# THE STRATIGRAPHIC AND SEDIMENTOLOGIC FRAMEWORK OF FINE-SCALE FAUNAL REPLACEMENTS IN THE MIDDLE MIOCENE OF THE VIENNA BASIN (AUSTRIA)

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## ABSTRACT

Fine-scale paleocommunity dynamics were studied in a short (~16 m) section in the Middle Miocene (Badenian Stage) of the Central Paratethys, which consists of siliciclastic, pelitic, and sandy-to-gravely shallow-water deposits. Two basal, coarsening- and shallowing-upward parasequences of a late highstand systems tract are separated by a third-order sequence boundary from the deepening-upward basal part of a transgressive systems tract at the top of the section. Benthic faunas in this succession are primarily autochthonous and storm-influenced, level-bottom assemblages, but a distinct oyster-vermetid boundstone occurs near the base of the transgressive systems tract. Additionally, three tempestitic shell beds were included, which were found out of sequence in an associated basinal setting; their faunal content relates them closely to the fine-grained deepest parts of the transgressive systems tract. Ordination of species and samples using detrended correspondence analysis and analysis of similarity suggest that two basic benthic assemblages can be distinguished. The oyster-vermetid boundstone is tied to a unique set of environmental conditions and indicates a major environmental change at the sequence boundary. The faunal assemblage in the boundstone shows a weak gradient into the pelitic (deeper and quiet-water) level-bottom assemblage, which in turn is characterized by strong overlaps with the fauna of sandy (shallower and more agitated) habitats. Therefore it is concluded that the benthic assemblages in the studied section belong to the same basic metacommunity, which was not seriously affected by the strong facies changes at the sequence boundary and at the flooding surfaces. Moreover, the species in the studied benthic assemblages reacted to changes in the environment by habitat tracking.

## INTRODUCTION

Patterns of recurrence in paleocommunities are scale dependent, and most case studies from marine soft substrata cover durations of several millions of years, with time resolutions of individual assemblages being in the range of hundreds of thousands to millions of years (for a review, see DiMichele et al., 2004). Only few studies have dealt with paleocommunity dynamics over shorter time spans and with higher time resolution of individual fossil assemblages (e.g., Holterhoff, 1996; Bonuso et al., 2002). At all temporal scales, however, sea-level changes and related depositional dynamics exert major influence on the composition of fossil assemblages, and the corresponding paleocommunity patterns are best interpreted within a sequence stratigraphic framework (Holland, 1995; Brett, 1998). Abrupt changes in biofacies are expected to occur at important sequence boundaries (e.g., Olszewski and Erwin, 2004), but considerable biotic replacement may also occur at major flooding surfaces, which induce rapid facies changes within depositional sequences (Holland, 2000).

The present study focuses on Middle Miocene shallow-water deposits of the Central Paratethys (Fig. 1) to study the paleocommunity dynamics

within and between three successive sequence stratigraphic units (two parasequences and a deepening-upward succession). No information is available on the absolute time preserved in these deposits, but parasequences typically cover only a few tens of thousands of years (Van Wagoner et al., 1990). The regional species pool for this stratigraphic succession of local assemblages comes from a metacommunity that was established during the early Middle Miocene transgression and diversified during a subsequent climatic optimum (Harzhauser et al., 2003; Zuschin et al., 2004). During the relatively short time span covered in this study, however, evolutionary turnover is assumed to be insignificant, and it can be expected that paleocommunity patterns reflect changes in local environmental conditions.

Our goal in this study is to recognize vertical changes of biota (i.e., community replacement) in the sedimentary deposits. Specifically, we ask if such replacements occur abruptly (indicating major environmental change) or along one or a few environmental gradients, which would indicate habitat tracking, the lateral migration of species or assemblages in response to shifting environments (Miller, 1990; Brett, 1998; Brett et al., 2007). We also attempt to identify the environmental factors that most likely shaped the benthic assemblages, the environmental disturbances that might have been responsible for community replacements, and the taphonomic factors that potentially influenced the composition of the benthic assemblages.

## STRATIGRAPHIC FRAMEWORK AND GEOLOGICAL SETTING

The Vienna Basin is a SSW–NNE-oriented rhombic Neogene pull-apart basin, about 200 km long and 55 km wide. It covers large parts of eastern Austria (Lower Austria, Vienna, and Burgenland) and reaches into the territories of the Czech Republic in the north and the Slovak Republic in the east (Fig. 2). The formation of the Vienna Basin started in the Early Miocene as an E–W trending piggyback basin on top of the Alpine thrust belt. Owing to rapid subsidence, the Miocene sedimentary successions reach up to 5,500 m thickness in the central part of the basin, and their depositional systems consist of alluvial plains, deltas, and shelf environments. These sediments were deposited during nine third-order cycles (defined as VB1–VB9 cycles by Kováč et al., 2004) of relative sea-level changes, which result from a combination of eustatic global sea-level changes, tectonic evolution of the basin, and sediment supply mostly from deltas (Kováč et al., 2004, and references therein).

The section we studied at the Gainfarn locality (Fig. 2) represents the late VB5 cycle and the early VB6 cycle of Kováč et al. (2004). The sequence stratigraphic framework of the section is made up of three fully marine depositional units, which consist of siliciclastic, pelitic, and sandy-to-gravely shallow-water deposits. They can be grouped into two basal coarsening- and shallowing-upward parasequences and a fining- and deepening-upward succession at the top (Fig. 3). Benthic faunas in this succession are fully marine and primarily occur as autochthonous and storm-influenced, level-bottom assemblages, but a distinct oyster-vermetid boundstone occurs near the base of the uppermost stratigraphic unit. Additionally, three tempestitic shell beds with a pelitic matrix from an associated basinal setting were also included. These shell beds were
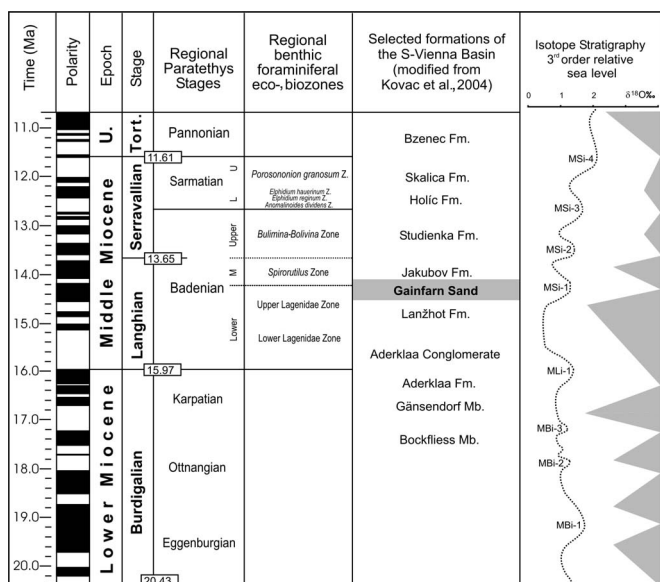
FIGURE 1—Miocene chronostratigraphy and biostratigraphy recalibrated according to Gradstein and Ogg (2004). Oxygen isotope stratigraphy is adapted after Abreu and Haddad (1998) and sequence stratigraphy after Hardenbol et al. (1998). Regional biozones have been modified from Grill (1941, 1943); some of the most important lithostratigraphic units are indicated after Kováč et al. (2004). The studied deposits are the Gainfarn sands—which are probably a nearshore facies of the Lanžhot Formation—and an overlying deepening-upward succession—which is most likely a lateral equivalent of the Jakubov Formation.
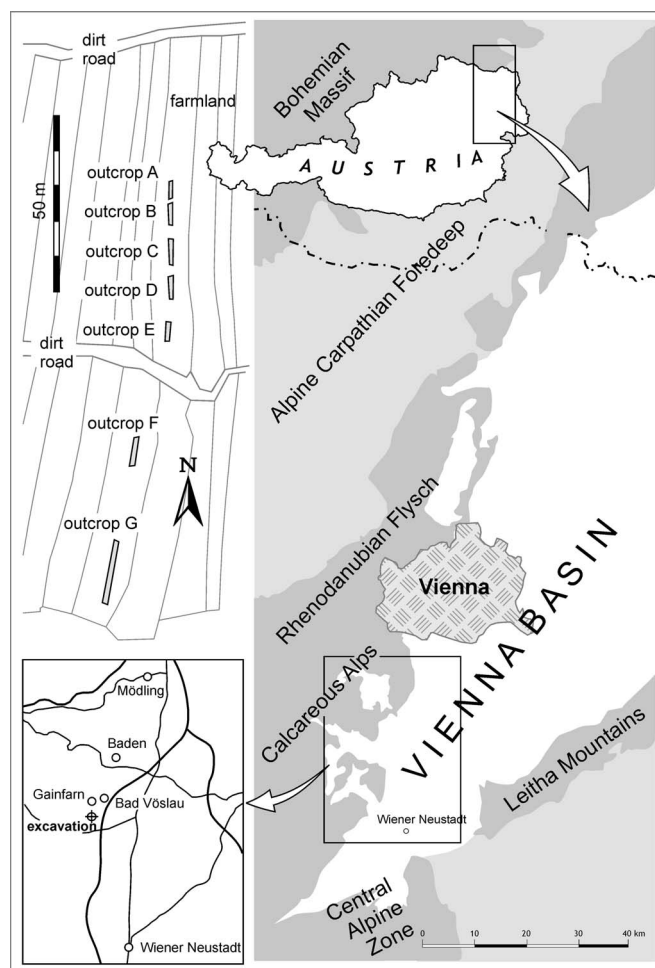


