indet. (4), *Scala* sp. (1), Pyramidellidae indet. (1), Gastropoda indet. (9)). These 11 taxa from poorly preserved material were excluded from the diversity analysis.

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-split curves) were computed for each sample using the program EstimateS, with 50 sample order randomizations without replacement (Colwell 1997). Species-split curves can be directly compared with each other because of standardized sampling intensity (the same number of splits from standardized bulk samples was used).

To evaluate the influence of transport on the diversity of the shell beds, the size frequency distributions of all molluscs combined, for bivalves only, gastropods only, and for the five quantitatively most important taxa were calculated for each sample. For this, the maximum diameter of each shell was measured by image analyses (Kontron Elektronik Imaging System KS 400) and standard calipers. Standard descriptive parameters (mean, median, mode, sorting, skewness, kurtosis) were calculated and the size frequency distributions of molluscs were compared by analysis of variance (ANOVA) between shell beds after loglog transformation to retain normally distributed data. To identify which of the shell parameters control the diversity of samples, a regression analysis (method stepwise) was performed with species richness as the dependent variable.

The statistical analyses were performed using the software package SPSS 10.0 (SPSS Base 10 Applications Guide, Prentice Hall, Chicago, 2000).

Results

Five artificial outcrops of Lower Badenian deposits were examined (Fig. 2), with special emphasis on sedimentological features, taphonomic characteristics and paleontological composition. The studied section of the Grund Formation shows a total thickness of approximately 9.5 m and is characterized by a rapid change of allochthonous psammitic and autochthonous pelitic sedimentation (Fig. 2). The sandy layers, especially in the lower part of the section, show abundant channel-structures and consist predominantly of thick polytaxic skeletal concentrations (*sensu* Kidwell et al. 1986), commonly with sharp erosional bases, graded bedding and a densely packed (bioclast-supported) biofabric (Fig. 3). Towards the top of the section the polytaxic skeletal concentrations are distinctly

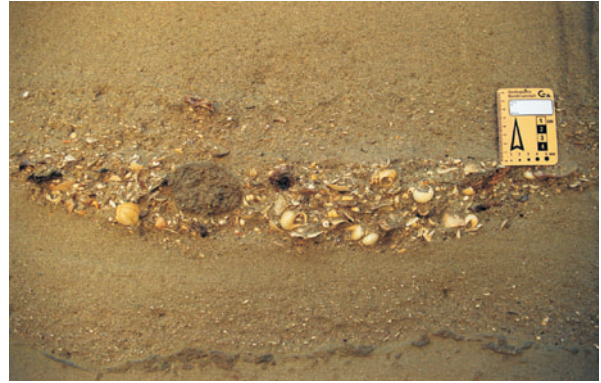


Fig. 3. Sharp erosional bases, graded bedding, and densely packed (bioclast-supported) biofabric of skeletal concentrations are typical features of the psammitic layers at Grund.

thinner and characterized by tabular beds and low-dip angle cross-bedding instead of channel-structures (Roetzel et al. 1999). The intercalated pelitic layers increase in thickness towards the top of the section and are characterized by intensive bioturbation. Many articulated shells of *Thyasira michelottii* occur in sandy sediments in a vertical position with the anterior end pointing upwards approximately 5–10 cm below a pelitic bed (Fig. 4).

Two species, *Timoclea marginata* and *Loripes dentatus*, strongly dominate the molluscan fauna of the shell beds at Grund. In the total assemblage, they make up 56 % of the shells, contributing 52.2–65.6 % to the shells in each of the 5 samples (Fig. 5, Fig. 6). The next three important species, *Sandbergeria perpusilla*, *Clausinella vindobonensis* and *Ervilia pusilla*, each contribute between 3.6 and 6.3 % to the total assemblage. Most species, however, contribute less than 1 % to the total fauna and to the fauna in each of the five samples (Fig. 5).

Diversity was evaluated for the total fauna and for the samples of the individual shell beds. Although the number of counted individuals is relatively high, species richness does not level off for the site (“alpha diversity”) or individual samples (“point diversities”) (Table 1, Fig. 7). In contrast to species richness, heterogeneity diversity is very stable within samples and for the site: the Shannon–Wiener index and the Simpson index do not increase with sample size (Fig. 7).

Huge differences are evident between the total number of species present (125) and the number of species in individual

Table 1: Number of individuals, number of species, values of the Shannon–Wiener index, and values of the Simpson index for each standardized sample.

| Sample | Number of individuals | Number of species | Shannon–Wiener index | Simpson index |
|--------|-----------------------|-------------------|----------------------|---------------|
| E5 | 763 | 43 | 2.00 | 4.04 |
| C3 | 467 | 48 | 2.37 | 5.23 |
| B7 | 982 | 83 | 2.74 | 5.71 |
| D2 | 915 | 71 | 2.48 | 5.11 |
| B2 | 978 | 74 | 2.67 | 5.09 |
| Total | 4105 | 125 | 2.59 | 5.09 |



Fig. 4. Photograph of *Thyasira michelottii* (Hoernes 1875) in situ, showing the life position of the specimen, the perfectly preserved inhalant tube, and the single long tunnel extending from the animal downwards deep into the underlying sediment.

samples, which range from 43 to 83 (Table 1). Also, the slopes of the diversity curves (species-split curves) differ strongly between samples (Fig. 7, see also Zuschin et al. submitted). For heterogeneity diversity, the comparatively low values of the Shannon-Wiener index and the Simpson index of sample E5, and the relatively high Simpson index of sample B7 are most evident (Table 1).

The size-frequency distributions of all molluscan shells combined, for gastropods only, for bivalves only and for each of the five quantitatively most important species differ significantly between samples from individual shell beds (Fig. 8, Fig. 9, Table 2).

Of the descriptive parameters (Table 3), only sorting is clearly related to diversity (Table 4). Between samples of individual shell beds, sorting explains nearly 85 % of the variance in species richness, nearly 98 % of the variance of the Shannon-Wiener index, and more than 77 % of the variance of the Simpson index (Fig. 10).

Most shells are taphonomically altered and show distinct evidence of abrasion (Fig. 6).

