

# Preservation of Autochthonous Shell Beds by Positive Feedback between Increased Hardpart-Input Rates and Increased Sedimentation Rates

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## ABSTRACT

The preservation of nonrapidly buried autochthonous shell concentrations with noncementing epifaunal animals in life position presents a taphonomic dilemma if in fact an increase in shelliness is driven by a decrease in sedimentation rate. A 150-cm-thick, densely packed shell bed with brachiopods from the Lower Jurassic of Morocco shows lower levels of postmortem alteration than shell-poor beds, indicating that its formation is primarily governed by variations in hardpart-input rates. Varying dominance and size structure of the main shell producer, brachiopod *Zeilleria rehmanni*, indicate that its increased population density was the main trigger in the shell bed formation. Thinner and less common microbial crusts in the shell bed than in shell-poor beds indicate that higher shelliness is not due to lack of sediment. On the basis of actualistic data from modern mussel and oyster shell beds, the suspension feeding of a high-density population leads to high biodeposition rates through production of feces and pseudofeces, which substantially exceed natural sedimentation rates. In addition, shell-rich areas preferentially trap more suspended sediment than shell-poor areas. Therefore, an increase in population density of shelly biodeposit producers should lead to higher biodeposition rates. This assumption is supported by a positive correlation between brachiopod shelliness and pellet abundance. Both active biodeposition and passive trapping of sediment would have increased sedimentation rate, thus leading to a decreased rate of shell destruction through suppression of predators or borers as well as stabilization and protection of the shell concentration. Under optimum ecologic conditions, these processes result in a positive feedback between an increased hardpart-input rate and increased biogenic sedimentation rate. This scenario thus provides one alternative pathway for formation of well-preserved shell concentrations formed by epifaunal suspension feeders. Identifying the importance of biodeposition is of environmental significance because it implies that carbonate sediment was produced largely in situ and was directly or indirectly related to the activity of shell producers. Recognizing the role of varying hardpart-input rates in shell concentration genesis is of ecologic significance because shelliness can directly reflect abundance fluctuations of shell producers.

**Online enhancement:** table.

## Introduction

Shell concentrations are repositories rich in paleobiologic and environmental information (Kidwell 1991a; Kowalewski et al. 1998) and reflect conditions when shell supply substantially exceeds shell loss and the net shell input is not diluted by sediment. Sites of slow net rate of sedimentation turn out to be more favorable for formation of denser shell concentrations than sites of higher net rate of

sedimentation (the low-dilution maxim of Kidwell [1991a] and Brett [1995]). Kidwell (1985, 1986a) found that most preservational variations of shell concentrations and their postmortem bias can be explained by variations in the rate of sedimentation. Sedimentologic or stratigraphic evidence supports the low-dilution maxim scenario (Beckvar and Kidwell 1988; Kidwell 1989, 1993; Abbott 1997, 1998; Naish and Kamp 1997; Kondo et al. 1998; del Río et al. 2001; Fürsich and Pandey 2003; Parras and Casadío 2005), implying that maximum shelliness is indeed more related to lack of dilution by sediment rather than to a peak in shell produc-

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tion. However, several studies proved the importance of dead shell production rates and shell destruction rates (i.e., hardpart-input rates in terms of Kidwell [1985, 1986a]) in shell concentration genesis (Allmon 1993; Meldahl 1993; Allmon et al. 1995; Boyajian and Thayer 1995; Kowalewski et al. 2000; Nebelsick and Kroh 2002; Carroll et al. 2003; Wehrmann 2003; Tomašových 2004).

Kidwell (1985, 1986a) showed that when varying sedimentation rates govern shell bed formation (i.e., R-sediment model), a positive correlation between the shelliness and assemblage-level alteration is predicted. This prediction reflects a paradoxical effect of decreased sedimentation rate on shell bed genesis, explicitly discussed by Kidwell (1985, 1986a, 1989): although reduced sedimentation rates can lead to a higher shell density via lower dilution and higher shell productivity, they also lead to higher alteration levels. Densely packed shell concentrations with shells less altered than in shell-poor deposits thus contradict this prediction. Such concentrations are typically explained by rapid burial events (Fürsich 1980). Nonevent shell concentrations with very low alteration levels thus require some scenarios that can lead to a negative correlation between shelliness and alteration. As an alternative to the R-sediment model, the R-hardpart model of Kidwell (1985, 1986a) states that the variations in shelliness are primarily driven by variations in hardpart-input rates (i.e., dead shell production and shell destruction rates). Tomašových et al. (2006) show that the R-hardpart model is also predictive and leads to a negative correlation between shelliness and assemblage-level alteration. Taphonomic pathways that are related to the R-hardpart model can thus be more suitable for an explanation of shell concentrations that show low alteration levels than pathways related to variations in sedimentation rates.

This study provides an example of how the prediction of the R-sediment and R-hardpart models can be evaluated with empirical data. We test whether variations in hardpart-input rates or variations in sedimentation rates better explain the genesis of a 150-cm-thick shell bed from the Lower Jurassic of the Central High Atlas (Morocco). The shell bed contrasts with shell-poor beds in the same formation, where brachiopods are highly altered. In the first part of this article, the trends observed in the shell bed are compared with the predictions of the R-sediment and R-hardpart models. In the second part, additional sedimentologic and stratigraphic evidence is used to assess possible covariations between sedimentation and hardpart-input rates. The study provides some general implica-

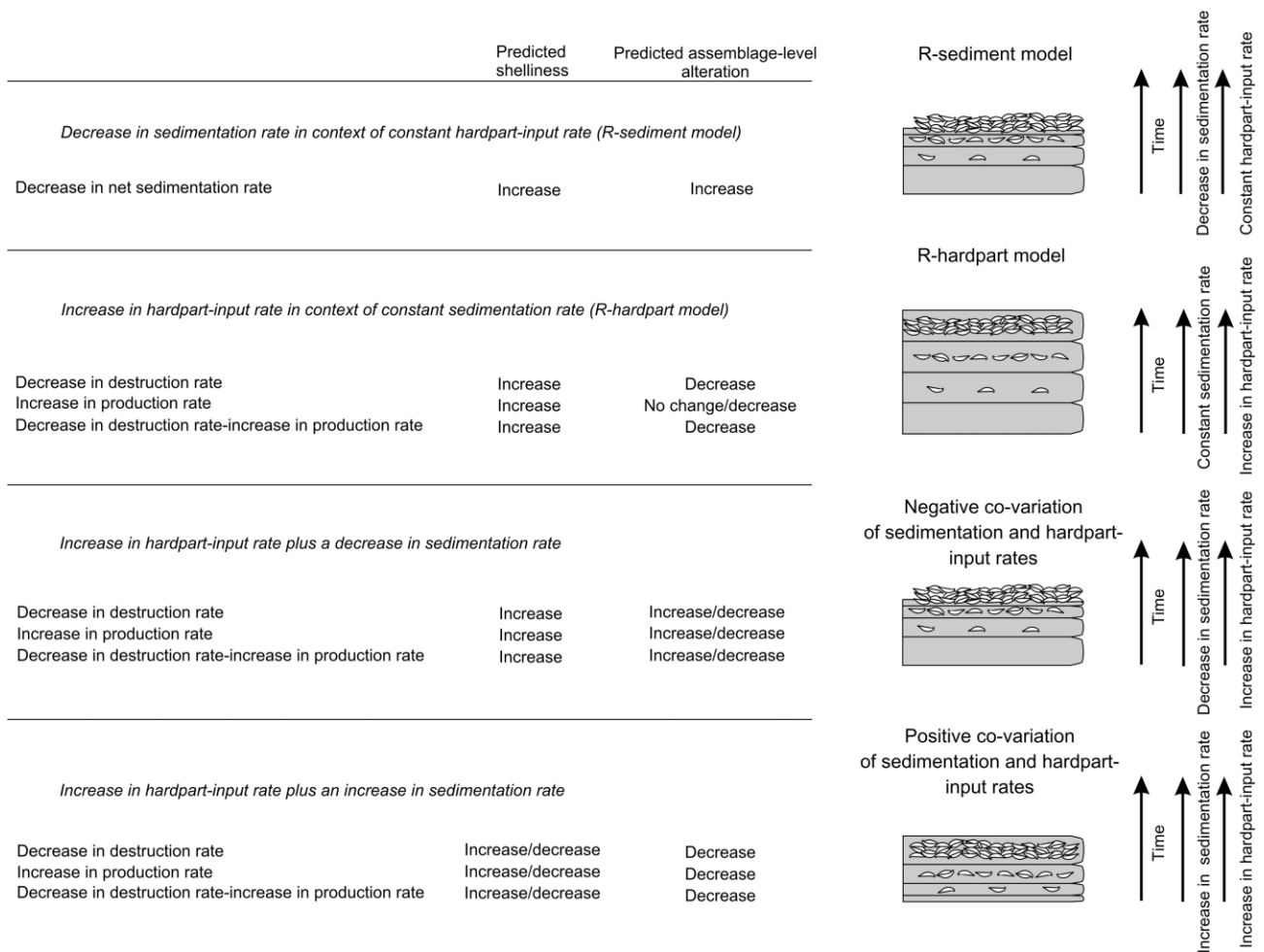
tions for taphonomic and environmental analyses. First, it indicates that variations in shelliness can directly reflect abundance fluctuations of shell producers. Second, the mechanism of shell bed origin proposed here can enlighten formation of other well-preserved nonevent shell concentrations dominated by epifaunal suspension-feeders (Kidwell 1985, 1986a). Third, the proposed explanation coupled with biodeposition provides specific information about sedimentary regime, so its recognition can be of significance in environmental analyses.