FIGURE 2—Study area and studied artificial trenches (log A–G) in the farmland north of the village Gainfarn, in the southwestern Vienna Basin in Lower Austria.

found out of sequence along an artificial street-parallel trench, made by a road construction company near the village of Gainfarn.

The mollusk fauna is indicative for the Badenian Stage of the Central Paratethys. The deposits of the second parasequence are dated as Upper Lagenidae Zone of the regional benthic foraminifera ecobiozonation (Steininger et al., 1978), allowing a correlation with the (upper) Langhian. The lower two parasequences are termed Gainfarn sands in the local literature (Brix and Plöchinger, 1988) and probably represent the nearshore facies of the Lanžhot Formation; they are interpreted as part of a highstand systems tract (HST) defined on seismic logs by Weissenbäck (1996). The overlying deepening-upward succession is most likely a lateral equivalent of the Jakubov Formation and is interpreted as part of a transgressive systems tract (TST) (see Fig. 1), which is very prominent in seismic sections (Weissenbäck, 1996). From this interpretation, we conclude that the second parasequence and the deepening-upward succession are separated by a third-order sequence boundary (cf. Weissenbäck, 1996).

## MATERIALS AND METHODS

### Sampling

No natural outcrops or roadcuts are available in the area of the Gainfarn sands. Therefore, we excavated seven deep trenches with power shovels in the farmland north of the village Gainfarn, in the southwestern Vienna Basin in Lower Austria (Fig. 2). These seven trenches yielded seven, mostly overlapping, sections, which are arranged in a composite section for the purpose of this study (Fig. 3). We took 28 bulk samples from sediments at this section, their weights ranging from 1,700 to 3,800 g (Fig. 3; Table 1). We included three samples from tempestitic shell beds in the basinal setting; they are characterized by comparatively high sample weights (Table 1). The sediment was wet sieved through a 1 mm screen, and material >1 mm was quantitatively picked under a binocular microscope for all biogenic components, which included sponges, corals, mollusks, polychaetes, decapods, bryozoans, echinoids, and vertebrates. For sponges, every bioeroded biogenic hard part with distinct traces of

the ichnogenus *Entobia* was counted as a sponge colony. For mollusks, every shell (gastropods, scaphopods), every isolated valve (bivalves), and every isolated plate (polyplacophorans) was counted as an individual. Identifiable fragments of mollusks were only considered to indicate the presence of a species in a sample, if no whole shells or valves were found. For bryozoans and serpulids, fragments > 0.5 cm were counted as individuals or colonies, but smaller fragments were only used to indicate the presence of a species. Each decapod claw, echinoid spine, and vertebrate hard part (including bones, teeth, and otoliths) was counted as an individual. In addition to these quantitative samples, each layer was scoured for large-sized species, which are likely underrepresented in bulk samples, and a species was added as present to the data matrix where appropriate.

Altogether, 9,101 fossils were counted and sorted into 198 species (see Supplementary Data 1[1]). For statistical analysis, samples containing <10 fossils and fossils occurring with only one specimen (singletons) were removed; the final data matrix contained 22 samples, 112 species, and 8,986 specimens (98.7% of the original data).

### Analysis of Faunal Composition

The faunal composition of the studied samples was analyzed with respect to the stratigraphic framework and with respect to the matrix and fabric of the bioclastic deposits. Accordingly, we distinguished four stratigraphic categories (parasequences 1 and 2, the deepening-upward suc-

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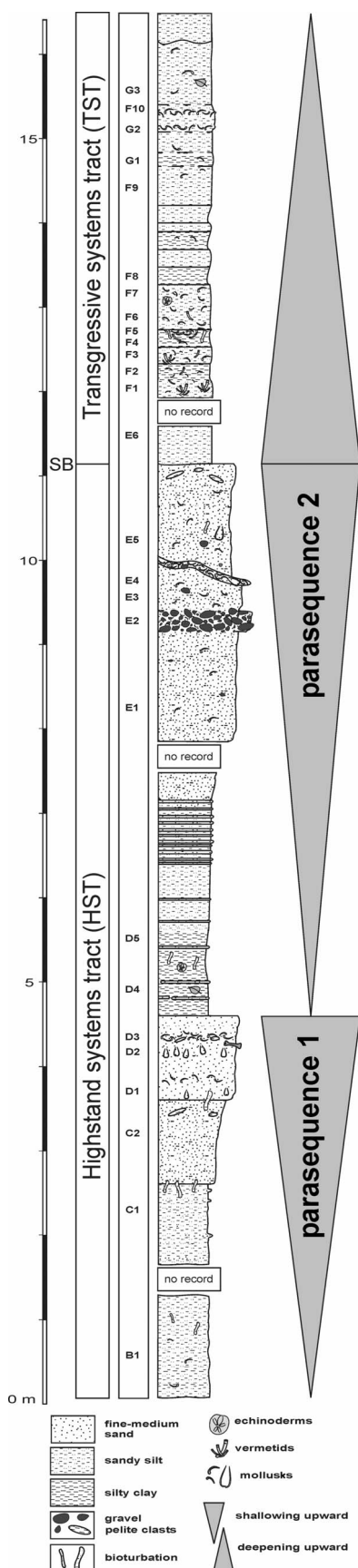
[1] www.sepm.org/archive/index.html

**FIGURE 3**—The studied section can be divided into two basal parasequences of a highstand systems tract (HST) and an uppermost deepening upward succession of a transgressive systems tract (TST). It consists of pelitic and sandy to gravely shallow-water deposits.

cession, and the basin shell beds) and five types of bioclastic accumulations (pelitic level-bottom assemblages, sandy-gravely level-bottom assemblages, tempestitic shell beds with pelitic matrix, tempestitic shell beds with sandy matrix, and boundstones; see Table 1).