Discussion

The tempestitic shell beds

Channel-structures, sharp erosional bases, and graded bedding identify the shell-rich psammitic layers as the product of high energy, short-term events; most likely they represent proximal tempestites (Kidwell 1991; Fürsich & Oschmann

Table 2: Analysis of variance (ANOVA) of the size-frequency distributions of molluscan taxa in shell beds after loglog transformation. df — degrees of freedom used to obtain the observed significance level, F — the ratio of mean squares between groups to mean squares within groups, *p* — significance level.

| Taxon | df | F | <i>p</i> |
|----------------------------------|----|---------|----------|
| Mollusca | 4 | 177.533 | <0.0001 |
| Bivalvia | 4 | 135.488 | <0.0001 |
| Gastropoda | 4 | 42.114 | <0.0001 |
| <i>Timoclea marginata</i> | 4 | 69.162 | <0.0001 |
| <i>Loripes dentatus</i> | 4 | 14.948 | <0.0001 |
| <i>Sandbergeria perpusilla</i> | 4 | 6.386 | <0.0001 |
| <i>Clausinella vindobonensis</i> | 4 | 21.568 | <0.0001 |
| <i>Ervilia pusilla</i> | 4 | 5.320 | <0.0001 |

Table 3: Descriptive parameters of the size-frequency distribution of all molluscs combined.

| | B2 | D2 | B7 | C3 | E5 | Total |
|----------|------|-------|-------|-------|-------|-------|
| N | 978 | 915 | 982 | 467 | 763 | 4105 |
| Mean | 4.67 | 3.39 | 4.30 | 2.92 | 2.60 | 3.71 |
| Median | 3.89 | 2.84 | 3.35 | 2.33 | 2.35 | 2.90 |
| Mode | 2.43 | 1.92 | 1.73 | 1.77 | 2.14 | 1.92 |
| Sorting | 2.75 | 2.06 | 3.09 | 1.85 | 0.97 | 2.49 |
| Skewness | 2.00 | 4.92 | 3.23 | 5.01 | 2.68 | 3.44 |
| Kurtosis | 6.33 | 42.66 | 19.19 | 41.58 | 12.63 | 21.48 |

Table 4: Results of regression analysis with diversity (species richness, heterogeneity diversity) as the dependent variable. Among the descriptive parameters of the shell size frequency distribution, only sorting is a significant predictor for diversity. Bold numbers indicate the statistically significant differences. *t* — the results of the *t*-statistics, *p* — significance level.

| Species richness | <i>t</i> | <i>p</i> |
|------------------|----------|--------------|
| (Constant) | 2.07 | 0.130 |
| Mean | 0.23 | 0.149 |
| Median | 0.31 | 0.309 |
| Mode | 0.12 | 0.992 |
| Sorting | 4.05 | 0.027 |
| Skewness | -0.06 | 0.971 |
| Kurtosis | -0.03 | 0.976 |

| Shannon-Wiener index | <i>t</i> | <i>p</i> |
|----------------------|----------|--------------|
| (Constant) | 25.13 | 0.000 |
| Mean | -0.22 | 0.844 |
| Median | -0.14 | 0.900 |
| Mode | -0.03 | 0.980 |
| Sorting | 11.72 | 0.001 |
| Skewness | 1.24 | 0.341 |
| Kurtosis | 1.43 | 0.289 |

| Simpson index | <i>t</i> | <i>p</i> |
|---------------|----------|--------------|
| (Constant) | 7.91 | 0.004 |
| Mean | -4.29 | 0.050 |
| Median | -3.97 | 0.058 |
| Mode | -2.54 | 0.126 |
| Sorting | 3.20 | 0.049 |
| Skewness | 3.83 | 0.062 |
| Kurtosis | 3.15 | 0.088 |

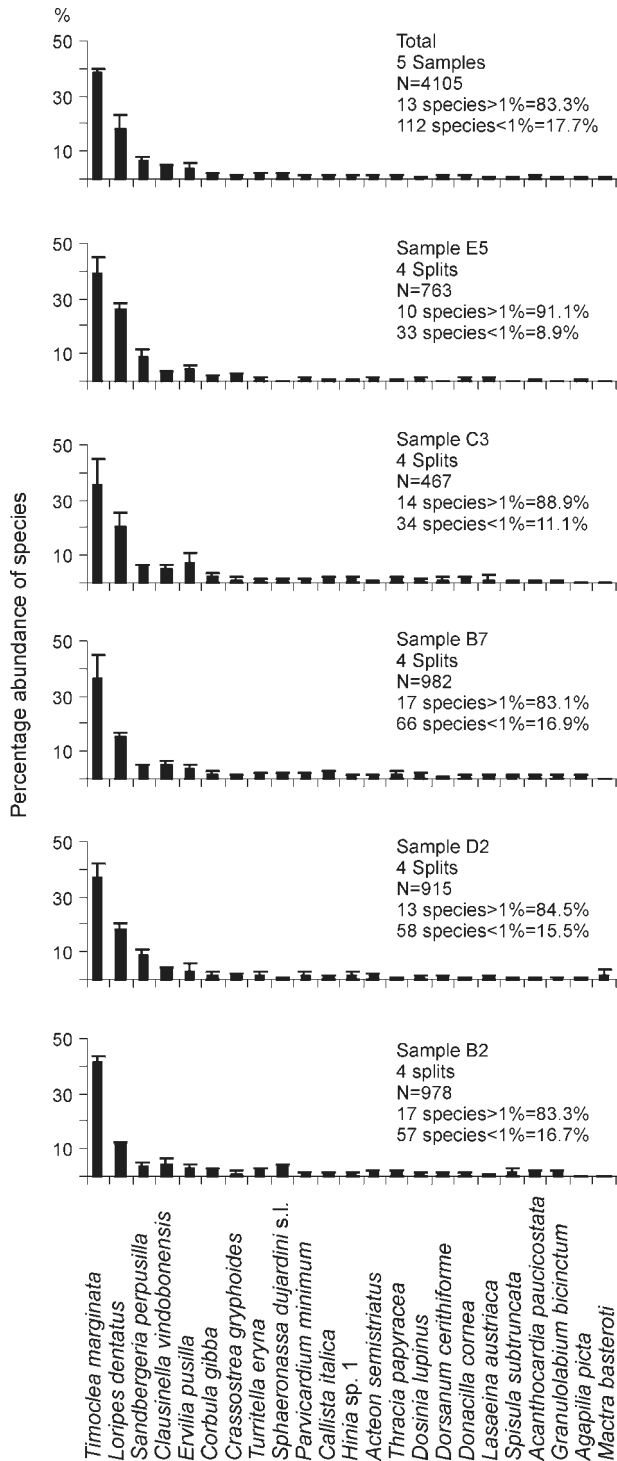


Fig. 5. Taxonomic composition and percentage abundance of the quantitatively important taxa with 95% confidence intervals in shell beds.

1993; Fürsich 1995). Decreasing hydrodynamic energy towards the top of the section is indicated by the geometries of the skeletal concentrations, which are distinctly thinner and characterized by tabular beds and low-dip angle cross-bedding instead of channel-structures (Roetzel et al. 1999). Correspondingly, the intercalated and intensely bioturbated pelitic

layers, which indicate quiet-water conditions, increase in thickness towards the top of the section.