### Theoretical Scenarios for Shell Concentration Genesis

Kidwell (1985, 1986a) proposed four basic heuristic scenarios for evaluation of genesis of shell concentrations, based on two parameters (i.e., net sedimentation rate and net hardpart-input rate). Two scenarios include (1) the R-sediment model (sedimentation rates vary and hardpart-input rates are constant) and (2) the R-hardpart model (sedimentation rates are constant and hardpart-input rates vary). They are complemented by two scenarios in which sedimentation rates and hardpart-input rates covary positively or negatively.

Owing to the fact that under reduced sedimentation rates shells accumulate at or just below the sediment-water interface and are also longer exposed to many postmortem processes, the R-sediment model predicts that there will be a positive correlation between shelliness and taphonomic alteration (Kidwell 1985, 1986a; Flessa et al. 1993; Meldahl et al. 1997). Although the R-sediment model was originally proposed to explain the strong association of shell concentrations with stratigraphic discontinuities (bedding planes to unconformities), this prediction should be applicable to any shell concentrations that are related to a decrease in net sedimentation rates.

If hardpart-input rates vary and sedimentation rates are kept constant, correlation between shelliness and alteration is expected to be negative owing to (1) the suppression of shell destruction rates, (2) a combination of decreased shell destruction rates and increased rate of production of dead shells, or, under some conditions, (3) increased rate of production of dead shells alone (fig. 1; Tomašových et al. 2006). This negative correlation exists because, on the one hand, an increase in net hardpart-input rate should lead to higher shelliness, all else being equal. On the other hand, a decrease in the rate of shell destruction also decreases the proportion of altered shells. A higher rate of dead



**Figure 1.** Summary of predictions for four scenarios with varying sedimentation and hardpart-input rates. Four scenarios are based on work by Kidwell (1985, 1986a). Four drawings graphically illustrate changes in sedimentation and hardpart-input rates. The predictions are based on works by Kidwell (1985, 1986a) and Tomašových et al. (2006). For simplification, the change in the thickness of beds in the drawings is equivalent to the change in the sedimentation rate.

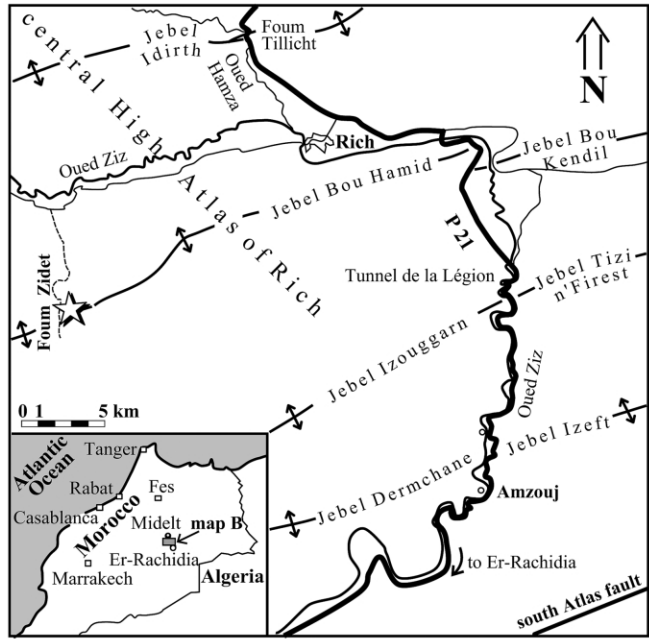
shell production might also lower the proportion of altered shells if it is associated with positive background sedimentation rates or if younger shells accumulate on top of older shells and thus decrease the postmortem exposure time of the older shells. Explicit comparison of shelliness and taphonomic alteration thus allows distinguishing the role of hardpart-input (R-hardpart model) and sedimentation rates (R-sediment model) in formation of shell concentrations.

If sedimentation rates covary with hardpart-input rates, predictions with respect to the shelliness and assemblage-level alteration depend on the relative difference between these two rates. Such covariation can also lead to negative correlation between the shelliness and assemblage-level altera-

tion (fig. 1). It is important to note that a negative correlation is primarily caused by the effect of varying hardpart-input rates and cannot be explained solely by variations in sedimentation rates. The predictions for four scenarios based on Kidwell's (1985, 1986a) approach are summarized in figure 1.

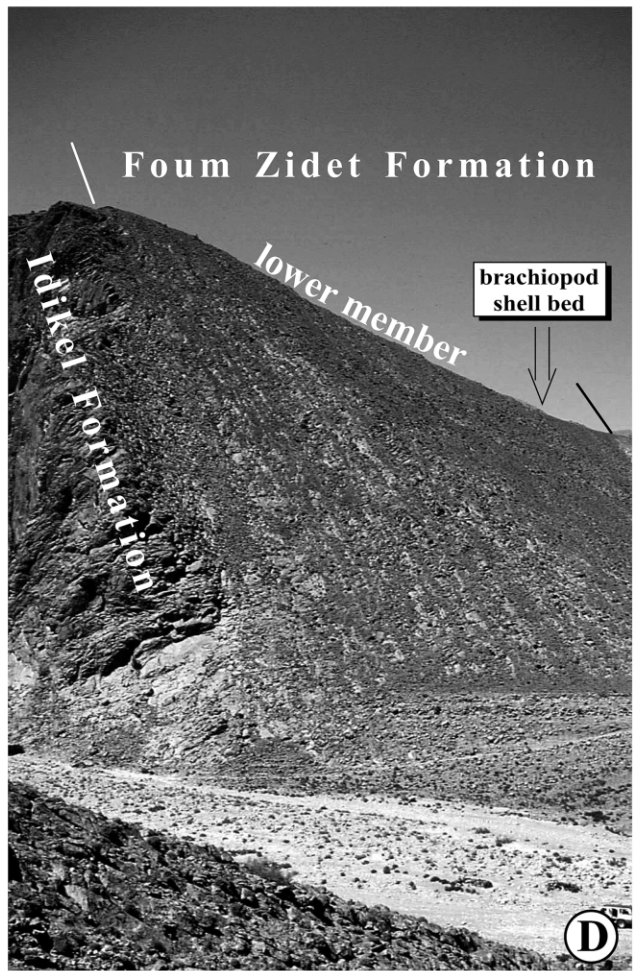
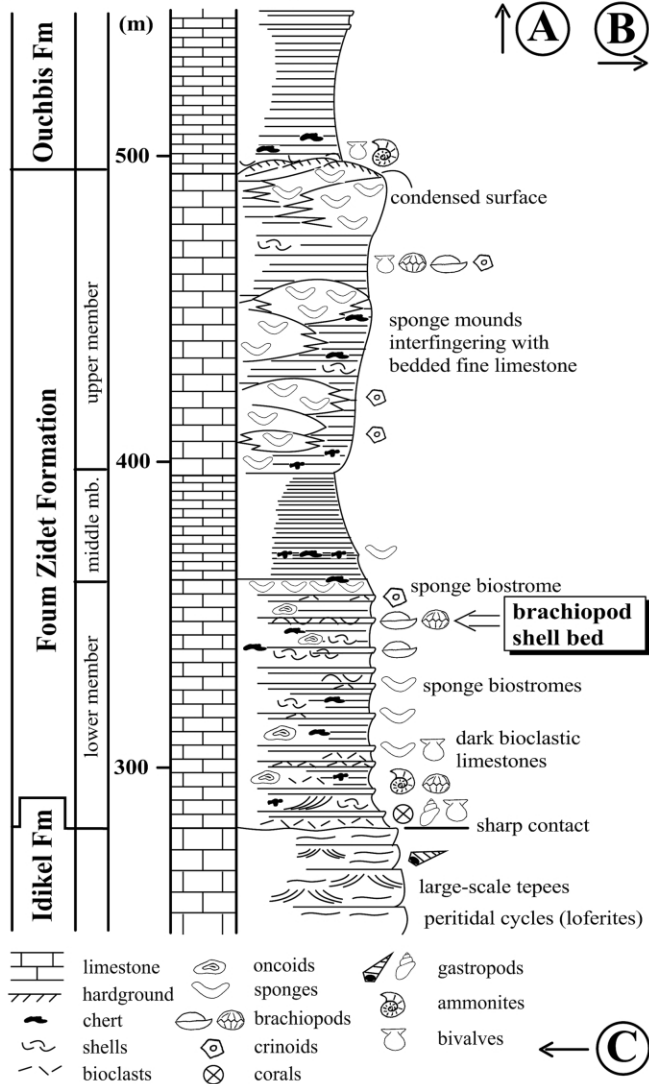
### The Brachiopod Shell Bed of the Lower Jurassic of Morocco