Percentage data were used for statistical analysis because differing volumes of sediment were sampled and the absolute numbers of individuals are not comparable between samples (Clarke and Warwick, 1994). Because some samples in this study are strongly dominated by few species, in a second series of analyses the percentage data were square-root transformed to de-emphasise the influence of the most abundant taxa. The results of these different statistical treatments, however, were almost identical, and therefore only those for the untransformed percentages are shown. Several explorative multivariate techniques were applied to the relative-abundance data matrix: nonmetric multidimensional scaling (nMDS), correspondence analysis (CA) and detrended correspondence analysis (DCA) were used as ordination methods, and analysis of similarity (ANOSIM) was used to identify significant differences in faunal composition between stratigraphic categories and bioclastic accumulations. Ordination methods are frequently used to detect ecological gradients in modern and ancient marine environments (e.g., Springer and Bambach, 1985; Olszewski and Patzkowsky, 2001; Zuschin et al., 2001). Detrended correspondence analysis especially has been successfully used to detect environmental gradients in paleoecological data sets (e.g., Holland et al., 2001; Scarponi and Kowalewski, 2004). Because severe distortions in axis 2 can occur in DCA (Kenkel and Orlóci, 1986; Minchin, 1987; Jackson and Somers, 1991), we also applied nMDS and CA, which are not prone to this distortion, to the data set. The different ordination methods yielded very similar results and suggest that axis 2 scores of our DCA can be environmentally interpreted. For the purpose of this study, we prefer DCA over CA as an ordination method because it minimizes the horseshoe effect (Hill and Gauch, 1980) and, as with normal correspondence analysis, it is still possible to study species and samples in the same system of axes (Gabriel, 1971). For comparison with DCA, the graphs of nMDS and CA are shown in Supplementary Data 2[1.]

To test the significance of taxonomic differences between stratigraphic categories and between types of bioclastic deposits, we applied ANOSIM based on the Bray-Curtis similarity coefficient (Bray and Curtis, 1957; Clarke and Warwick, 1994). Of the numerous similarity coefficients that have been suggested over the years, the Bray-Curtis coefficient has become particularly common in ecological work (Clarke and Warwick, 1994). The important message of the pairwise tests of the ANOSIM analysis is usually not so much the significance level (which can often be low because of few replicates in each group) but the pairwise R-values; the latter give an absolute measure of how separated the groups are, on a scale of zero (indistinguishable) to one (all similarities within groups are less than any similarity between groups). With R-values $> 0.75$, groups are well separated; with R-values $> 0.5$, groups are overlapping but clearly different; with R-values $> 0.25$, groups strongly overlap; and with R-values $< 0.25$, groups are barely separable (Clarke and Gorley, 2001). We used these categories of R-values to evaluate overlaps in faunal composition between benthic assemblages and to identify gradual and disjunct faunal replacements. We performed a similarity percentage analysis (SIMPER; see Clarke and Warwick, 1994) to determine which species were responsible for the greatest similarity within stratigraphic categories and bioclastic accumulations. Those species for which the ratio of mean similarity to standard deviation of similarity is $>1$ typify the sample group. The ecological software package PRIMER (Clarke and Warwick, 1994) was used to perform ANOSIM and SIMPER; the program PAST (Hammer et al., 2001, 2004) was used to perform DCA; and the program PC-ORD (McCune and Mefford, 1999) was used to perform CA and nMDS.

## RESULTS

The two basal, coarsening-upward parasequences largely share the same species and show high proportional abundances of the gastropods

**TABLE 1**—Basic data for the studied samples. Samples with <10 fossils were excluded from further analyses; PS = parasequence, DUS = deepening upward succession, BSB = basin shell bed, PLA = pelitic level-bottom assemblage, SLA = sandy level-bottom assemblage, TSBP = tempestitic shell bed with pelitic matrix, TSBS = tempestitic shell bed with sandy matrix, B = boundstone.

| Sample number | Stratigraphic unit | Bioclastic accumulation | Description | Sample weight (in g) | Number of fossils | Number of species |
|---|---|---|---|---|---|---|
| B1 | PS1 | PLA | silty clay with layers of sandy silt | 3800 | 0 | 0 |
| C1 | PS1 | PLA | silty clay with layers of sandy silt | 3590 | 6 | 5 |
| C2 | PS1 | SLA | poorly sorted fine sand | 3440 | 3 | 3 |
| D1 | PS1 | SLA | coarse sand with *in situ Panopaea* | 3110 | 44 | 23 |
| D2 | PS1 | SLA | coarse sand with *in situ Panopaea* | 2990 | 1 | 1 |
| D3 | PS1 | TSBS | tempestitic shell bed with coarse-sandy matrix | 2900 | 111 | 63 |
| D4 | PS2 | PLA | silty clay with layers of sandy silt | 3140 | 3 | 3 |
| D5 | PS2 | PLA | silty clay with layers of sandy silt | 2500 | 49 | 14 |
| E1 | PS2 | SLA | fine-medium sand | 2480 | 0 | 0 |
| E2 | PS2 | SLA | conglomerate with sandy matrix | 3055 | 114 | 33 |
| E3 | PS2 | SLA | poorly sorted coarse sand | 2610 | 52 | 27 |
| E4a | PS2 | TSBS | tempestitic shell bed with sandy matrix | 2370 | 143 | 51 |
| E4b | PS2 | TSBS | tempestitic shell bed with sandy matrix | 2220 | 159 | 58 |
| E5 | PS2 | SLA | fine-medium sand | 2320 | 103 | 35 |
| E6 | DUS | PLA | silty clay with *in situ* oysters | 2200 | 9 | 3 |
| F1 | DUS | B | oyster-vermetid boundstone with pelitic matrix | 1810 | 39 | 13 |
| F2 | DUS | B | oyster-vermetid boundstone with pelitic matrix | 1700 | 418 | 34 |
| F3 | DUS | B | oyster-vermetid boundstone with pelitic matrix | 2140 | 1208 | 72 |
| F4 | DUS | B | oyster-vermetid boundstone with pelitic matrix | 1970 | 84 | 20 |
| F5 | DUS | B | oyster-vermetid boundstone with pelitic matrix | 1750 | 512 | 69 |
| F6 | DUS | PLA | silty clay with *in situ* oysters | 2120 | 117 | 11 |
| F7 | DUS | PLA | sandy silt with *in situ* oysters | 2330 | 268 | 28 |
| F8 | DUS | PLA | silty clay | 1920 | 62 | 11 |
| F9 | DUS | PLA | sandy silt | 2250 | 2 | 2 |
| F10 | DUS | TSBP | tempestitic shell bed with pelitic matrix | 2240 | 170 | 20 |
| G1 | DUS | PLA | silty clay | 2060 | 6 | 1 |
| G2 | DUS | TSBP | tempestitic shell bed with pelitic matrix | 2360 | 142 | 22 |
| G3 | DUS | PLA | silty clay | 2470 | 87 | 9 |
| S1 | BSB | TSBP | tempestitic shell bed with pelitic matrix | 24,568 | 954 | 29 |
| S2 | BSB | TSBP | tempestitic shell bed with sandy silt matrix | 22,420 | 1851 | 33 |
| S3 | BSB | TSBP | tempestitic shell bed with sandy silt matrix | 4715 | 2384 | 23 |
| Total | | | | 121,548 | 9101 | 198 |

*Bittium* and *Tricolia* and the bivalve *Loripes* (Table 2). These three taxa and the bivalve *Glycymeris* are also the most characteristic faunal elements in these stratigraphic units (Table 3). The gastropods *Bittium* and *Alvania ampulla*, the bivalves *Corbula* and *Ostrea*, and the bryozoan *Schizostomella* account for almost 70% of the assemblage in the deepening-upward succession (Table 2), which is typified by *Ostrea* (Table 3). The basin shell beds, finally, are strongly dominated and best characterized by *Corbula gibba* (Tables 2 and 3). The three tempestitic basin shell beds are faunistically most similar to the uppermost parau-

tochthonous assemblage and corresponding winnowed shell beds of the section (Fig. 4A). Because of this similarity, the three basin shell beds are not significantly different from fossil assemblages in the deepening-upward succession (Table 4). The two lower, coarsening-upward parasequences cannot be distinguished from each other, but both differ significantly from the uppermost pelitic succession and the three tempestitic basin shell beds. The differences between parasequences 1 and 2 and the basin shell beds are very strong (R-values > 0.8), but different degrees of overlap in faunal composition are evident between the two lower par-

**TABLE 2**—Quantitatively important species (contributing 1% to the total assemblage or 5% to one of the four sample groups) in the stratigraphic categories. See Table 1 for abbreviations.