The molluscan fauna of Grund

From a historical perspective, the molluscan fauna from various localities in the area of Hollabrunn such as Immendorf, Guntersdorf, Braunsdorf, and Windpassing have been labelled in collections and were referred to in the literature simply as "Grund". Hence, the fauna of the Grund Formation contains taxa not only from its type locality at Grund, but also from the above localities. All in all the so-called "Grunder fauna" consists of 138 bivalve species and about 170 gastropod species (database in preparation). The taxonomic inventory seems to be quite complete because during the recent intense investigations only four new species were added to this faunal list (Mandic 2004).

From a taphonomic perspective, however, the molluscan fauna of the type locality Grund can be divided into the monospecific occurrence of autochthonous, chemosymbiotic *Thyasira michelottii* and the polytaxic fauna of the bioclast-supported allochthonous, tempestitic shell beds.

The bivalve *T. michelottii* is the only molluscan species of the diverse fauna at Grund occurring in life position. This is confirmed by articulated valves and preservation of the inhalant and postero-ventral tunnel networks (Fig. 4, see also Pervesler & Zuschin 2004). This bivalve burrowed in sandy sediments in an anterior up position approximately 5–10 cm below a pelitic bed, to which it was connected by the inhalant tube. Based on the comparative ecology of modern thyasirid bivalves we suppose that active ventilation of the inhalant tube was the mode of oxygen acquisition and that the prominent postero-ventral tunnel reflects the search of the vermiform foot for short-lived pockets of sulphidic material in an otherwise low-sulphide environment (see Zuschin et al. 2001 for a detailed discussion of the life habit of this bivalve).

In contrast to the depauperate autochthonous fauna, the skeletal concentrations contain a highly diverse molluscan fauna, which is strongly dominated by two bivalve species, *Timoclea marginata* and *Loripes dentatus*. These quantitatively most important species differ strongly from those species that were considered to be important elements of the fauna by shell collectors and taxonomists. For example, the first report of molluscs from Grund (Foetterle 1850) mentioned a crate of molluscs of 59 Pfund, which was stored at the Geological Survey in Vienna, and emphasized the large numbers of *Turritella vindobonensis*, *Pyrula rusticola* and *Crepidula* among other gastropods and of *Cytherea chione* and *Venus brocchii* among the bivalves. This weighting of certain conspicuous, large-sized taxa is the typical collector's approach and is strongly contrasted by the quantitative data presented in the current study. Similarly, Hörnes (1851) enumerated *Ancillaria glandiformis*, *Murex trunculus*, *Pyrula rusticola* and *Fasciolaria burdigalensis* along with 10 other species as the most frequent taxa in the Grund fauna. In fact, these species comprise less than 1% of the quantitative samples. Even those species noted by Sieber (1947a,b, 1949) as frequent or very frequent in the Grund fauna are hardly important in respect to a rigorous quantitative treatment.

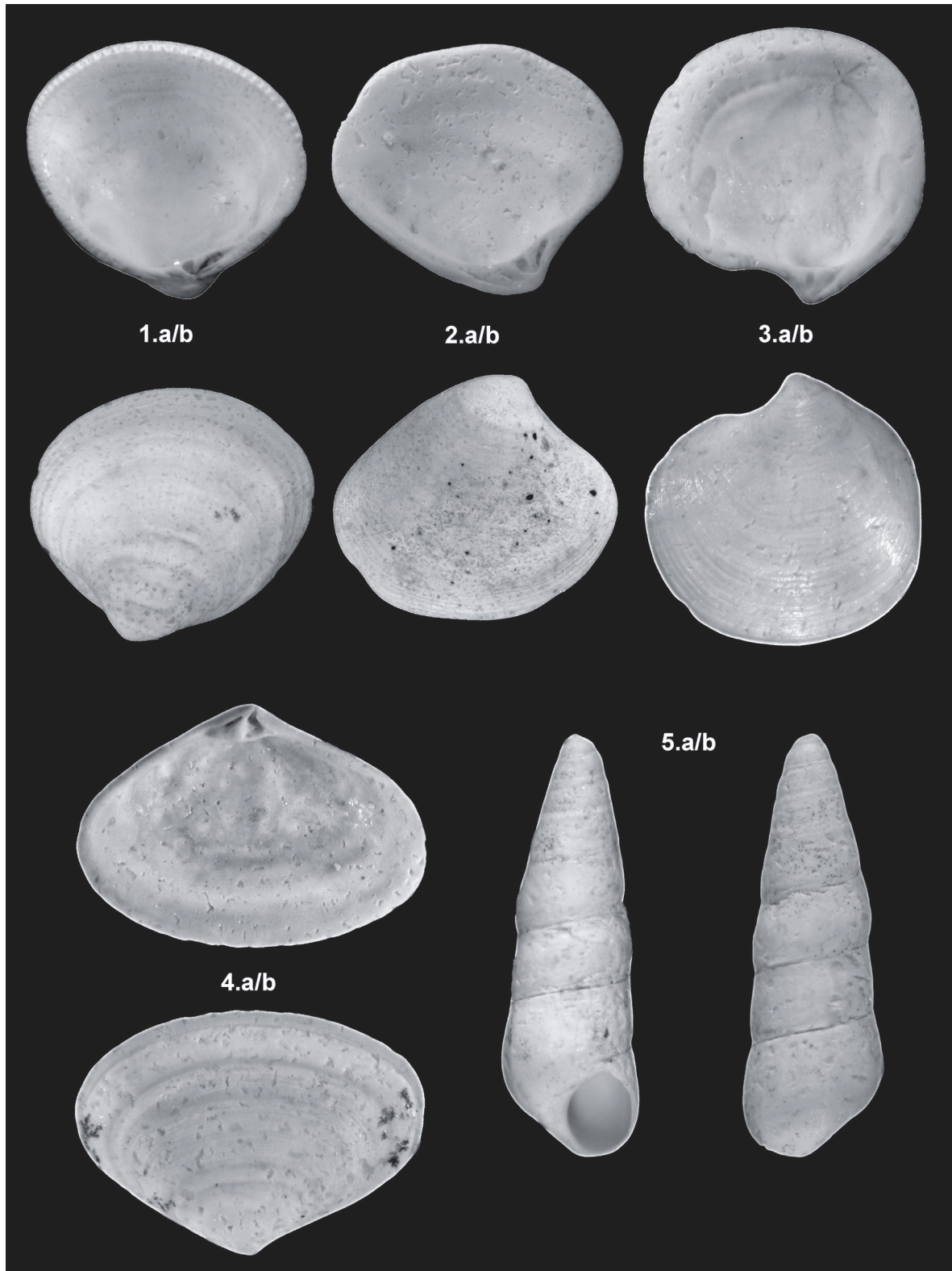


Fig. 6. The quantitatively most important species with typical taphonomic features. The external views of the species demonstrate the strong abrasive reduction of sculptural features (best seen in *Timoclea* and *Clausinella*). Additionally, the numerous point-like holes in the shells (here best seen on *Ervilia*) result from compactional pressure of quartz-sand grains into the shells. **1** – *Timoclea marginata* [L = 5.2 mm]. **a** – internal view of right valve; **b** – external view of right valve. **2** – *Clausinella vindobonensis* [L = 7.6 mm]. **a** – internal view of right valve; **b** – external view of right valve. **3** – *Loripes dentatus* [L = 3.7 mm]. **a** – internal view of right valve; **b** – external view of right valve. **4** – *Ervilia pusilla* [L = 3.7 mm]. **a** – internal view of right valve; **b** – external view of right valve. **5** – *Sandbergeria perpusilla* [L = 4.0 mm]. **a** – apertural view; **b** – adapertural view.