The central High Atlas forms part of an inverted basin that developed in response to widespread Triassic/Jurassic intracontinental rifting during the opening of the Atlantic system and a westward-proceeding enlargement of the Tethyan Realm (e.g., Jacobshagen et al. 1988). The Central High Atlas



Series	Stage	Substage	ammonite biozonation	central High Atlas of Rich		
				Tunnel de la Légion	Foum Zidet	Foum Tillicht
Lower Jurassic	Toarcian	Lower	<i>falciferum</i>	Tagoudite Formation		
			<i>tenuicostatum</i>			
	Pliensbachian	Upper	<i>spinatum</i>	Ouchbis Formation		
			<i>margaritatus</i>			
		Lower	<i>davoiei</i>			
			<i>ibex</i>			
Sinemurian	Upper		<i>jamesoni</i>	Aberdouz Fm		
			<i>rari-costatum</i>			
		<i>oxynotum</i>	Foum Zidet Formation			
		<i>obtusum</i>				
Lower		not zoned	Idikel Formation			

ammonite data  
 dolomites  
 limestone  
 rhythmites  
 marl



- limestone
- hardground
- chert
- shells
- bioclasts
- oncoids
- sponges
- brachiopods
- crinoids
- corals
- gastropods
- ammonites
- bivalves



Basin opened at a paleolatitude of ca. 15°–20°N, reaching a maximum width of ca. 110 km (Beauchamp et al. 1999; Arboleya et al. 2004). During the Late Sinemurian, it formed an intrashelf basin subdivided into fault-controlled tectonic blocks, possibly with one or more central basin highs. The section at Fom Zidet with the brachiopod shell bed is situated in the Rich area (fig. 2A, 2B) and corresponds to the hanging wall of the Rich fault block. It exposes a 280-m-thick package of peritidalites of the Idikel Formation, which is unconformably overlain by shallow to deeper subtidal limestones of the 220-m-thick Fom Zidet Formation of Late Sinemurian age (Lachkar et al. 1998; Wilmsen et al. 2002; Mehdi et al. 2003). A ca. 500-m-thick succession of the Ouchbis Formation of Late Sinemurian–Pleinsbachian age completes the section at Fom Zidet.

The Fom Zidet Formation, at the base with a marked transgressive event, reflects a relative sea level rise, probably leading to restricted within-basin circulation and development of the oxygen-minimum zone in deep-water parts of the basin (Neuweiler et al. 2001). It contains three informal members (fig. 2C; Mehdi et al. 2003). The lower member consists of dark-colored, micrite-rich bioclastic limestones with abundant brachiopods, oysters, siliceous sponges, crinoid fragments, ferruginous oncoids, and microbialites. Near the top of the lower member, a 1.5-m-thick and laterally persistent shell bed of densely packed brachiopods occurs. It is underlain by an interval formed by bioclastic floatstones and less common oncoidal floatstones and overlain mainly by oncoidal floatstones with several bioclastic floatstone interbeds. This bed is the scope of this study. The presence of brachiopods in this member corresponds to an initial phase during which brachiopods dominate in level-bottom communities in the southwestern Tethys (Dubar 1942; Colo 1961; Almérás 1993; Almérás and Elmi 1993). The middle member consists of an alternation of bioturbated argillaceous limestones and silty marls. The upper member consists of meter- to decameter-scale thrombolitic siliceous sponge mounds embedded in rhythmically bedded

argillaceous limestones (Neuweiler et al. 2001). The distribution of extensive sponge mounds seems to be preferentially bounded to the upturned, foot wall edges of fault blocks that formed during the initial rifting (Evans and Kendall 1977; Milhi et al. 2002).

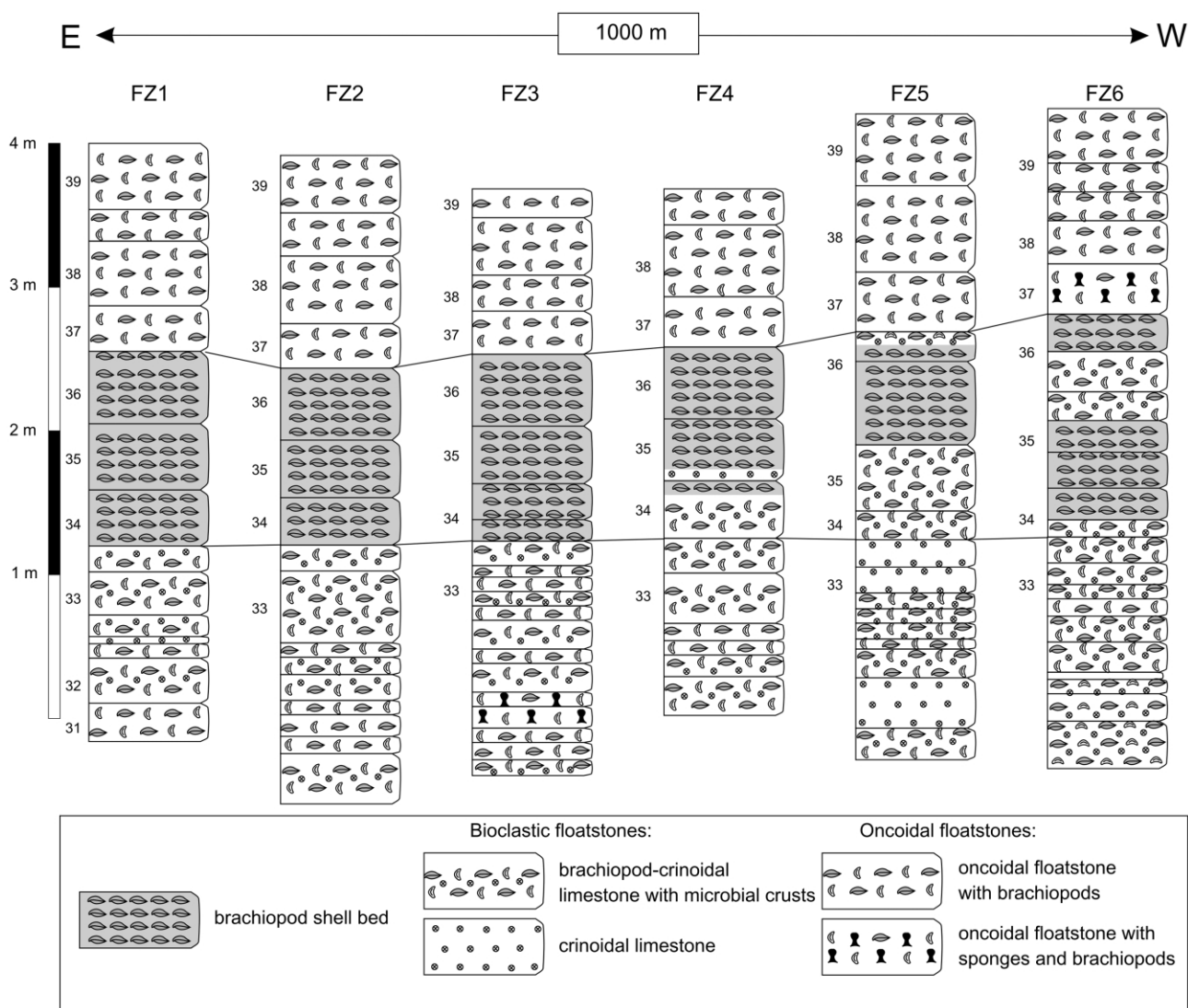
### Methods

The brachiopod shell bed was traced in six stratigraphically equivalent sections (fig. 3), with a between-section distance of about 200 m. Fifteen thin sections were analyzed in total, including four thin sections from the 7-m-thick interval below the shell bed, five thin sections from the brachiopod shell bed, one thin section from its lateral equivalent, and five thin sections from the overlying 5-m-thick interval with shell-poor beds (fig. 3; table A1 available in the online edition or from the *Journal of Geology* office). The shelliness and pellet abundance were estimated by a semiquantitative comparative method as the areal proportion of components in thin sections (Schäfer 1969). Because of the difference in the percent area measures of articulated shells and disarticulated valves, the grain-solid method (area of solid skeletal material is estimated only) and the grain-bulk method (solid skeletal material plus all voids enclosed in the shell are estimated) give different results of shelliness (Jaanusson 1972). The grain-bulk method could lead to artificial differences in shelliness if samples with differential proportions of articulated shells are compared. Because of this inflation, the grain-solid method is used in this study. We use the terms “shell-rich bed” for the shell bed and “shell-poor beds” for the underlying and overlying beds. Because the shell bed contains predominantly brachiopods, only brachiopod shelliness was compared among the samples in order to minimize the effect of other taxa on measured shelliness.