| Species | PS1 (N = 183) % | PS2 (N = 544) % | DUS (N = 3077) % | BSB (N = 5182) % | Total (N = 8986) % |
|---|---|---|---|---|---|
| *Corbula gibba s.l.* | 2.7 | 15.4 | 19.1 | 94.5 | 62.0 |
| *Bittium reticulatum* | 10.4 | 10.7 | 22.4 | 0.0 | 8.5 |
| *Ostrea digitalina* | 1.6 | 2.4 | 14.8 | 1.3 | 6.0 |
| *Schizostomella grinzingensis* | 1.1 | 0.0 | 7.1 | 0.0 | 2.4 |
| *Alvania ampulla* | 0.0 | 0.4 | 6.5 | 0.0 | 2.3 |
| *Anadara diluvii* | 0.5 | 5.7 | 2.6 | 0.7 | 1.7 |
| *Venus nux* | 0.5 | 0.4 | 1.0 | 1.6 | 1.3 |
| Serpulidae indet. (incl. *Protula protensa*) | 2.2 | 1.1 | 3.2 | 0.0 | 1.2 |
| *Vermetus arenarius* | 0.0 | 1.3 | 3.1 | 0.0 | 1.1 |
| *Alvania transiens* | 0.0 | 0.0 | 3.3 | 0.0 | 1.1 |
| *Loripes dentatus* | 7.7 | 5.7 | 0.2 | 0.1 | 0.6 |
| *Tricolia eichwaldi* | 7.7 | 5.0 | 0.0 | 0.0 | 0.5 |
| *Alveinus nitidus* | 13.1 | 0.0 | 0.1 | 0.0 | 0.3 |

**TABLE 3**—Characteristic species in the stratigraphic categories using similarity percentage analysis (SIMPER; see Clarke and Warwick, 1994). Characteristic species are those for which the ratio of average abundance to standard deviation of abundance is >1.

| Species | Average abundance | Average similarity | Sim/SD | Contrib% | Cum.% |
|---|---|---|---|---|---|
| **Parasequence 1** (2 samples) | | | | | |
| Average similarity: 39.77 | | | | | |
| *Bittium reticulatum* | 8 | 9.47 | — | 23.82 | 23.82 |
| *Tricolia eichwaldi* | 5.5 | 7.37 | — | 18.53 | 42.34 |
| *Gouldia minima* | 3.5 | 4.76 | — | 11.97 | 54.32 |
| *Glans subrudista* | 3 | 3.16 | — | 7.94 | 62.26 |
| *Paroxystele orientalis* | 2.5 | 2.38 | — | 5.99 | 68.24 |
| *Gibbula buchi* | 2 | 2.11 | — | 5.29 | 73.53 |
| *Gibbula pseudangulata* | 2.5 | 2.11 | — | 5.29 | 78.83 |
| *Ostrea digitalina* | 1.5 | 2.11 | — | 5.29 | 84.12 |
| *Polinices redemptus* | 1.5 | 1.05 | — | 2.65 | 86.77 |
| *Semibittium turritella* | 1 | 1.05 | — | 2.65 | 89.41 |
| *Turritella tricincta* | 1.5 | 1.05 | — | 2.65 | 92.06 |
| **Parasequence 2** (6 samples) | | | | | |
| Average similarity: 36.77 | | | | | |
| *Bittium reticulatum* | 10.17 | 5.92 | 5.17 | 16.1 | 16.1 |
| *Glycymeris cf. pilosa deshayesi* | 1.33 | 1.17 | 2.14 | 3.17 | 19.27 |
| *Tricolia eichwaldi* | 5 | 3.07 | 1.72 | 8.34 | 27.61 |
| *Loripes dentatus* | 6.17 | 4.78 | 1.65 | 13 | 40.61 |
| *Antalis cf. quindeciesstriata* | 1.33 | 0.84 | 1.14 | 2.28 | 42.89 |
| *Conus dujardini* | 1.5 | 0.79 | 1.05 | 2.15 | 45.04 |
| *Gibbula pseudangulata* | 3.67 | 2.01 | 1.03 | 5.47 | 50.51 |
| **Deepening-upward succession** (11 samples) | | | | | |
| Average similarity: 32.51 | | | | | |
| *Ostrea digitalina* | 41.45 | 10.81 | 1.04 | 33.25 | 33.25 |
| **Basin shell beds** (3 samples) | | | | | |
| Average similarity: 91.50 | | | | | |
| *Corbula gibba s.l.* | 1632.33 | 90.3 | 46.87 | 98.69 | 98.69 |

asequences on one side and the deepening-upward succession on the other side (Fig. 4A; Table 4).

The pelitic level-bottom assemblages show a very high proportional abundance of *Corbula*, *Ostrea* and *Anadara* (Table 5), but only the bivalve *Venus nux* typifies this sample group (Table 6). The strong dominance of *Corbula* in tempestitic shell beds with pelitic matrix is striking (Table 5), and this species also best characterizes these deposits (Table 6). Sandy level-bottom assemblages and tempestitic shell beds with sandy matrix share the same species and are both dominated by *Corbula* and *Bittium* (Table 5). Sandy level-bottom assemblages are typified by three gastropods (*Gibbula*, *Bittium*, *Tricolia*) and two bivalves (*Glycymeris*, *Ostrea*), whereas the tempestitic shell beds with sandy matrix are characterized by a multitude of taxa, most notably the bivalves *Loripes*, *Venus*, *Pelecyora*, *Panopea*, and *Acanthocardia* and the gastropod *Turritella erronea* (Table 6). The oyster-vermetid boundstone, finally, is dominated by *Bittium*, *Ostrea*, *Schizostomella*, and *Alvania ampulla* (Table 5) and typified by the bivalves *Ostrea* and *Chama* and the gastropods *Alvania*, *Vermetus*, and *Petaloconchus* (Table 6). Except for sandy level-bottom assemblages and tempestites with sandy matrix, all bioclastic deposits differ significantly from each other in their faunal content. Five pairs of assemblages are very well separated (sandy level-bottom assemblages versus boundstones and tempestites with pelitic matrix, tempestites with sandy matrix versus boundstone and tempestites with pelitic matrix, and boundstone versus tempestites with pelitic matrix), as indicated by high R-values (>0.8). The other four pairs of assemblages also differ from each other but show considerable overlap in their faunal content (R-values < 0.5; Fig. 4B; Table 7).

Ordination of species in the detrended correspondence analysis demonstrates the presence of two strong faunal gradients (Fig. 4C). The first gradient occurs in the HST and includes species with DC1 scores above 3 and DC2 scores below 2. The species of this gradient stem from sandy level-bottom assemblages and their storm-influenced shell beds. An ex-

ception is the assemblage in the pelitic sample D5, which is characterized by the unusual relative abundance of otherwise rare species (most notably the bivalve *Alveinus nitidus*). The second gradient occurs in the TST and includes species with DC1 scores between 0 and 5 and D2 scores higher than 1.8. The species of this gradient stem from tempestitic shell beds with pelitic matrix, pelitic level-bottom assemblages, and the oyster-vermetid boundstone. As a general feature of both gradients, DC2 scores increase with increasing DC1 scores. The two gradients are not completely separated, and a series of species with DC1 scores between 2.5 and 5.5 and D2 scores between 1 and 2 indicate various degrees of overlap, mostly between sandy and pelitic level-bottom assemblages (Fig. 4C).

## DISCUSSION

### The Habitats and Depositional Environments in the Gainfarn Section

The fossils of this section are generally indicative of a fully marine, warm-water, inner-shelf setting, but the range of sediments present and the different life habits of the fauna suggest very heterogeneous habitats and depositional environments.