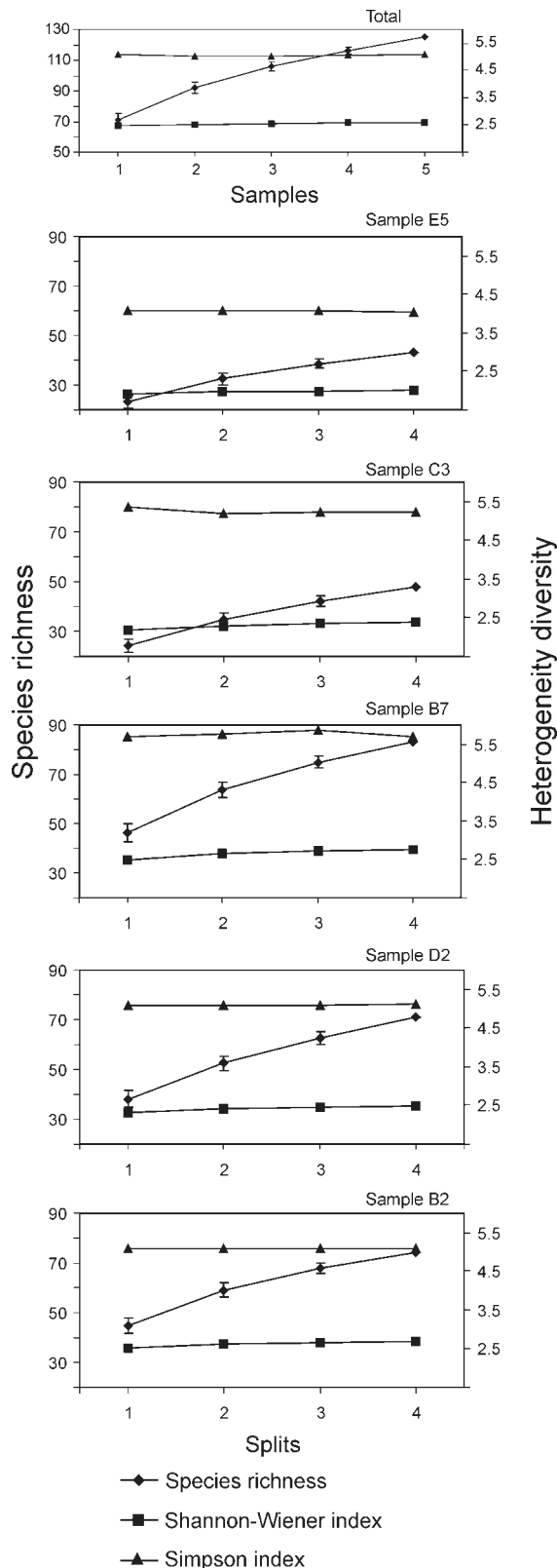


Fig. 7. Species richness (number of species) and heterogeneity diversity (measured with the Shannon-Wiener index and the Simpson index) for the total tempestitic fauna and for the samples of the individual shell beds. Within samples and for the site, species richness does not level off, but heterogeneity diversity is very stable. The slopes of the species-split curves differ strongly between samples.

From an ecological point of view most of the fauna in the shell beds at Grund indicates a shallow to moderately deep sublittoral, soft bottom environment (e.g. infaunal suspension-feeding venerids and cardiids, chemosymbiotic lucinids, deposit-feeding tellinids, suspension-feeding turritellids, scavenging nassariid). But species with other habitat characteristics also occur. The herbivorous Potamididae probably lived in a nearshore brackish-water environment, and some terrestrial gastropods of the genus *Cepaea* (as well as disarticulated bones of terrestrial mammals) are also found in the skeletal concentrations. The abrasive features of most shells in the skeletal concentrations can be interpreted to stem from continuous reworking by waves or currents in the source area of the tempestites, because the tempestitic transport itself is very unlikely to affect the preservation quality of single shells (Davies et al. 1989; for review see Fürsich & Oschmann 1993).

Species richness versus heterogeneity diversity

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 both, individual samples and the site (Fig. 6). This indicates that incorporating more samples or more individuals per sample would simply add more rare species, but would not change the rank order of the most abundant and the middle ranked species.

The influence of transport on diversity measurements

The diversity (species richness and heterogeneity diversity) of the shell beds at the locality Grund decreases with increasing sorting of the shells indicated by the size-frequency distribution. This feature clearly points to transport of the assemblages (e.g. Cummins et al. 1986; Miller & Cummins 1990). The alternative scenario, that is that differences in sorting are only apparent because the shell beds consist of different taxa, can be ruled out because 1) the quantitatively most important species are the same in the five shell beds, 2) the ecological composition of the fauna in the different shell beds is very similar and 3) the size frequency distribution of all molluscs combined, gastropods only, bivalves only, and the five quantitatively most important species follows the same pattern of differences between samples. It is therefore safe to conclude that the studied shell beds consist of shells from the same source area and that their differences in species richness reflect different transport histories, most probably due to different storm intensities. Therefore, all the samples are inappropriate for measuring the diversity of the original habitat, although poorly sorted samples (indicating relatively minor transport) will approximate the diversity of single samples of the habitat better than well-sorted samples (which indicate stronger transport).