The relative abundance of disarticulated, fragmented, encrusted, surface-altered, and bored brachiopods and brachiopods coated with microbial crusts in each thin section was scored under magnification up to  $\times 50$ . The number of scored spec-

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**Figure 2.** A, Locality details of the Fom Zidet section (*star*) in the central High Atlas of Rich, Morocco. B, Litho- and biostratigraphic framework of the central High Atlas of Rich (modified after Wilmsen et al. 2002). The stratigraphic interval of the section in figure 1C is indicated. C, Generalized section of the Fom Zidet Formation at Fom Zidet. The studied brachiopod shell bed occurs near the top of the lower member of the formation. D, Field photograph of the section FZ2 showing the lower part of the Fom Zidet Formation, with approximate position of the brachiopod shell bed.



**Figure 3.** Variations in vertical and horizontal features of the Fom Zidet shell bed and its relationship to underlying and overlying beds in six correlated sections (FZ1–FZ6); 33–39 = bed numbers.

imens varies between 29 and 91 (see table A1). Brachiopods are incompletely silicified. Fragmentation refers to any breakage visible in a thin section. Encrustation refers to foraminifers, bryozoans, serpulids, agglutinated polychaetes, sponges, and oysters. Surface alteration (sensu Best and Kidwell 2000) denotes any microscopic irregularities, pitting, or delamination on the interior or exterior surfaces of brachiopod valves (i.e., it can be related to abrasion, maceration, dissolution, or very fine microbioerosion). Bioerosion refers to borings larger than 10  $\mu\text{m}$  in diameter. Microbial crusts refer to dark, nondestructive, micritic, or peloidal coatings. Because sieve size affects alteration levels in taphofacies analyses (Kidwell et al. 2001), only brachio-

pods larger than 1 mm were scored. Counting all fragments can be too conservative when evaluating proportions of disarticulation and fragmentation because number of disarticulated valves and number of fragments can be inflated. However, we found that differences between shell-rich and shell-poor beds are still significant with this conservative measure. Because the recognition of interior and exterior surfaces is difficult in small fragments, only those specimens that showed a given type of taphonomic alteration on both surfaces of the valves were scored. This method ensures that the estimated alteration is of postmortem origin. The difference in median proportions for each taphonomic variable between shell-rich and shell-poor

beds was evaluated with the Wilcoxon rank sum test. Correlation between brachiopod shelliness and a proportion of a given type of taphonomic variable (i.e., assemblage-level alteration) was evaluated with the Spearman rank correlation coefficient. In order to estimate community composition, two samples from the shell bed and two samples from shell-poor beds were dissolved with diluted hydrochloric acid and sieved through a 0.1-mm mesh sieve. The absolute abundances were converted into number of individuals as the sum of articulated shells plus the dominating number of either brachial or pedicle valves and converted to relative abundances. All measurable specimens were used for size-frequency distributions based on the length of pedicle valve.

## Results

**Brachiopod Shell Bed.** The shell bed is a biomicritic limestone with densely packed and poorly sorted brachiopods (fig. 4). It is dominated by the smooth terebratulid *Zeilleria rehmanni*, reaching sizes of 15–25 mm in the adult stage. Size-frequency distributions of *Z. rehmanni* are dominated by adult individuals, in contrast to the under- and overlying shell-poor beds that contain abundant juveniles (fig. 5). The multicostate rhynchonellid *Prionorhynchia* sp., small rhynchonellid *Squamirhynchia* sp., spiriferinids (*Liospiriferina* sp.), and inarticulate brachiopods (*Discinisca* sp.) are less common or rare. Bivalves are represented by relatively abundant epibyssate *Oxytoma* sp. reaching 1–2 mm in size.

The shell bed is internally subdivided into three layers by bedding planes, but the texture is homogeneous, with very minor vertical or lateral variations in shell packing, sorting, or community composition (fig. 4). There are no traces of erosion, omission, or macroscopic bioturbation. The matrix between the articulated brachiopod shells consists of a pelmicritic wackestone or packstone, with dispersed, poorly sorted, and randomly oriented millimeter-sized brachiopod and bivalve fragments, crinoids, microbial clasts, pellets, and nonrigid sponges. Pellets (5%–17.5%) reach 80–250  $\mu\text{m}$  in size. Thirty-five to 45 brachiopod shells counted per 100  $\text{cm}^2$  of top bedding plane gives about 3500–4500 individuals/ $\text{m}^2$ . The proportion of bioclasts (predominantly brachiopods) in thin sections reaches 60%–80% with the grain-bulk method and 15%–30% with the grain-solid method (fig. 6). Brachiopods are rarely disarticulated (6%–35%) and fragmented (6%–24%; fig. 7A). Only one sample

showed an anomalously higher proportion of disarticulation (71%) and fragmentation (69%).

Brachiopod shells are filled with micrite and abundant fecal pellets. In contrast to the matrix between the shells, the fillings are locally enriched with microbial coatings, sponge spicules, and polychaete tubes (*Terebella*). The shells are commonly oriented with pedicle openings downward, toward the adjacent shells. Based on analysis of 681 shells in side view, more than 50% of shells are oriented with their anteroposterior axis in oblique position with respect to bedding, at an angle higher than 25°. Thirty-three percent of shells are concordant to bedding, and 11% are vertically oriented. Small, several-centimeters-large shell clusters with partial or complete sparitic fillings are rarely observable. Encrustation and surface alterations are low (0%–9% and 0%–17%, respectively). Bioerosion is rare or absent (0%–2%). The proportion of specimens with microbial crusts is moderate (23%–48%); the external microbial crusts are very thin (<1 mm) and do not coalesce into a microbial framework. In contrast, the microbial crusts on internal shell surfaces can be several millimeters thick. Microbial crusts on external shell surfaces mostly do not cross the commissure.

**Shell-Poor Bioclastic and Oncoidal Floatstones.** In contrast to the shell bed, *Z. rehmanni* is less dominant, and the other brachiopods *Squamirhynchia* sp., *Liospiriferina* sp., and *Prionorhynchia* sp. and thecideid *Moorellina* sp. are common. Brachiopods are predominantly disarticulated (88%–100%) and fragmented (73%–95%), with a moderate or high proportion of microbial crusts (30%–79%) and encrustations by bryozoans, sponges, and foraminifers (7%–44%). The proportion of surface alteration attains 5%–31%. Pellets are less common than in the shell bed (1%–15%). Two deposit types are distinguished on the basis of the bioclast abundance and abundance and thickness of microbial crusts. The proportions of alteration in these two types are similar (fig. 7B, 7C).

Oncoidal floatstones are mainly overlying the shell bed and consist of dispersed, poorly sorted, and randomly oriented brachiopods (fig. 8A). They contain very common microbial crusts (25%–45% of thin section area). Planar or wavy microbial crusts are structureless or peloidal and commonly contain laminae stained with ferruginous pigment. They are mostly more than 2–3 mm thick and locally form several-centimeters-thick microbial oncoids. Microbial layers also alternate with crustose bryozoans and foraminifers. With the grain-solid method, the areal proportion of all bioclasts reaches



5%–20%, and that of brachiopods reaches 3.5%–10%.

Bioclastic floatstones are mainly present below the shell bed and consist of loosely packed, poorly/moderately sorted, and randomly or concordantly oriented brachiopods (fig. 8B, 8C). Bivalves, gastropods, crinoids, and siliceous sponges are also common. They contain 1–2-mm-thick microbial crusts that constitute only 2%–6% of thin section area. The proportion of all bioclasts attains 17.5%–22.5%; the brachiopod shelliness is between 7.5% and 15%. The oyster *Nanogyra nana* can be locally very common. Some beds of bioclastic floatstones show signs of complex stratification formed by centimeter-thick layers with variable shell packing. Articulated shells are commonly filled with sparite.