Actualistic comparisons suggest that the biostrome near the base of the TST of the early VB6 cycle, whose framework was built by the oyster *Ostrea digitalina* and the vermetid gastropod *Vermetus arenarius*, developed in intertidal to very shallow subtidal conditions (e.g., Safriel, 1975). Solitary, loosely aggregated vermetid gastropods are subordinate constructors in algal cup reefs (e.g., Gischler et al., 1998), but can be quantitatively important components of recent intertidal to shallow subtidal coral reefs (e.g., Hadfield et al., 1972; Hughes and Lewis, 1974; Zuschin et al., 2001). Colonial vermetids can form dense intertidal thickets (Keen, 1961; Hughes, 1978), and such biostromes are, for example, reported from Hawaii (Hadfield et al., 1972), southwest Florida (Shier, 1969), Bermuda (Ginsburg and Schroeder, 1973), and the Mediterranean (e.g., An-

1= *Entobia*, 2=*Siderastrea*, 3=*Nucula nucleus*, 4=*Nuculana fragilis*, 5= *Striarca lactea*, 6=*Anadara diluvii*, 7=*Glycymeris* cf. *pilosa*, 8=*Aeqipecten elegans*, 9=*Aequipecten malvinae*, 10= *Aequipecten scabrellus / macrotis*, 11=*Costellamussiopecten cristatus*, 12=*Crassadoma multistriata*, 13=*Plicatula striata*, 14=*Anomia ephippium*, 15=*Ostrea digitalina*, 16=*Loripes dentatus*, 17=*Ctena exigua*, 18=*Chama gryphoides*, 19=*Acanthocardia turonica*, 20=*Cerastoderma* cf. *arcellum*, 21=*Parvicardium papillosum*, 22= *Parvicardium subhispidum*, 23=*Parvicardium* cf. *minimum*, 24=*Cardiocardita partschi*, 25= *Megacardita jouanneti*, 26=*Cardites scalaris*, 27=*Glans subrudista*, 28=*Abra alba*, 29=*Ervilia pusilla*, 30=*Alveinus nitidus*, 31=*Venus nux*, 32=*Gouldia minima*, 33=*Circomphalus subplicatus*, 34=*Pelecyora islandicoides*, 35=*Corbula gibba* s.l., 36=*Corbula carinata*, 37=*Panopea menardi*, 38=*Antalis* cf. *quindeciesstriata*, 39=*Gadilina jani*, 40=*Gibbula buchi*, 41=*Gibbula pseudangulata*, 42=*Paroxystele orientalis*, 43=*Tricolia eichwaldi*, 44=*Teinostoma woodi*, 45=*Smaragdia expensa*, 46=*Bittium reticulatum*, 47=*Cerithium bronni*, 48=*Cerithium europaeum*, 49=*Semibittium multiliratum*, 50=*Semibittium turritella*, 51=*Turritella badensis*, 52=*Turritella bicarinata*, 53=*Turritella erronea*, 54=*Turritella laevissimus*, 55=*Turritella spirata*, 56=*Turritella tricincta*, 57=*Alaba anomala*, 58=*Sandbergeria perpusilla*, 59=*Turboella acuticosta*, 60=*Alvania ampulla*, 61=*Alvania transiens*, 62=*Alvania* sp. 1, 63=*Manzonia miocrassicosta*, 64=*Cingula vitrea*, 65=*Aporrhais pespelecani*, 66=*Strombus bonelli*, 67=*Crepidula crepidula*, 68=*Calyptrea chinensis*, 69=*Vermetus arenarius*, 70=*Petaloconchus intortus*, 71=*Euspira helicina*, 72=*Natica* cf. *tigrina*, 73=*Polinices redemptus*, 74=*Cerithiopsis* sp. 75=*Triphora* sp., 76=*Latirus valenciennesi*, 77=*Nassarius coloratus*, 78=*Nassarius dujardini*, 79=*Nassarius serraticosta*, 80=*Nassarius striatulus*, 81=*Narona calcarata*, 82=*Vexillum* cf *pseudorecticosta*, 83=*Mitrella semicaudata*, 84=*Amalda glandiformis*, 85=*Conus dujardini* 86=*Asthenotoma festiva*, 87=*Clavatula granulatocincta*, 88=*Cythara rugulosa*, 89=*Perronea jouanneti*, 90=*Turricula dimidiata*, 91=*Carinorbis burdigalica*, 92=*Odostomia* sp. 1, 93=*Odostomia* sp. 3, 94=*Turbonilla* sp. 1, 95=*Turbonilla* sp. 2, 96=Retusidae sp. 1, 97=*Ringicula buccinea*, 98=Serpulidae indet (incl. *Protula protensa*), 99="*Spirorbis*", 100=Portunidae sp. indet, 101=Xanthidae sp. indet, 102=*Discoporella umbellata*, 103=*Schizostomella grinzingensis*, 104=Celleporidae sp. indet, 105=*Tripneustes* sp., 106=?*Brissopsis*/?*Schizaster* sp., 107=*Pantuichthys subglaber*,108=Cyprinidae sp. Indet, 109=*Micromesistius* sp., 110=*Diaphus debilis*, 111=*Echiodon* sp., 112=*Gobius* sp.
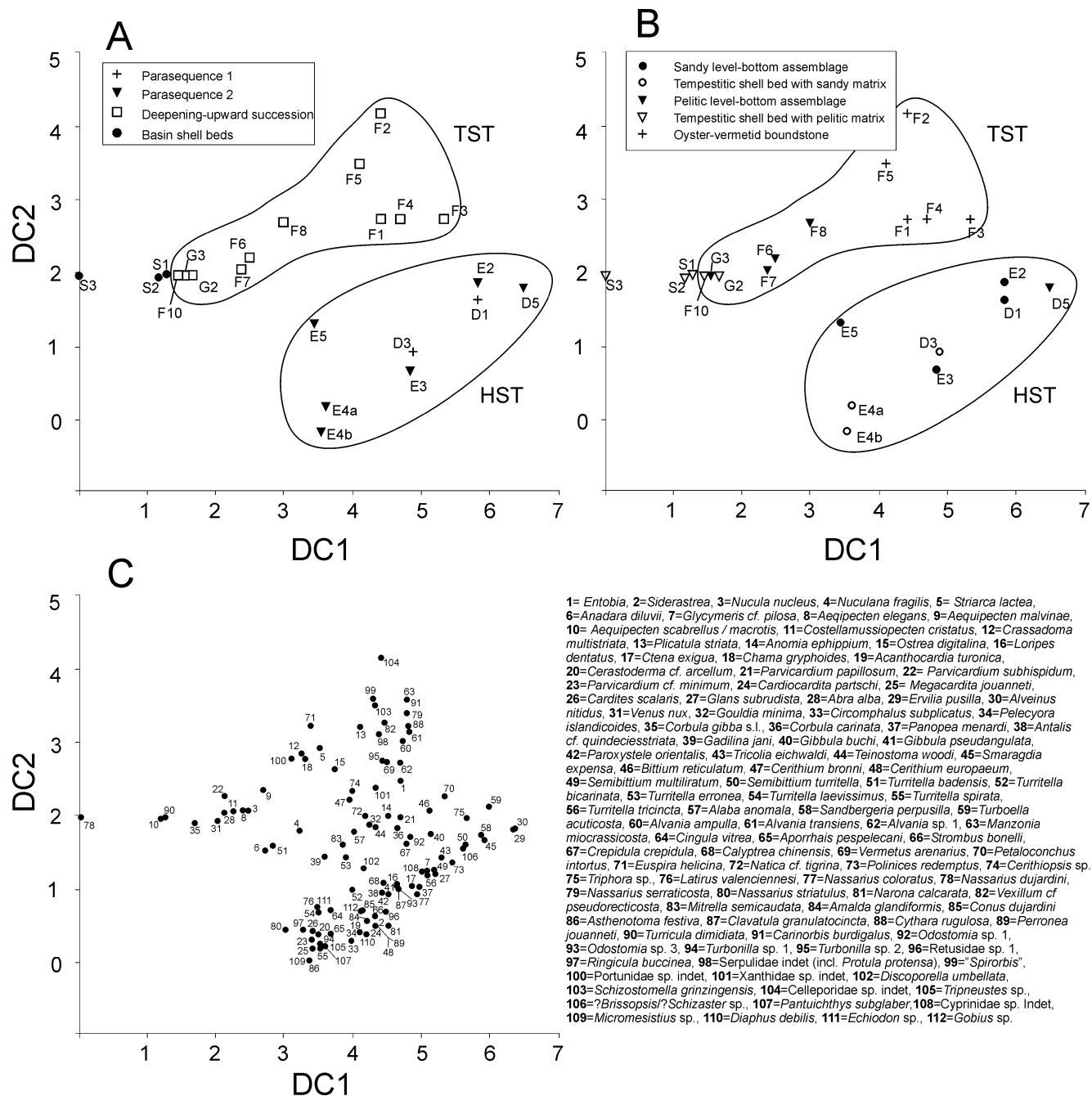
FIGURE 4—Ordination of samples and species using dimension 1 and dimension 2 of the detrended correspondence analysis (DCA). A) Samples plotted by stratigraphic units. B) Samples plotted by bioclastic units. C) Ordination of species, which indicates the presence of two faunal gradients. DCA was calculated with PAST (Hammer et al., 2001; 2004). Detrending is based on the division of axes into 26 segments (Ø. Hammer, personal communication, January 2006). HST = highstand systems tract; TST = transgressive systems tract.