Paleoenvironment

The short distance of estimated 15–20 km to the paleo-coastline, along with the faunal composition of the skeletal

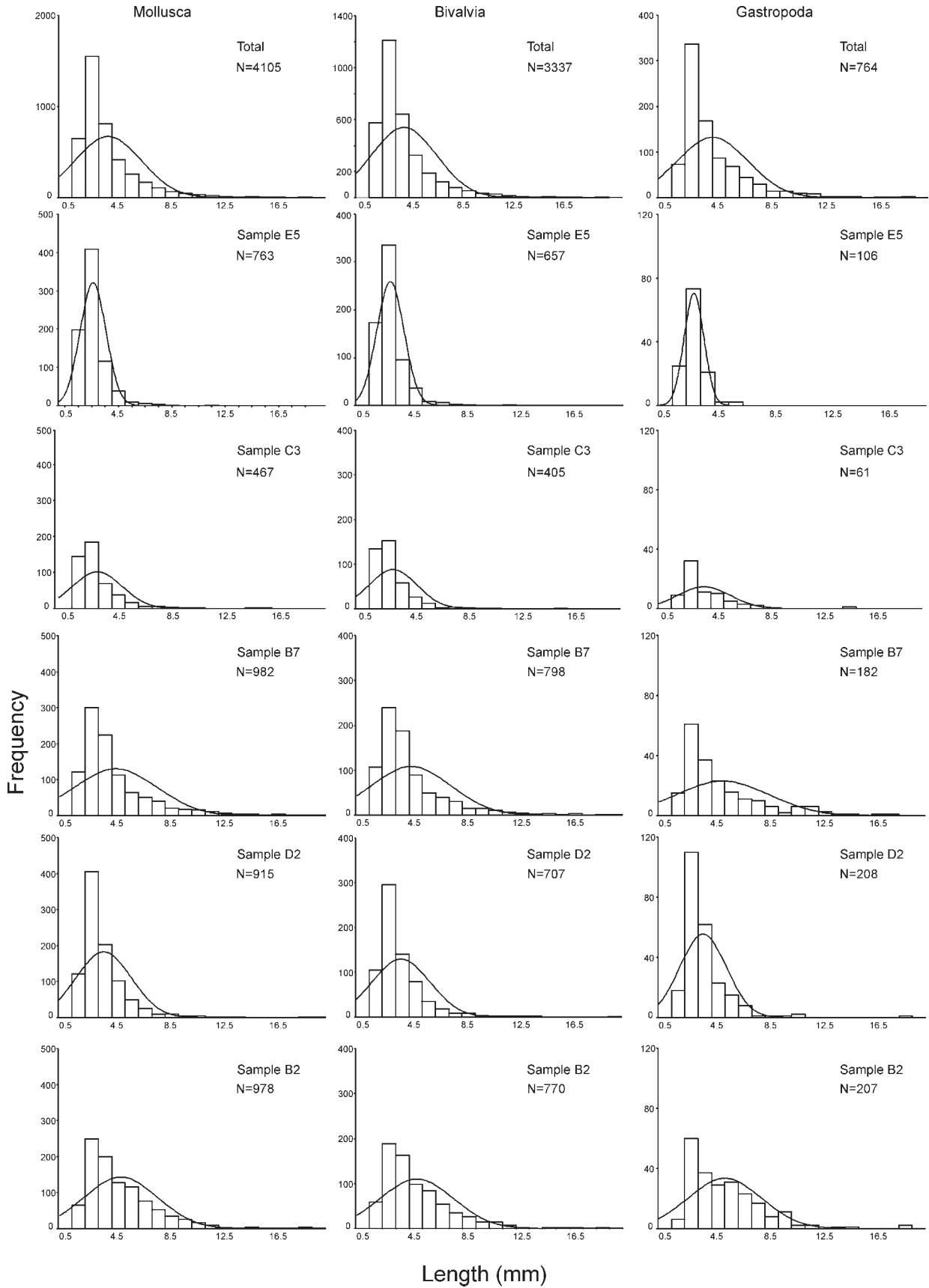


Fig. 8. Size-frequency distribution with normal curve of all molluscs combined, gastropods only, and bivalves only for each sample of shell beds as well as for the total tempestitic fauna.

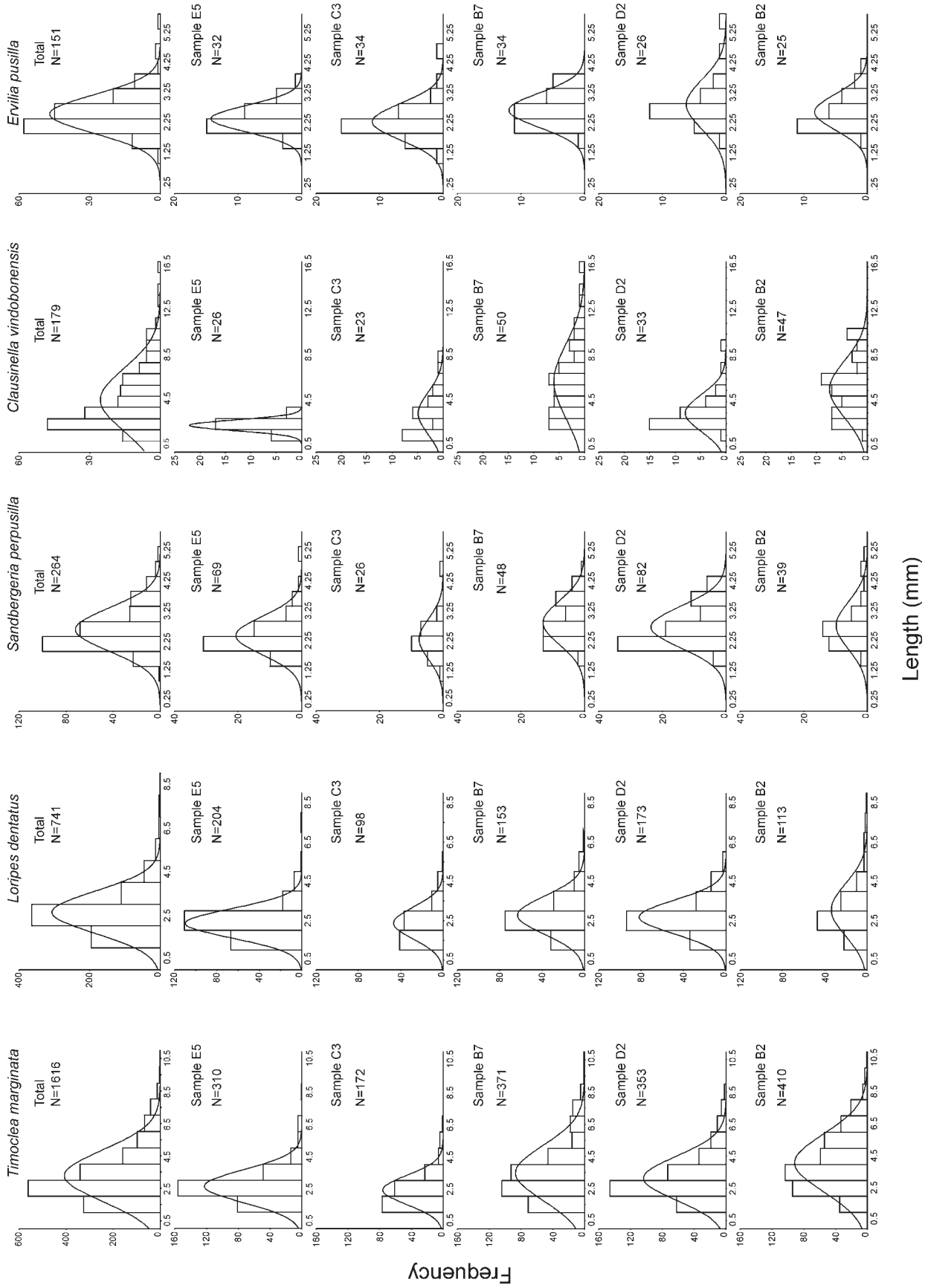


Fig. 9. Shell size-frequency distribution with normal curve of the five quantitatively most important species for each sample of shell beds and the total tempestitic fauna.