**Spatial Extent and Variations in Shell Bed Biofabric.** For a distance of about 600 m, the brachiopod bed exhibits a consistent thickness (1.5 m) and biofabric (sections FZ1–FZ3). Further to the west, the shell bed gradually passes into a bed of more or less the same thickness but that is formed by alternations of shell-rich layers (equivalent in fabric to the shell bed) and shell-poor, bioclastic floatstone layers (sections FZ4–FZ6). The shell-poor bed type is similar to the observed bioclastic floatstone underlying the shell bed itself in the east. In section FZ4, the basal, 40-cm-thick layer is internally stratified. It consists of a 10-cm-thick, shell-poor bioclastic floatstone with dispersed, small clusters of four to five articulated brachiopod shells, abruptly replaced by a 5-cm-thick, loosely to densely packed crinoidal packstone and followed again by a 15-cm-thick, shell-poor bioclastic floatstone with small clusters of articulated brachiopod shells. This gradually passes into a 10-cm-thick brachiopod shell-rich interval in the uppermost part of layer 34 (fig. 8D). Layer 35 starts similarly with a floatstone with small dispersed brachiopod clusters and is abruptly replaced by a 5-cm-thick crinoidal packstone (with sharp basal boundary and concordantly oriented crinoids), which is sharply overlain by a 30-cm-thick concentration with densely packed, articulated brachiopod shells. Such small-scale alternations of shell-rich and shell-poor layers are typical also of sections FZ5 and FZ6. Note that two cri-

noidal layers in section FZ4 are at the same stratigraphic level as bedding planes in adjacent sections FZ3 and FZ5.

**Comparing Shelliness and Assemblage-Level Alteration between Shell-Rich and Shell-Poor Beds.** Although semiquantitative estimation of shelliness in thin sections can be affected by large error and uncertainty, the resulting correlations between the proportions of taphonomic variables and brachiopod shelliness are consistently negative and of high or borderline significance. Brachiopods are consistently densely packed in the shell bed and dispersed or loosely packed in the underlying and overlying shell-poor beds (*sensu* Kidwell and Holland 1991). The estimated brachiopod shelliness is highest in the shell bed, followed by medium levels in the bioclastic floatstones and low levels in the oncoidal floatstones (fig. 9).

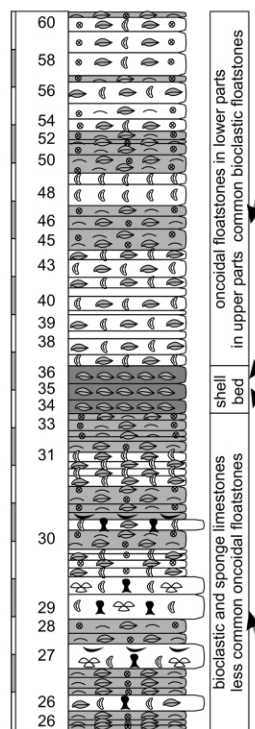
Comparing the samples from shell-rich and shell-poor beds, the Spearman rank correlation between brachiopod shelliness and assemblage-level alteration is always negative (fig. 10; table 1) and significant for disarticulation ( $P = 0.0026$ ), fragmentation ( $P = 0.023$ ), and surface alteration ( $P = 0.033$ ). It is negative but insignificant for bioerosion, microbial crusts, and encrustation. The Spearman rank correlation between pellet relative abundance and brachiopod shelliness is significantly positive ( $r = 0.57$ ,  $P = 0.0239$ ). The difference in the median proportion of pellets between shell-rich (10%) and shell-poor beds (3.75%) is also significant (Wilcoxon [Mann-Whitney  $U$ ] test,  $Z = 2.14$ ,  $P = 0.0311$ ).

The median proportions of disarticulation, fragmentation, and encrustation are significantly lower in shell-rich beds than in shell-poor beds (Wilcoxon [Mann-Whitney  $U$ ] test,  $P = 0.0022$  for the first two variables,  $P = 0.0143$  for the third variable; fig. 7D; table 2). Note that the  $P$  values can be the same because, due to low number of samples, the sums of ranks for the shell-rich and shell-poor beds are equivalent in some tests. The differences between median proportions of microbial crusts and surface alteration between shell-rich and shell-poor beds are of borderline significance ( $P = 0.05$  for both variables; table 2). We use noncorrected  $P$  values in the multiple testing because applying the Bonfer-

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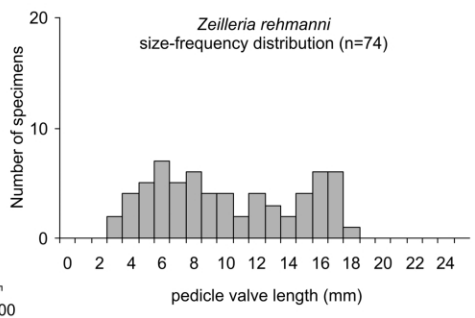
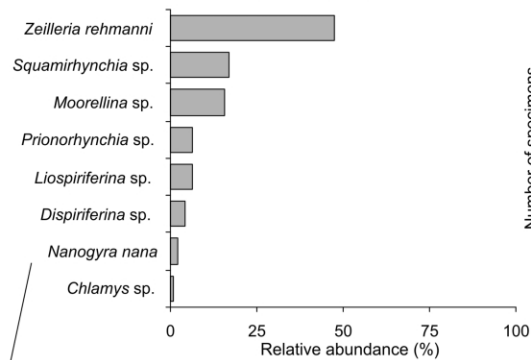
**Figure 4.** Field photographs of the Foug Zidet shell bed. *A*, Brachiopod shell bed (150 cm thick) in the Foug Zidet section (FZ1). *B*, Upper part of the shell bed (FZ1). *C*, Detailed view of the biofabric of the shell bed in its typical development (FZ1). *D*, Lateral equivalents of beds 35 and 36 in section FZ4, with crinoidal packstone at the base. Hammer (*A*) and lens cap (*B–D*) for scale.

Uppermost part of lower member of the Four Zidet Fm (FZ1)



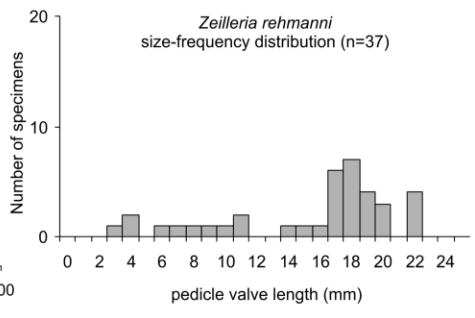
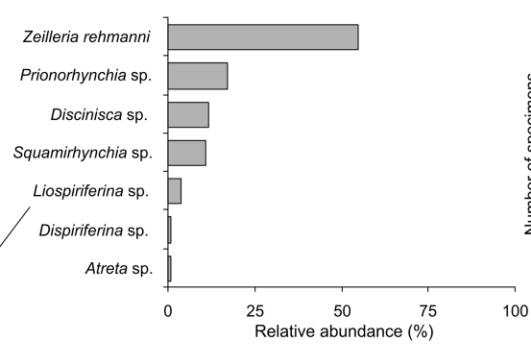
Shell-poor oncoidal floatstone - FZ1-38.2

Assemblage composition (n=95)



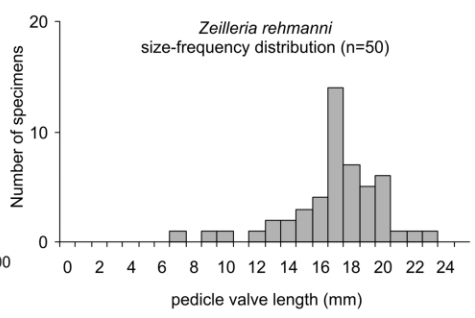
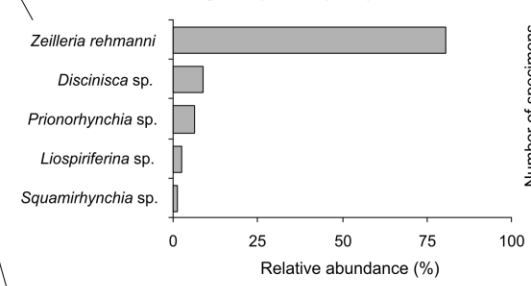
Brachiopod shell bed - FZ1-36

Assemblage composition (n=128)



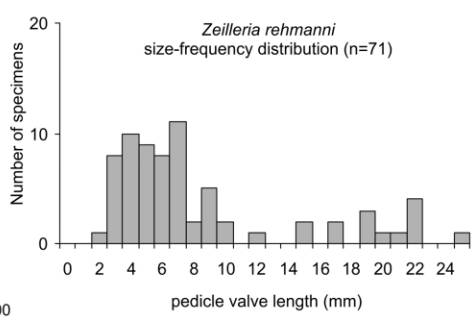
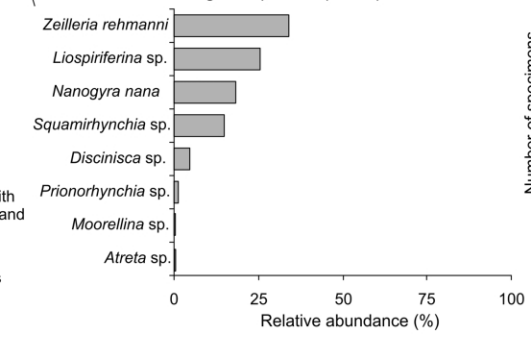
Brachiopod shell bed - FZ1-35

Assemblage composition (n=78)



Shell-poor bioclastic floatstone - FZ2-25

Assemblage composition (n=168)



roni correction for the dependent tests based on the same specimens would be highly conservative. If the Bonferroni correction would be used for correction of the multiple testing ( $\alpha = 0.05/6$ ), some significant results will become of borderline significance.