TABLE 4—Results of ANOSIM (analysis of similarity) for the stratigraphic categories. Statistical decisions are based on R-values, which give an absolute measure of how separated the groups are. For high R-values, significance levels can be low because of few replicates in each group (for more information, see the Materials and Methods section). For explanation of abbreviations, see Table 1; s = significant; ns = not significant.

| Parasequences | R-stat | Description (based on R-values) | *P*-value | Statistical decision |
|---|---|---|---|---|
| total | 0.374 | assemblages strongly overlap | 0.003 | s |
| PS1 versus PS2 | 0.042 | assemblages barely separable | 0.357 | ns |
| PS1 versus DUS | 0.472 | assemblages strongly overlap | 0.013 | s |
| PS1 versus BSB | 1 | assemblages well separated | 0.1 | s |
| PS2 versus DUS | 0.405 | assemblages strongly overlap | 0.002 | s |
| PS2 versus BSB | 0.747 | assemblages well separated | 0.012 | s |
| DUS versus BSB | 0.09 | assemblages barely separable | 0.228 | ns |

**TABLE 5**—Quantitatively important species (contributing 1% to the total assemblage or 5% to one of the five sample groups) in the different types of bioclastic deposits. For explanation of abbreviations, see Table 1.

| Species | PLA (N = 574) % | TSBP (N = 5494) % | SLA (N = 298) % | TSBS (N = 383) % | B (N = 2237) % | Total (N = 8986) % |
|---|---|---|---|---|---|---|
| *Corbula gibba s.l.* | 45.8 | 93.9 | 10.1 | 15.4 | 2.9 | 62.0 |
| *Bittium reticulatum* | 0.5 | 0.0 | 15.8 | 7.0 | 30.8 | 8.5 |
| *Ostrea digitalina* | 16.7 | 1.4 | 2.7 | 2.1 | 15.7 | 6.0 |
| *Schizostomella grinzingensis* | 0.9 | 0.0 | 0.7 | 0.0 | 9.5 | 2.4 |
| *Alvania ampulla* | 0.0 | 0.0 | 0.3 | 0.3 | 9.0 | 2.3 |
| *Anadara diluvii* | 10.5 | 0.9 | 2.3 | 6.5 | 0.4 | 1.7 |
| *Venus nux* | 2.6 | 1.8 | 0.0 | 0.8 | 0.1 | 1.3 |
| Serpulidae indet. (incl. *Protula protensa*) | 0.5 | 0.0 | 0.7 | 1.8 | 4.2 | 1.2 |
| *Vermetus arenarius* | 0.2 | 0.0 | 2.3 | 0.0 | 4.2 | 1.1 |
| *Alvania transiens* | 0.0 | 0.0 | 0.0 | 0.0 | 4.5 | 1.1 |
| *Petaloconchus intortus* | 0.2 | 0.0 | 6.7 | 0.3 | 2.2 | 0.8 |
| *Loripes dentatus* | 1.4 | 0.1 | 4.7 | 6.5 | 0.0 | 0.6 |
| *Tricolia eichwaldi* | 0.5 | 0.0 | 8.1 | 3.7 | 0.0 | 0.5 |

tonioli et al., 1999; Safriel, 1974, 1975). Comparison with a fossil study suggests that such vermetid framestones in the Miocene may also have formed in somewhat deeper water, below 15–20 m (Betzler et al., 2000). The pelitic sediments associated with the vermetid bioconstruction in this study indicate low-energy conditions, and the distinct upward growth of individual vermetids points to high-sedimentation rates (Fig. 5). The oyster-vermetid assemblage developed in a shallow quiet-water embayment that requires a shallow water depth near the base of the uppermost succession. Although the biostrome occurs near the base of the TST, it was not developed on the transgressive surface itself, and there is no evidence for a firmground or hardground that was colonized by the encrusting organisms.

In the level-bottom assemblages, *Panopea menardi* was the only bivalve found *in situ* (Fig. 6). This can be related to the deep-burrowing life habit of this genus, which is probably an adaptation to frequent disturbances of the seafloor by storms (e.g., Kondo, 1998; Hanken et al., 2001). Modern representatives of *Panopea* live in sandy and muddy substrata and are recorded from the lower intertidal zone to water as deep as 100 m. Usually, however, they prefer shallow subtidal habitats down to 20 m, where they bury themselves 60 cm to 2 m below the seabed (Yonge, 1971; Ludbrook and Gowlett-Holmes, 1989). In the studied section, *Panopea* in life position occurred in coarse sands of the HST of the late VB5 cycle, which were in the reach of storm waves, as indicated by the presence of tempestitic shell beds. The *Panopea* horizons are overlain by only 20–30 cm sediment, and thus a storm-induced loss of several decimeters of sediment seems likely.

The composition of the sandy level-bottom assemblages and the sandy tempestitic shell beds suggests the presence of shallow sublittoral sea grass– and algae-dominated habitats in the HST, as indicated by abundant *Tricolia eichwaldi* and *Gibbula* spp. Also, the relatively rare *Smaragdia* cling to sea grasses in modern environments (Bandel and Wedler, 1987). Sea grass meadows, finally, would also have served as a food supply for sirenians (Domning, 2001), whose presence is documented by an isolated scapula. Shells in these coarse-grained sediments experienced some degree of corrosion and abrasion. In certain samples from sandy sediments, the shelly assemblage was obviously strongly reduced by such taphonomic processes. The best example is sample D2, whose macroscopic appearance is very similar to sample D1 (both are classified as coarse sands with *in situ Panopea*). In contrast to sample D1, however, sample D2 contained only disintegrated and unidentifiable shell hash.

The subtidal, infaunal, suspension-feeding *Corbula* dominates the composition of the pelitic level bottom assemblages and the pelitic tempestitic shell beds. Its high abundance and the low species richness in these deposits could indicate that these faunas at least occasionally experienced stress, most likely from oxygen deficiency (Hrs-Brenko, 1981; Weigelt

and Rumohr, 1986). The presence of nuculid and nuculanid bivalves in the highest parts of parasequence 3 could indicate a deepening-upward trend (Knudsen, 1970; Allen, 1978). An exception is sample D5, the only sample from pelitic level-bottom assemblages in the HST, which is characterized by the unusual abundance of an otherwise rare species (*Alveinus nitidus*). Therefore it is positioned with the samples from sandy sediments in the ordination, and we consider it to represent an ecological epibole (Brett et al., 1990). It may also indicate, however, that pelitic level-bottom assemblages in the HST differed strongly from those in the TST.

Macroscopic bioerosion and encrustation were generally rare. This points to high-sedimentation rates (especially for the pelitic deposits) and high-water energy in sandy-gravely sediments. The coral *Siderastrea*, however, whose recent representatives are known to colonize environmentally highly variable habitats with fluctuating temperature, salinity, and turbidity (e.g., Guzman and Tudhope, 1998), colonized some of the cobbles present in parasequence 2, which indicates their relatively stable position at the seafloor (Fig. 7).