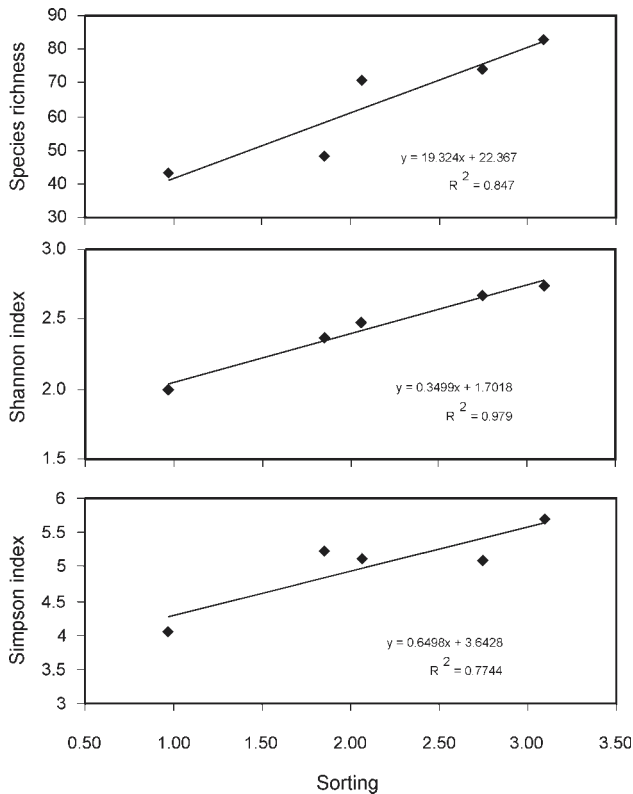


Fig. 10. Diversity (species richness and heterogeneity diversity) as a function of sorting of the shell size frequency distribution of molluscs.

concentrations (mainly representative of a sublittoral soft bottom environment), whose geometries suggest proximal tempestites, indicate a shelf environment of less than one hundred meters water depth (Spezzaferri 2004). The deepening-upward trend in the section is interpreted as coinciding with the major transgressive cycle of the Lower Badenian; a proximal facies at the base passes into a slightly more distal facies towards the top of the Grund section. Alternatively, the change in sedimentation may be due to a local influence, such as the fluctuating input and changing course of a fluvial system in the hinterland.

The autochthonous occurrence of monospecific *Thyasira* indicates that the chemical and physical conditions of the sediment were preferred by this thyasirid species, but were unsuitable for other molluscs. The bivalves' prominent postero-ventral tunnel network (Fig. 4, see also Pervesler & Zuschin 2004) probably reflects the search of the vermiform foot for short-lived pockets of sulphidic material in an otherwise low-sulphide environment (cf. Cary et al. 1989; see Zuschin et al. 2001 for a detailed discussion). The combination of bioturbated pelitic sediments and a monospecific macro-fauna suggests a dysaerobic biofacies (Tyson & Pearson 1991). Global warming, coinciding with a far-reaching transgression at the base of the Middle Miocene, indicates warm water conditions (Rögl 1998).

Conclusions

1. The original, restricted outcrops at the locality Grund were sufficient to identify the taxonomic composition of the shelly assemblage. A reliable paleoecological and taphonomic treatment of the fauna, however, was only possible with artificial outcrops, which allowed the taphonomic framework of the deposit to be evaluated.

2. Instead of the anticipated simple parautochthonous paleo-community, the fauna has to be divided into a monospecific autochthonous assemblage of *Thyasira michelottii* in life position, and a distinctly transported and highly diverse assemblage present in shell beds.

3. For the five samples from individual shell beds the taxonomic composition of the most abundant species and the taphonomic features of the shells are very similar, but species richness and the size frequency distribution of the shells differ strongly. Therefore, the ecological characteristics and taphonomical features of the molluscan fauna in the shell beds allow the original habitats and the source area of the tempestites to be reconstructed. The diversity, however, depends on sorting and is therefore very sensitive to transport.

4. The present study shows that extensive field work is necessary to evaluate the paleoecological and taphonomic features of shelly assemblages and that especially diversity measurements should not be made from samples taken from restricted outcrops.

Acknowledgments: We thank Gudrun Höck, Peter Pervesler and Reinhard Roetzel for help with field work, Fred Rögl and Michael Stachowitsch for stimulating discussions, Johann Hohenegger for comments on our statistical results, and Franz T. Fürsich and Barbara Studencka for their careful review of the manuscript. The study was supported by project P-13745-Bio of the Austrian Science Fund (FWF).

References

- Cary S.C., Vetter R.D. & Felbeck H. 1989: Habitat characterization and nutritional strategies of the endosymbiont-bearing bivalve *Lucinoma aequizonata*. *Marine Ecology Progress Series* 55, 31–45.
- 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>.
- Čorić S., Harzhauser M., Hohenegger J., Mandic O., Pervesler P., Roetzel R., Rögl F., Scholger R., Spezzaferri S., Stingl K., Švábenická L., Zorn I. & Zuschin M. 2004: Stratigraphy and correlation of the Grund Formation in the Molasse Basin, northeastern Austria (Middle Miocene, Lower Badenian). *Geol. Carpathica* 55, 2, 207–215.
- Cummins H., Powell E.N., Stanton R.J. Jr. & Staff G. 1986: 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. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 72, 317–356.