### Variations in Hardpart-Input Rates

Because the proportions of disarticulation, fragmentation, surface alteration, microbial crusts, and encrustation are higher in shell-poor beds than in the shell bed, the negative correlation between shelliness and assemblage-level alteration indicates a driving role of variations in hardpart-input rates in governing shelliness and assemblage-level alteration in the Foum Zidet shell bed. The higher shell density in the Foum Zidet shell bed is thus primarily a consequence of higher hardpart-input rate and not due to a passive accumulation of shells caused by nonsedimentation.

The role of increased rate of dead shell production in formation of the Foum Zidet shell bed is supported by two arguments. First, relatively lower proportions of juveniles of *Zeilleria rehmanni* in the shell bed than in shell-poor beds indicate a decreased juvenile mortality and higher production of adult shells (fig. 5). Second, the change in community composition between the shell bed and shell-poor beds also indicates the increased rate of dead shell production via an increase in community-level abundance of the main shell producer *Z. rehmanni* (fig. 5). Because thinner and less common microbial crusts demonstrate that the shell bed was not characterized by lower sedimentation rates than shell-poor beds, the higher shelliness is not related to decreased sediment dilution. A decrease in shell destruction rates and/or shorter exposure time due to higher sediment input could lead to lower alteration levels in the shell bed.

The spatial change in hardpart-input rate between the shell bed and its lateral shell-poor equivalents can be explained either by spatial patchiness of the brachiopod populations produced by irregular larval settlement and mortality or by the presence of a small-scale environmental gradient that governed the decrease in hardpart-input rate toward

the west. Lateral equivalents of the shell bed would thus correspond to zones of higher disturbance of brachiopod populations via either failed recruitment or locally more intense shell destruction (e.g., higher predation).

### Variations in Sedimentation Rates

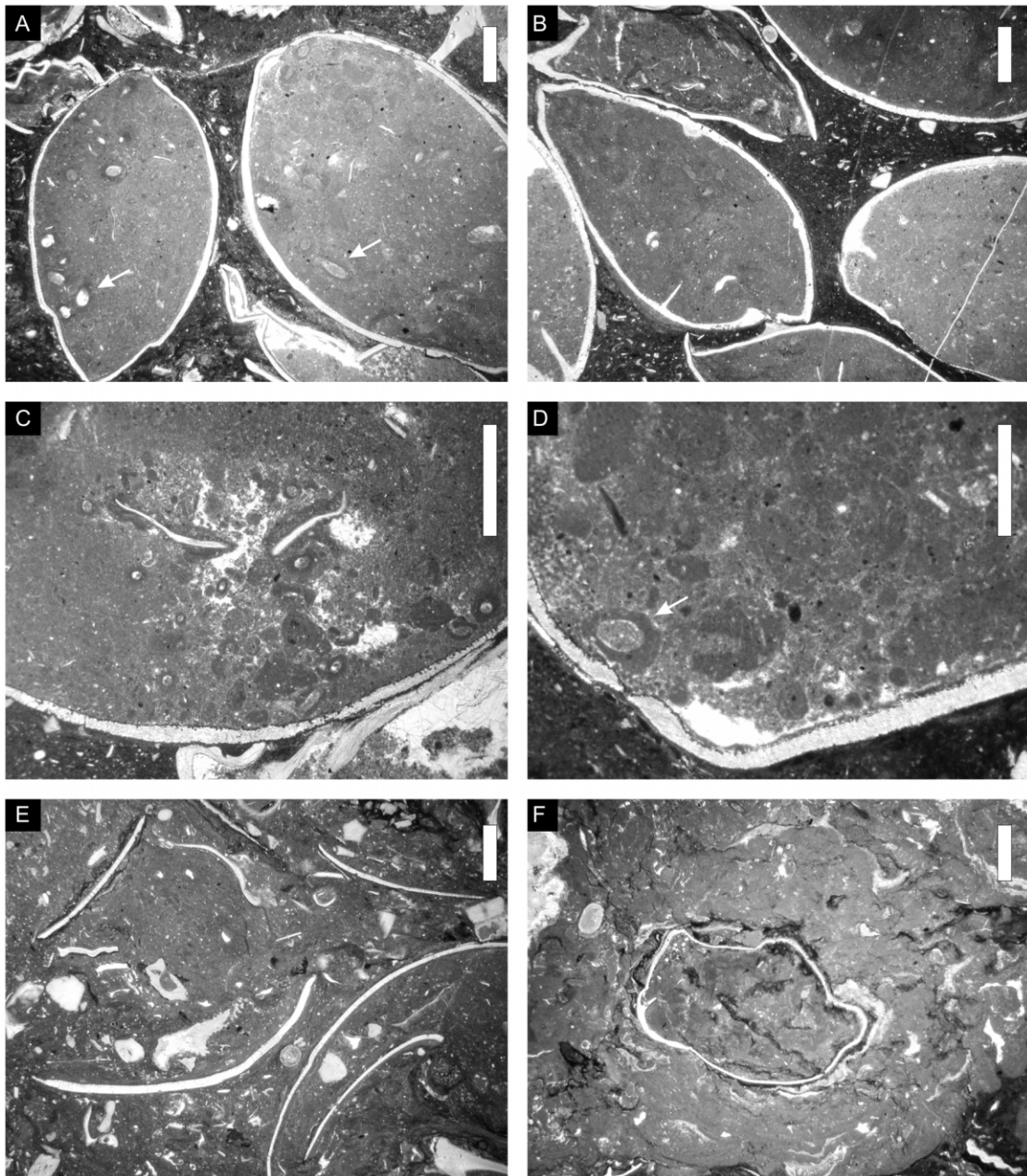
**Difference in Microfacies between Shell-Rich and Shell-Poor Beds.** The higher frequency and higher thickness of microbial crusts in shell-poor beds suggest that the sedimentation rate in those beds was distinctly lower than in the shell bed (Schmid et al. 2001). The presence of thin microbial crusts, encrusters, and cryptic biota within the brachiopod shells in the shell bed indicates that the dead shells were not immediately buried (Holland 1988). This intermediate stage of exposure did not last for a very long time after death of the brachiopods because micritic sediment completely fills most of the shells and microbial crusts do not coalesce into a continuous framework from shell to shell. Given that observed alteration levels are relatively uniform within the shell bed and micritic infillings are typical of the entire shell bed, this indicates an approximate equilibrium between net sediment accumulation and brachiopod growth. Although some brachiopods are probably displaced, inclined shells with the pedicle opening directed downward and close to other shells are probably still in their life position. Using two alternative estimates of brachiopod longevity (5 and 10 yr; James et al. 1992), if one generation forms a continuous shell cover that is 1 cm thick, then a 150-cm-thick shell bed will form in approximately 750 or 1500 yr. The shell bed thus grew gradually by attritional mortality of brachiopod clusters and developed gradually over a period of numerous generations, probably hundreds of years to millennia. The order of at least several hundred years indicates relatively stable conditions to enable this equilibrium growth.

**Actualistic Extrapolations from Bivalve Shell Concentrations.** Although continuous growth of the shell bed can be unrealistic, actualistic data from modern bivalve shell concentrations provide a plausible mechanism, which might have been re-

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**Figure 5.** Assemblage compositions and size-frequency distributions in four samples show higher dominance and lower proportions of juveniles of *Zeilleria rehmanni* in the shell bed than in the shell-poor bioclastic and oncoidal floatstones. The relative abundance plots were computed without the micromorphic bivalve *Oxytoma* sp. (1–2 mm in size) that can be numerically abundant in the shell bed.