### Community Replacement

The temporal pattern of biotic change recorded in particular vertical stratigraphic sections has been referred to as community replacement, and gradational faunal replacements commonly reflect a process termed habitat tracking (Miller, 1990; Brett, 1998). The replacements we observed in this study are better explained by the matrix and fabric of the bioclastic deposits than by stratigraphic categories. For example, the similarities in faunal composition between the basin shell beds and the uppermost benthic assemblages in the TST, and between parasequences 1 and 2 of the HST, are most likely due to similarities in sedimentary facies. The basin shell beds and the uppermost benthic assemblages in the TST are pelitic level-bottom assemblages and tempestitic shell beds with pelitic matrix. Samples in parasequence 1 and 2 are mostly from sandy level-bottom assemblages and tempestitic shell beds with sandy matrix. Conversely, the differences in sedimentary facies most likely explain the strong differences in faunal composition between the two basal parasequences and the basin shell beds.

Community replacements in the studied section correspond strongly to changes in the matrix and fabric of the bioclastic deposits and therefore reflect differences in the environmental conditions that shaped the benthic assemblages, but they also show taphonomic influences. The biostromal community in the oyster-vermetid boundstone shows faunistic overlaps with the pelitic level-bottom assemblage (R-value = 0.496), but it is well separated from all other bioclastic deposits (R-value > 0.8 in all cases). Correspondingly, the oyster-vermetid boundstone appears abruptly near the base of the TST, only few decimeters above a third-order sequence

**TABLE 6**—Characteristic species in the bioclastic deposits, calculated with similarity percentage analysis (SIMPER; see Clarke and Warwick, 1994). Characteristic species are those for which the ratio of average abundance to standard deviation of abundance is >1.

| Species | Average abundance | Average similarity | Sim/SD | Contrib% | Cum.% |
|---|---|---|---|---|---|
| **Sandy level-bottom assemblages** (4 samples) | | | | | |
| Average similarity: 36.03 | | | | | |
| *Gibbula pseudangulata* | 3.75 | 4.36 | 3.17 | 12.1 | 12.1 |
| *Glycymeris cf. pilosa* | 1.5 | 1.48 | 2.39 | 4.11 | 16.21 |
| *Bittium reticulatum* | 11.75 | 8.11 | 1.79 | 22.52 | 38.73 |
| *Ostrea digitalina* | 2 | 1.92 | 1.54 | 5.33 | 44.06 |
| *Tricolia eichwaldi* | 6 | 4.71 | 1.48 | 13.09 | 57.15 |
| **Tempestitlc shell beds with sandy matrix** (3 samples) | | | | | |
| Average similarity: 55.61 | | | | | |
| *Loripes dentatus* | 8.33 | 5.9 | 234.4 | 10.6 | 10.6 |
| *Turritella erronea* | 3.67 | 2.73 | 13.57 | 4.91 | 15.51 |
| *Venus nux* | 1 | 0.68 | 13.57 | 1.23 | 16.74 |
| *Pelecyora islandicoides* | 1 | 0.68 | 13.57 | 1.23 | 17.97 |
| *Panopea menardi* | 1 | 0.68 | 13.57 | 1.23 | 19.2 |
| *Acanthocardia turonica* | 1 | 0.68 | 13.57 | 1.23 | 20.43 |
| *Amalda glandiformis* | 2 | 1.14 | 7.74 | 2.05 | 22.48 |
| *Bittium reticulatum* | 9 | 5.95 | 4.73 | 10.71 | 33.19 |
| *Conus dujardini* | 2 | 0.84 | 4.69 | 1.52 | 34.71 |
| *Turritella tricincta* | 1.33 | 0.84 | 4.69 | 1.52 | 36.23 |
| *Circomphalus subplicatus* | 1.33 | 0.84 | 4.69 | 1.52 | 37.75 |
| *Antalis cf. quindeciesstriata* | 1.33 | 0.84 | 4.69 | 1.52 | 39.27 |
| *Tricolia eichwaldi* | 4.67 | 2.29 | 3.97 | 4.13 | 43.4 |
| *Gibbula pseudangulata* | 4 | 1.57 | 3.41 | 2.83 | 46.23 |
| *Ostrea digitalina* | 2.67 | 1.57 | 3.41 | 2.83 | 49.06 |
| *Glycymeris cf. pilosa* | 1.33 | 0.79 | 3.41 | 1.41 | 50.47 |
| *Aporrhais pespelecani* | 3 | 1.36 | 2.58 | 2.44 | 52.91 |
| *Turritella bicarinata* | 5 | 2.88 | 2.14 | 5.19 | 58.1 |
| *Glans subrudista* | 2 | 0.93 | 1.94 | 1.67 | 59.77 |
| Serpulidae indet (incl. *Protula protensa*) | 2.33 | 1.15 | 1.63 | 2.06 | 61.83 |
| *Paroxystele orientalis* | 3.67 | 2.11 | 1.52 | 3.79 | 65.62 |
| *Corbula gibba s.l.* | 19.67 | 9.39 | 1.31 | 16.89 | 82.51 |
| *Gouldia minima* | 3.33 | 1.37 | 1.26 | 2.46 | 84.97 |
| **Pelitic level bottom assemblages** (5 samples) | | | | | |
| Average similarity: 31.81 | | | | | |
| *Venus nux* | 3 | 0.85 | 1.12 | 2.66 | 91.34 |
| **Tempestitic shell beds with pelitic matrix** (5 samples) | | | | | |
| Average similarity: 89.45 | | | | | |
| *Corbula gibba s.l.* | 1031.8 | 85.83 | 25.5 | 95.95 | 95.95 |
| **Oyster-vermetid boundstone** (5 samples) | | | | | |
| Average similarity: 43.61 | | | | | |
| *Ostrea digitalina* | 70.4 | 17.21 | 2.01 | 39.46 | 39.46 |
| *Alvania ampulla* | 40.2 | 6.35 | 2.01 | 14.56 | 54.02 |
| *Vermetus arenarius* | 18.8 | 3.72 | 1.94 | 8.54 | 62.56 |
| *Petaloconchus intortus* | 9.8 | 1.66 | 1.79 | 3.81 | 66.37 |
| *Alvania transiens* | 20.2 | 1.6 | 1.48 | 3.67 | 70.04 |
| *Chama gryphoides* | 8.8 | 0.88 | 1.05 | 2.02 | 72.06 |

**TABLE 7**—Results of ANOSIM (analysis of similarity) for the five types of bioclastic deposits. Statistical decisions are based on R-values, which give an absolute measure of how separated the groups are. For high R-values, significance levels can be low because of few replicates in each group (for details, see the Materials and Methods section). For explanation of abbreviations, see Table 1; s = significant; ns = not significant.

| Bioclastic accumulations | R-stat | Description of assemblages (based on R-values) | *P*-value | Statistical decision |
|---|---|---|---|---|
| total | 0.635 | overlapping but clearly different | 0.001 | s |
| SLA vs. TSBS | 0.13 | barely separable | 0.257 | ns |
| SLA vs. PLA | 0.381 | strongly overlap | 0.063 | s |
| SLA vs. B | 0.838 | well separated | 0.008 | s |
| SLA vs. TSBP | 0.944 | well separated | 0.008 | s |
| TSBS vs. PLA | 0.303 | strongly overlap | 0.089 | s |
| TSBS vs. B | 1 | well separated | 0.018 | s |
| TSBS vs. TSBP | 1 | well separated | 0.018 | s |
| PLA vs. B | 0.496 | overlapping but clearly different | 0.008 | s |
| PLA vs. TSBP | 0.366 | strongly overlap | 0.008 | s |
| B vs. TSBP | 1 | well separated | 0.008 | s |

FIGURE 5—The oyster-vermetid boundstone showing distinct upward growth of the vermetid gastropods and the pelitic matrix.

boundary; in samples above the biostrome (F6, F7, F8), however, vermetids as well as oysters gradually decrease and infaunal elements become more abundant. Therefore, the biostrome development reflects a unique but brief set of environmental conditions connected to an important transgressive episode that did not seriously affect the long-term metacommunity. The strong overlap between sandy and pelitic level-bottom assemblages (R-value = 0.381) probably indicates gradational faunal replacements along an onshore-offshore gradient. The sandy level-bottom assemblages and their storm-influenced shell beds are barely separable (R-value = 0.130), and pelitic level-bottom assemblages show strong overlaps in faunal composition with their tempestitic derivates (R-value = 0.366). This suggests that storms more strongly influenced the faunal composition of the tempestitic shell beds with pelitic matrix than those with sandy matrix. Strong similarities in faunal composition between pelitic level-bottom assemblages and sandy tempestites (R-value = 0.366), however, could indicate considerable storm-induced habitat mixing between assemblages from sandy substrates and pelitic substrates. Conversely, the strong separation of sandy level-bottom assemblages and pelitic, presumably distal tempestites (R-value = 0.944) suggests that the respective storms did not mix assemblages from different substrates but only concentrated faunas from fine-grained offshore habitats.