- Foetterle F. 1850: Verzeichnis der an die k.k. geologische Reichsanstalt gelangten Einsendungen von Mineralien, Petrefacten, Gebirgsarten u. s. w. *Jb. K.-Kön. Geol. Reichsanst.* 1, 350–364.
- Fürsich F.T. 1995: Shell concentrations. *Eclogae Geol. Helv.* 88, 643–655.
- Fürsich F.T. & Oschmann W. 1993: Shell beds as tools in basin analysis: the Jurassic of Kachchh, western India. *J. Geol. Soc., London* 150, 169–185.
- Gray J.S. 2000: The measurement of marine species diversity with an application to the benthic fauna of the Norwegian continental shelf. *J. Experimental Marine Biology and Ecology* 250, 23–49.
- Hörnes M. 1851: Die fossilen Mollusken des Tertiär-Beckens von Wien. *Jb. K.-Kön. Geol. Reichsanst.* 2, 193–134.
- Hörnes M. 1856: Die fossilen Mollusken des Tertiär-Beckens von Wien. Univalven. *Abh. K.-Kön. Geol. Reichsanst.* 3, 1–736.
- Hörnes M. & Reuss A.E. 1859–1870: Die fossilen Mollusken des Tertiär-Beckens von Wien. II. Bivalven. *Abh. K.-Kön. Geol. Reichsanst.* 4, 1–479.
- Hoernes R. 1875: Die Fauna des Schliers von Ottnang. *Jb. K.-Kön. Geol. Reichsanst.* 25, 333–431.
- Hoernes R. & Auinger M. 1879–1882: Gasteropoden der Meeresablagerungen der ersten und zweiten miocänen Mediterranstufen in der österreichisch-ungarischen Monarchie. *Abh. K.-Kön. Geol. Reichsanst.* 12, 1–382.
- Kidwell S.M. 1991: The stratigraphy of shell concentrations. In: Allison P.A. & Briggs D.E.G. (Eds.): *Taphonomy: Releasing the data locked in the fossil record*. Plenum Press, New York and London, 211–290.
- Kidwell S.M., Fürsich F.T. & Aigner T. 1986: Conceptual framework for the analysis and classification of fossil concentrations. *Palaios* 1, 228–238.
- Kowalewski M., Nebelsick J.H., Oschmann W., Piller W.E. & Hoffmeister A.P. 2002: Multivariate hierarchical analyses of Miocene mollusk assemblages of Europe: Paleogeographic, paleoecological, and biostratigraphic implications. *Bull. Geol. Soc. Amer.* 114, 239–256.
- Magurran A.E. 1988: *Ecological diversity and its measurement*. Princeton University Press, Princeton, New Jersey, 1–179.
- Mandic O. 2004: Pectinid bivalves from the Grund Formation (Lower Badenian, Middle Miocene, Alpine-Carpathian Foredeep) — taxonomic revision and stratigraphic significance. *Geol. Carpathica* 55, 2, 129–146.
- Miller A.I. & Cummins H. 1990: A numerical model of the formation of fossil assemblages: Estimating the amount of post-mortem transport along environmental gradients. *Palaios* 5, 303–316.
- Peet R.K. 1974: The measurement of species diversity. *Ann. Reviews of Ecology and Systematics* 5, 285–307.
- Pervesler P. & Zuschin M. 2004: A lucinoid bivalve trace fossil *Saronichnus abeli* igen. et isp. nov. from the Miocene molasse deposits of Lower Austria, and its environmental significance. *Geol. Carpathica* 55, 2, 111–115.
- Roetzel R. & Pervesler P. 2004: Storm-induced event deposits in the type area of the Grund Formation (Middle Miocene, Lower Badenian) in the Molasse Zone of Lower Austria. *Geol. Carpathica* 55, 2, 87–102.
- Roetzel R., Pervesler P., Daxner-Höck G., Harzhauser M., Mandic O., Zuschin M. & Cicha I. 1999: C4 Grund — Kellergasse. In: Roetzel R. (Ed.): *Arbeitstagung Geol. Bundesanst.* 1999, Retz-Hollabrunn, 3.–7. Mai 1999. *Geol. Bundesanst.*, Wien, 328–334.
- Rögl F. 1998: Palaeogeographic considerations for Mediterranean and Paratethys Seaways (Oligocene to Miocene). *Ann. Naturhist. Mus. Wien* 99A, 279–310.
- Sieber R. 1937: Neue Beiträge zur Stratigraphie und Faunengeschichte des österreichischen Jungtertiärs. *Petroleum* 13, 1–8, 17–26.
- Sieber R. 1947a: Die Fauna von Windpassing bei Grund in Niederösterreich (Bez. Hollabrunn). *Verh. Geol. Bundesanst.* 1945, 7–9, 155–163.
- Sieber R. 1947b: Die Grunder Fauna von Braunsdorf und Groß-Nondorf in Niederösterreich (Bezirk Hollabrunn). *Verh. Geol. Bundesanst.* 1945, 1–3, 46–55.
- Sieber R. 1949: Eine Fauna der Grunder Schichten von Guntersdorf und Immendorf in Niederösterreich. *Verh. Geol. Bundesanst.* 1946, 7–9, 107–122.
- Sieber R. 1955: Systematische Übersicht der jungtertiären Bivalven des Wiener Beckens. *Ann. Naturhist. Mus. Wien* 60, 169–201.
- Spezzaferri S. 2004: Foraminiferal paleoecology and biostratigraphy of the Grund Formation (Molasse Basin, Lower Austria). *Geol. Carpathica* 55, 2, 155–164.
- Zuschin M., Harzhauser M. & Mandic O. submitted: Influence of size-sorting on diversity estimates from tempestitic shell beds. *Palaios*.
- Zuschin M., Mandic O., Harzhauser M. & Pervesler P. 2001: Fossil evidence for chemoautotrophic bacterial symbiosis in the thyasirid bivalve *Thyasira michelottii* from the Middle Miocene (Badenium) of Austria. *Historical Biology* 15, 223–234.

Appendix: The species list contains the 130 distinct morphospecies used in this study plus 11 taxa of poorly preserved gastropods, which were mostly summarized at the genus and family level because the shelly material was taphonomically strongly altered (*Granulolabium?* sp., Potamididae indet., *Turritella* sp., *Calyptrea* sp., Naticidae indet. juv., Nassariidae indet. juv., *Perrona* sp., Turridae indet. *Scala* sp., Pyramidellidae indet., Gastropoda indet.).