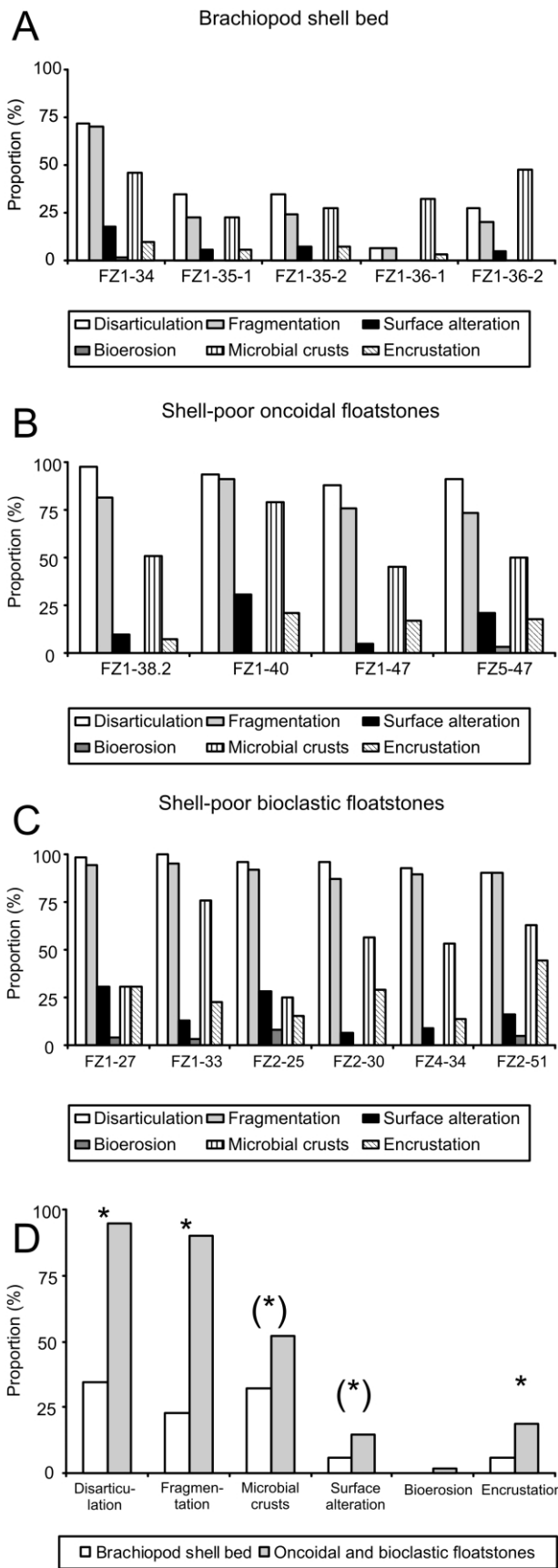


**Figure 6.** Shell-rich (A–D) and shell-poor beds (E, F) in thin sections show marked differences with respect to the thickness and abundance of microbial crusts. A, Brachiopods filled with abundant agglutinated polychaete tubes (*Terebella*; arrows). Sample FZ1-35, scale = 2 mm. B, Brachiopod shells probably still in growth position, covered with thin microbial crusts. Sample FZ1-36, scale = 2 mm. C, Interior of brachiopod shell with preserved brachidium coated with thin microbial crusts. Sample FZ1-36, scale = 2 mm. D, Interior of brachiopod shell with thin microbial crust, loosely packed microbial clasts, and *Terebella* (arrow). Sample FZ1-35, scale = 1 mm. E, Bioclastic floatstone with high proportion of disarticulated and fragmented valves. Sample FZ2-30, scale = 2 mm. F, Oncoidal floatstone with brachiopod shell coated by thick microbial crust. Sample FZ1-47, scale = 2 mm.

responsible for the equilibrium of brachiopod growth and sedimentation. Two main processes through which increased sedimentation consistently positively correlates with an increased hardpart-input

rate include (1) high biodeposition of feces and pseudofeces and (2) preferential trapping of sediment. These processes are typical of habitats where epifaunal bivalves (e.g., mussels and oysters) form



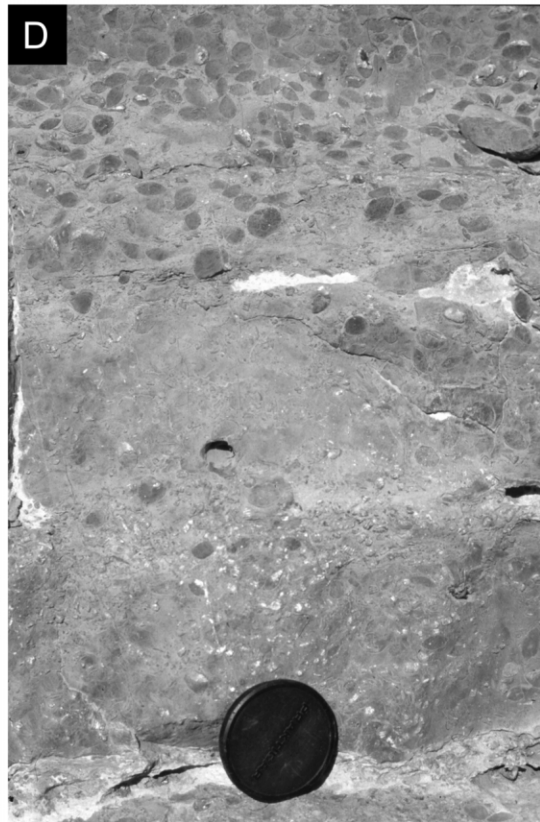


dense concentrations and substantially modify their own habitat (Kidwell and Jablonski 1983; Kidwell 1991*b*; Jones et al. 1997; Gutiérrez et al. 2003; Cohen 2005). Dense shell concentrations can influence their habitat by several interrelated processes, including altered burial rates; an altered hydraulic flow regime; altered community structure; an increase of delivery of food, oxygen, and sediment particles to the bottom; and an increase in habitat complexity and heterogeneity (Kidwell and Jablonski 1983; Kidwell 1986*b*; Pullen and La-Barbera 1991; Crooks and Khim 1999; Commito and Dankers 2000; Hartstein and Rowden 2004).

1. Dense populations of suspension feeders induce high production of feces and pseudofeces (i.e., biodeposition; Arakawa 1970; Haven and Morales-Alamo 1972; Graf and Rosenberg 1997; Jie et al. 2001). In habitats with dense shell concentrations (e.g., mussel farms), biodeposition rates can be substantially higher than natural net sedimentation rates (Jaramillo et al. 1992; Klerks et al. 1996; Jie et al. 2001; Norkko et al. 2001; Widdows et al. 2004). In addition, biodeposits usually have much higher settling velocities than their constituent particles, enhancing sedimentation rate (Miller et al. 2002; Giles and Pilditch 2004). Biodeposition rates can reduce turbidity and phytoplankton abundance and increase light penetration to the bottom (Klerks et al. 1996; Newell 2004), but they also shade and bury potential encrusters and borers (Albrecht 1998). Under very rapid biodeposition, the resulting microbial respiration reduces the oxygen content in organic-rich sediment, leading to reducing conditions (Mirto et al. 2000; Tsuchiya 2002; Christensen et al. 2003).

The high biodeposition rates in some bivalve shell concentrations may not be applicable to brachiopods because of known differences in metabolic and clearance rates between bivalves and brachiopods (Thayer 1986; Peck et al. 1987; Rhodes and Thayer 1991; Rhodes and Thompson 1993; Peck 1996). Because of their blind-ending guts, articulate brachiopods fill the stomach, process a batch of food, and must eliminate waste before they

**Figure 7.** Relative proportions of taphonomic variables. *A*, Foux Zidet brachiopod shell bed. *B*, Oncoidal floatstones. *C*, Bioclastic floatstones. *D*, Comparison of median proportions of taphonomic variables between shell-rich and shell-poor beds. Asterisks mark a significant difference according to the Wilcoxon test; asterisks in parentheses mark borderline significance (see table 2).



can refill their gut (Peck 2001). This mechanism thus probably limits the potential of brachiopods for high feces production (Peck et al. 2005). Although we do not assume that brachiopods can account for biodeposition comparable to that of bivalves, the difference in shelliness between shell-poor beds and the Foux Zidet shell bed should indicate the potential for relatively higher biodeposition rates in shell-rich than in shell-poor areas. The role of increased biodeposition via pellet production by brachiopods or other organisms in formation of the Foux Zidet shell bed is supported by the positive correlation between pellet abundance and brachiopod shelliness. An absolute density of about 4000 individuals/m<sup>2</sup> in the Foux Zidet shell bed would indicate that the sea floor was entirely covered by living or dead brachiopod shells. Given the sedimentologic evidence (e.g., poorly sorted bioclasts among brachiopod shells, brachiopods in orientations inconsistent with hydrodynamic modification in the shell bed, microbialites in shell-poor beds), alternative scenarios about secondary shell enrichment via sediment winnowing or lower sediment dilution are unlikely.

2. Shell concentrations formed by live and dead shells trap more sediment from suspension than shell-poor zones (Mullins et al. 1981; Gutiérrez and Iribarne 1999). Field experiments with blocks with dead shells and blocks with live shells showed higher sedimentation rates than blocks without shells (Ricciardi et al. 1997; Mortl and Rothhaupt 2003). In addition, sticky surfaces on the sea floor such as biofilms can hold particles that could be otherwise resuspended (i.e., biostabilization). The trapping can also be related to siliciclastic sediment (Krautter et al. 2001).

**Horizontal Changes in Shell Bed Preservation.** The horizontal replacement of the shell bed by interval with the same thickness formed by alternations of shell-rich with shell-poor layers indicates that net accretion rate of the shell-poor areas laterally adjacent to the shell bed was probably the same as that of the shell-rich area. In addition to the evidence from the microfacies, this replacement also suggests that the shell bed grew in equilibrium with

the sediment-water interface of the surrounding areas on the scale that substantially exceeded the timescale of population turnover.