Environmental Factors

In this study, we interpret the first axis (DC1) as water depth. Species with low DC1 scores occur in offshore pelitic sediments, and species
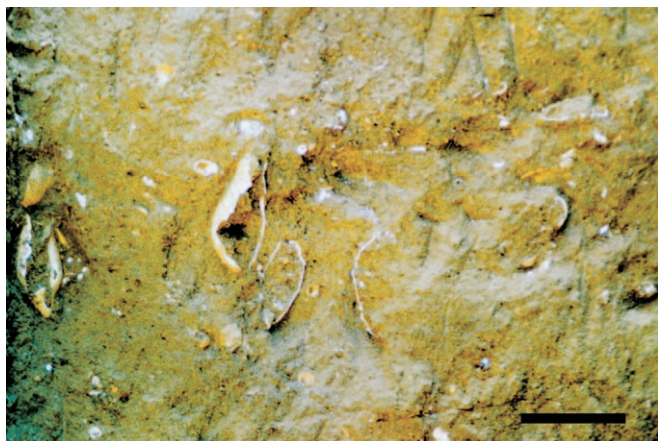


FIGURE 6—The deep infaunal *Panopea menardi* was the only bivalve in the level-bottom assemblages found in life position. Scale bar = 10 cm.



FIGURE 7—Cobbles in parasequence 2, encrusted by the coral *Siderastrea*, indicating stable position at the seafloor. Scale bar = 1 cm.

with high DC1 scores occur in onshore sandy sediments or boundstones. We interpret the second axis (DC2) as reflecting hydrodynamic energy (or, alternatively, substrate consistency) because this factor separates the onshore sandy assemblages (indicating higher hydrodynamic regimes) from the onshore biostrome, which developed in a very shallow, but quiet-water, regime. Water depth is therefore the dominant source of faunal variation in this study and most likely reflects the combined influence of many environmental parameters that are highly correlated and that change systematically with water depth and distance from the shore (e.g., wave shear stress, grain size, temperature, salinity, oxygen concentration, nutrient levels, and biotic interactions; for a short discussion and references, see Holland, 2005). The influence of depth, however, is certainly scale dependent. Previous paleoecological studies have already shown that, when a significant amount of shelf area is examined, the dominant source of faunal variation is highly correlated with bathymetry (Holland et al., 2001; Scarponi and Kowalewski, 2004). If a limited range of water depths is sampled, other factors will become the dominant control on community composition. For example, in the environmentally complex recent Red Sea, the basin-scale distribution pattern of bivalves is well explained by bathymetry (Grill and Zuschin, 2001), but at the scale of a highly structured shallow-water bay, the distribution pattern of mollusks occurs primarily along substrate gradients, which are only partly influenced by water depth (Zuschin and Hohenegger, 1998; Zuschin et al., 2001).

Environmental disturbances recognized in the studied section are of two types, each with different consequences for paleocommunity dynamics. The disjunct biotic replacement, manifested in the oyster-vermetid biostrome, occurs above a third-order sequence boundary (i.e., the VB5 and VB6 cycle) in the Vienna Basin (Weissenbäck, 1996; Kováč et al., 2004). Therefore, this sea-level change had a strong impact on short-term environmental conditions but did not seriously affect the long-term composition of biofacies. This is indicated by the faunal gradient from the biostrome into normal pelitic level-bottom assemblages, the latter showing overlaps in faunal composition with sandy level-bottom assemblages.

Episodic, short-term disruptions by storms are documented throughout the section by frequent winnowed and allochthonous shell beds. These events shaped the faunal composition in the benthic assemblages, probably because of size sorting and shape sorting during transport (e.g., Westrop, 1986; Zuschin et al., 2005); this is supported by differences between level-bottom assemblages and their tempestitic derivates. The storms also influenced the faunal gradients because samples from tempestitic shell beds tend to have lower DC1 scores than the respective samples from sandy and pelitic level-bottom assemblages. The storms are also responsible for some degree of habitat mixing, as indicated by the overlap in faunal composition between tempestitc shell beds with sandy matrix and pelitic level-bottom assemblages. The storms, however, had no major affect on overall biofacies composition because parautochthonous level-bottom assemblages are still present in the section and paleocommunity composition corresponds well to the matrix and fabric of the bioclastic deposits. Any other evidence for local and short-term disruptions was presumably smoothed out by time averaging (Schopf and Ivany, 1998).

### Habitat Tracking and the Nature of Paleocommunities

Habitat tracking is the lateral migration of species or associations of species in response to shifting environments; it implies the persistence of relatively stable environmental gradients through time (Brett et al., 2007). Evidence for habitat tracking can be established by comparing biotic contents between the same types of lithofacies in similar environments (Ivany, 1996). In our study, only the assemblages from coarse-grained shoreface sediments are sufficiently abundant to allow a quantitative comparison between stratigraphic units. These sediments are characterized by very similar, storm-influenced, benthic assemblages and suggest the recurrence of largely the same assemblage, when environmental conditions are appropriate.

Additional evidence for habitat tracking is provided by the results of explorative multivariate techniques, which suggest that the benthic assemblages are characterized by different degrees of mutual overlap in faunal composition. Sandy and pelitic level-bottom assemblages are very similar to each other, and pelitic level-bottom assemblages show a gradient into the oyster-vermetid boundstone; the latter, however, differs strongly from the sandy level-bottom assemblage. This suggests that the benthic assemblages belong to the same basic metacommunity, whose species "track" their favored environmental conditions. Accordingly, most species assemble in transient associations along the dominant environmental gradients, without evidence of tight community integration (Hoffman, 1979; Jablonski and Sepkoski, 1996). The comparatively distinct benthic assemblage in the oyster-vermetid biostrome, however, is tied to the very unique set of environmental conditions that prevailed during the early transgression above the third-order sequence boundary and, therefore, occurs only once in the studied section.

### CONCLUSIONS

The fossils of this section generally indicate a fully marine, warm-water, inner-shelf setting, but the range of sediments present and the different life habits of the fauna suggest very heterogeneous habitats and depositional environments. These environments were frequently disturbed by storms, which shaped the faunal composition in the level-bottom assemblages. Storms were responsible for some degree of habitat mixing and influenced the faunal gradients, but they had no significant influence on the long-term development of the benthic assemblages.

The most important structuring environmental parameters of the benthic assemblages are bathymetry and hydrodynamic energy. Level-bottom assemblages are from sandy to gravely shoreface habitats and offshore pelitic habitats, and they show strong overlaps in faunal composition. The comparatively distinct assemblage from the oyster-vermetid biostrome occurs in a shallow, but quiet-water, environment with high-sedimentation rates.

The faunal replacements observed in the studied interval are gradual and well explained by changes in the matrix and fabric of the bioclastic deposits. The sudden appearance of an oyster-vermetid biostrome is associated with the transgression above a third-order sequence boundary. Nevertheless, the oyster-vermetid biostrome stands for a very unique, but short-lasting, set of environmental conditions that did not seriously affect the long-term metacommunity.

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