| Subclass | Superfamily | Family | Species | Subclass | Superfamily | Family | Species |
|------------|----------------|----------------|---|----------|-------------------|----------------|--|
| Gastropoda | Fissurelloidea | Fissurellidae | <i>Scutum bellardii</i> <i>Diodora</i> sp. | | | | Pyramidellidae indet. |
| | Trochoidea | Phasianellidae | <i>Tricolia</i> sp. | | Philinoidea | Acteonidae | <i>Acteon semistriatus</i> <i>Acteon tornatilis</i> |
| | | Trochidae | <i>Paroxystele amedei</i> | | | Retusidae | <i>Retusa truncatula</i> |
| | | Vitrinellidae | <i>Tornus pseudotinostoma</i> <i>Circulus planorbillus</i> | | | Ringiculidae | <i>Ringicula auriculata</i> ssp. |
| | Neritoidea | Neritidae | <i>Agapilla picta</i> | | | Scaphandridae | <i>Acteocina lajonkaireana heraclitica</i> |
| | Rissooidea | Rissoidae | <i>Alvania (Taramellia) alexandrae</i> <i>Alvania curta</i> <i>Alvania montagui</i> ssp. <i>Alvania venus transiens</i> <i>Alvania zetlandica</i> <i>Alvania</i> sp. <i>Sandbergeria perpusilla</i> <i>Turboella acuticosta</i> <i>Turboella</i> sp. (cf. <i>johannaedilemma</i>) | | Helicoidea | Helicidae | <i>Cepaea</i> cf. <i>etelkae</i> |
| | | | | | Gastropoda indet. | | Gastropoda indet. |
| | Cerithioidea | Cerithiidae | <i>Semibittium</i> sp. <i>Hemicerithium</i> sp. <i>Bittium spina</i> <i>Bittium</i> cf. <i>reticulatum</i> | Bivalvia | Nuculanoidea | Mallettiidae | <i>Saturnia</i> cf. <i>pusio</i> |
| | | Potamididae | <i>Granulolabium bicinctum</i> <i>Granulolabium?</i> sp. <i>Potamides theodiscus?</i> Potamididae indet. | | | Nuculanidae | <i>Nuculana (Lembulus) emarginata</i> <i>Nuculana (Saccella) fragilis</i> <i>Nucula (Nucula) nucleus</i> |
| | | Turritellidae | <i>Turritella eryna</i> <i>Turritella spirata</i> <i>Turritella</i> sp. | | | Nuculoidea | Nuculidae |
| | | | | | Arcoidea | Arcidae | <i>Anadara (Anadara) adametzi</i> <i>Anadara (Anadara) diluvii</i> |
| | Crepiduloidea | Crepidulidae | <i>Calyptrea chinensis</i> <i>Calyptrea</i> sp. <i>Crepidula (Janacus) crepidula</i> | | | Noetiidae | <i>Striarca lactea</i> |
| | | | | | Mytiloidea | Mytilidae | <i>Gregariella</i> sp. |
| | Naticoidea | Naticidae | <i>Neverita olla</i> <i>Natica tigrina</i> <i>Euspira helicina</i> <i>Polinices redemptus</i> Naticidae indet. | | Pectinoidea | Pectinidae | <i>Aequipecten malvinae</i> <i>Aequipecten</i> aff. <i>zenonis</i> <i>Crassadoma multistriata</i> |
| | | | | | | | |
| | Cypraeoidea | Triviidae | <i>Trivia (Sulcotrivia) dimidiatoaffinis</i> | | Limoidea | Limidae | <i>Limea (Limea) strigilata</i> |
| | Tonnoidea | Cymatiidae | Cymatiidae indet. | | Anomioidea | Anomiidae | <i>Anomia (Anomia) ephippium</i> |
| | Muricoidea | Buccinidae | Buccinidae indet. | | Ostroidea | Ostreidae | <i>Crassostrea gryphoides</i> |
| | | Cancellariidae | <i>Narona (Aneurystoma) austropolonica</i> | | | Gryphaeidae | <i>Neopycnodonte navicularis</i> |
| | | Columbellidae | <i>Mitrella</i> sp. juv. | | Lucinoidea | Lucinidae | <i>Divalinga ornata</i> <i>Loripes (Microloripes) dentatus</i> <i>Pterolucina schencki</i> |
| | | Nassariidae | <i>Dorsanum cerithiforme</i> <i>Hinia notterbecki</i> <i>Hinia rosthorni</i> <i>Hinia serraticosta</i> <i>Hinia signata</i> <i>Hinia</i> sp. 1 (cf. <i>toulai</i>) <i>Hinia</i> sp. 2 (cf. <i>styriaca</i>) <i>Hinia</i> sp. 3 <i>Hinia</i> sp. 4 <i>Hinia</i> sp. 5 <i>Hinia</i> sp. 6 <i>Hinia</i> sp. 7 <i>Sphaeronassa dujardini</i> s.l. Nassariidae indet. | | | Thyasiridae | <i>Thyasira (Thyasira) michelottii</i> |
| | | | | | | Ungulinidae | <i>Felaniella trigonula</i> <i>Diplodonta rotundata</i> |
| | | | | | Chamoidea | Chamidae | <i>Chama (Psolopus) gryphoides</i> |
| | | | | | Galeommatoidea | Galeommatidae | <i>Spaniorinus bobiesi</i> |
| | | | | | | Kelliidae | <i>Pseudolepton bayeri</i> <i>Pseudolepton insigne</i> <i>Properycina sallomacensis</i> |
| | | | | | | Leptonidae | <i>Lasaena austriaca</i> |
| | | | | | | Sportellidae | <i>Lasaena austriaca</i> |
| | | | | | Carditoidea | Carditidae | <i>Cardita elongata</i> <i>Scalaricardita scalaris</i> |
| | | | | | | | |
| | | | | | Cardioidea | Cardiidae | <i>Acanthocardia pancicostata</i> <i>Cerastoderma praeplicata</i> <i>Parvicardium minimum</i> <i>Parvicardium papillosum</i> |
| | | | | | | | |
| | | | | | Mactroidea | Mactridae | <i>Lutraria (Lutraria) lutraria</i> <i>Maetra (Eomactra) basteroti</i> <i>Spisula (Spisula) subtruncata</i> |
| | | | | | | | |
| | | | | | | Mesodesmatidae | <i>Donacilla cornea</i> |
| | | | | | Solenioidea | Rzehakiidae | <i>Rzehakia dubiosa</i> |
| | | | | | Tellinoidea | Donacidae | <i>Donax (Paradonax) intermedia</i> <i>Donax (Paradonax) sallomacensis</i> <i>Donax (Paradonax) variegatus</i> |
| | | | | | | | |
| | | | | | | Psammbiidae | <i>Gari (Psammbia) uniradiata</i> |
| | | | | | | Mesodesmatidae | <i>Ervilia pusilla</i> |
| | | | | | | Tellinidae | <i>Angulus (Peronidia) bipartitus</i> <i>Angulus (Moerella) donacinus</i> <i>Quadrans (Serratina) schoenni</i> |
| | | | | | Dreissenoidae | Dreissenidae | <i>Mytilopsis sandbergeri</i> |
| | | | | | Arcticoidea | Kelliellidae | <i>Alveinus nitidus</i> |
| | | | | | Veneroidea | Petricolidae | <i>Petricola (Rupellaria) lithophaga</i> |
| | | | | | | Veneridae | <i>Callista italica</i> <i>Clausinella basteroti</i> <i>Clausinella vindobonensis</i> <i>Dosinia (Asa) lupinus</i> <i>Gouldia minima</i> <i>Pitar (Pitar) cf. rudis</i> <i>Tapes (Ruditapes) decussatus</i> <i>Timoclea marginata</i> |
| | | | | | | | |
| | | | | | Myoidea | Corbulidae | <i>Corbula (Caryocorbula) basteroti</i> <i>Corbula (Varicorbula) gibba</i> |
| | | | | | Hiatelloidea | Hiatellidae | <i>Hiatella (Hiatella) arctica</i> |
| | | | | | Pandoroidea | Thraciidae | <i>Thracia papyracea</i> |
| | | | | | Scaphopoda | | Scaphopoda indet. |