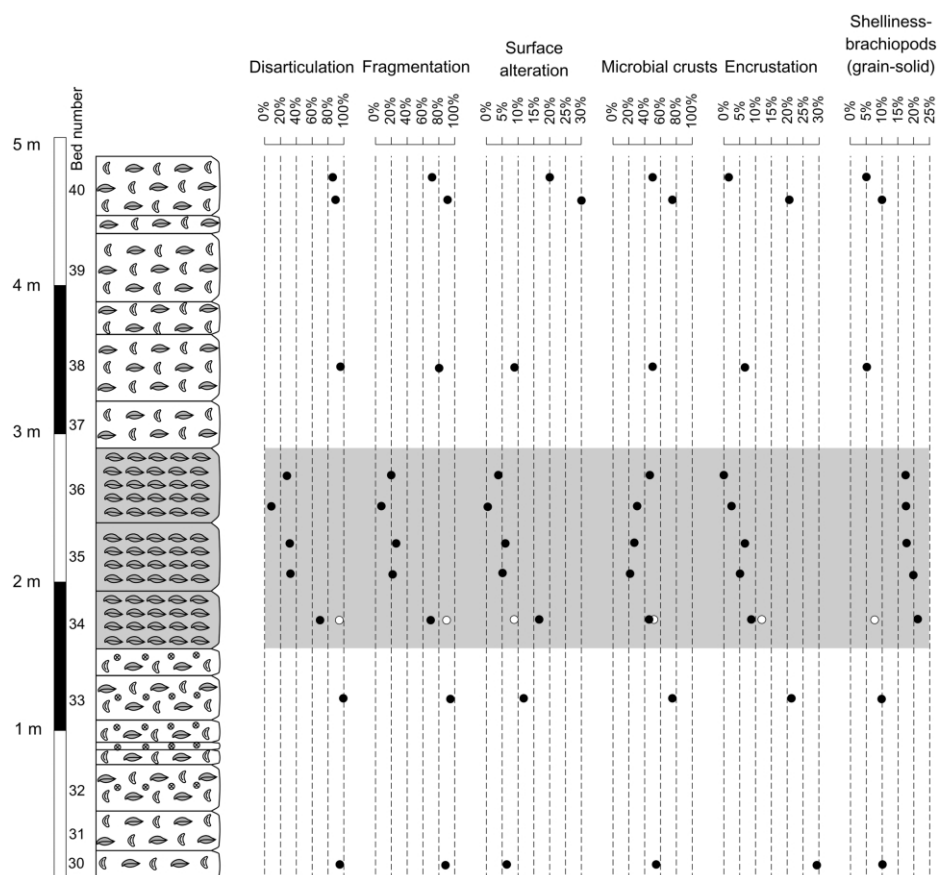
A shell concentration of in situ brachiopods, which could be stabilized by sediment trapping and biodeposition, was lacking in shell-poor areas most likely because of localized disturbance of live brachiopod populations. Under such conditions, disarticulation and fragmentation rates were rapid enough to be effective. High biodeposition and trapping in shell-rich areas would provide enough sediment, which could continually accumulate also in the shell-poor areas, even without extensive sediment transport. A settling velocity of soft carbonate pellets is lower than that of quartz spheres of a similar size (e.g., aragonite pellets settle as quartz spheres 60%–25% in size; Wanless et al. 1981), and the pelletization of the sediment surface can substantially decrease its erosional threshold in contrast to sediments without pellets (e.g., due to high near-surface porosity; Rhoads 1974; Andersen 2001). Therefore, relatively low-velocity currents could be sufficient for small-scale transport of pellets. We assume that, although the biofabric of the lateral shell-bed equivalents can be similar to the underlying shell-poor beds, the shell bed and its lateral equivalents probably grew more rapidly than shell-poor beds above and below.

### Environmental Variations

Relative abundances and size structure of the main shell producer *Zeilleria rehmanni* demonstrate that the main trigger for the shell bed formation was its increased population density, most likely reflecting the species optimum along environmental gradient (fig. 11). Sedimentologic features indicate that deposition of the shell bed took place in a comparatively deep, offshore, low-energy environment below normal storm wave base. Some short-term disruption of local brachiopod populations in the shell bed may be indicated by the bedding planes dividing the shell bed because they are at similar levels as thin, sharp-based crinoidal packstones in its lateral equivalents in sections FZ4–

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**Figure 8.** Field photographs of oncoidal and bioclastic floatstones below and above the shell bed. *A*, Oncoidal floatstone with dispersed brachiopod fragments. *B*, Bioclastic floatstone with loosely packed fragments of brachiopods. *C*, Bioclastic floatstones with loosely packed fragments of crinoids, brachiopods, and microbial oncoids. *D*, Lateral equivalent of shell bed; bed number 34 in section FZ4, showing small brachiopod clusters in the middle part. They pass into shell-poor bioclastic floatstone that is several centimeters thick, grading upward into a typical shell-rich layer. Lens cap for scale.



**Figure 9.** Proportions of taphonomic variables and shelliness in section at Fom Zidet. For legend, see figure 3.

FZ6. However, the rarity or poor destructive power of such events was necessary for the continued existence of shell concentrations. In the lateral equivalents of the shell bed in sections FZ4–FZ6, the presence of thin crinoidal packstones with sharp bases points to occasional, possibly storm-induced rapid burial or concentration events. Some sedimentologic data (e.g., common sparitic shell infills or concordantly oriented bioclasts) indicate that bioclastic floatstones can reflect episodically increased reworking or rapid burial events, in contrast to the rarely disturbed shell bed. Oncoidal floatstones do not show any evidence of high-energy disturbance. They can represent the deepest habitats with minimum current velocities. Therefore, the stratigraphic replacement of bioclastic floatstones by the shell bed and finally by oncoidal floatstones may indicate a net decrease in water energy levels, perhaps linked to an increase in water depth.

Sedimentologic variations thus indicate that the production peak and ecologic success of *Z. rehmanni* correlate with change in water depth and

current velocity. On the basis of the composition and preservation of sponge mounds, Neuweiler et al. (2001) supposed that the oxygen-minimum zone (OMZ) developed in the Central High Atlas Basin during the Late Sinemurian, probably because of rapid sea level rise and subsequent water column stratification. They assumed that abundance of sponges in the Fom Zidet Formation can be related to the oxygen-minimum zone edge effects that lead to greater nutrient concentrations (Mullins et al. 1985). Macroinvertebrates that are able to tolerate low oxygen levels can thus form dense populations near OMZ edges (Levin 2003). The variations in brachiopod abundance could thus be directly or indirectly related to variations in oxygen concentration or nutrient supply via changes in the depth range of OMZ. Brachiopods with low metabolic rates are able to tolerate low oxygen levels (Tunncliffe and Wilson 1988) and could profit from high nutrient supply conditions where possible competitors or predators with higher oxygen demands are excluded.

### Scenario for the Fom Zidet Shell Bed

**Stage 1: Life Assemblage.** A live population of brachiopods of the first generation occupied a stable, micrite-rich substrate. External shell surfaces became encrusted probably still during life by foraminifers, bryozoans, and serpulids and were covered by thin microbial crusts. Suspension feeding of brachiopods led to initial biodeposition of feces and pseudofeces.

**Stage 2: Death Assemblage with Shells Colonized by Biota.** The second generation of live brachiopods attached themselves to dead or alive individuals of the previous generation. In addition to external surfaces, internal surfaces of dead shells became encrusted and were covered with thin microbial crusts. Some empty shell cavities were occupied by the polychaete *Terebella* living in an agglutinated tube. The bioturbated fill of some shells indicates the presence of small infauna. After decay of the pedicle, the dead shell concentration was stabilized by dense packing and was probably supported by thin microbial crusts. In addition to biodeposition induced by suspension feeding, the initial concentration of dead and live shells started to trap the sediment.

**Stage 3: Death Assemblage with Shells Trapping the Sediment.** The next generations of live brachiopods attached themselves to the concentration of live and dead shells of previous generations. Recently dead shells were empty and supported encrusters and cryptic biota or became partially filled with sediment. Shell cavities of shells having been dead for a long time became mostly completely filled with internal sediment, as did cavities between shells. Thus, the shell concentration became protected by the sediment produced by biodeposition, trapping, and biostabilization. Biodeposition and trapping of sediment by the shell concentration probably generated a sediment veneer, which restricted and/or inhibited encrustation, bioerosion, and other destructive processes. Probably only live shells and the most recently dead shells not yet filled with sediment formed a several-centimeters-thick shell concentration extending above the sediment-water interface. Areas affected by interruptions in the growth of brachiopod populations or by too high biodeposition leading to their burial could be rapidly recolonized from adjacent local populations.

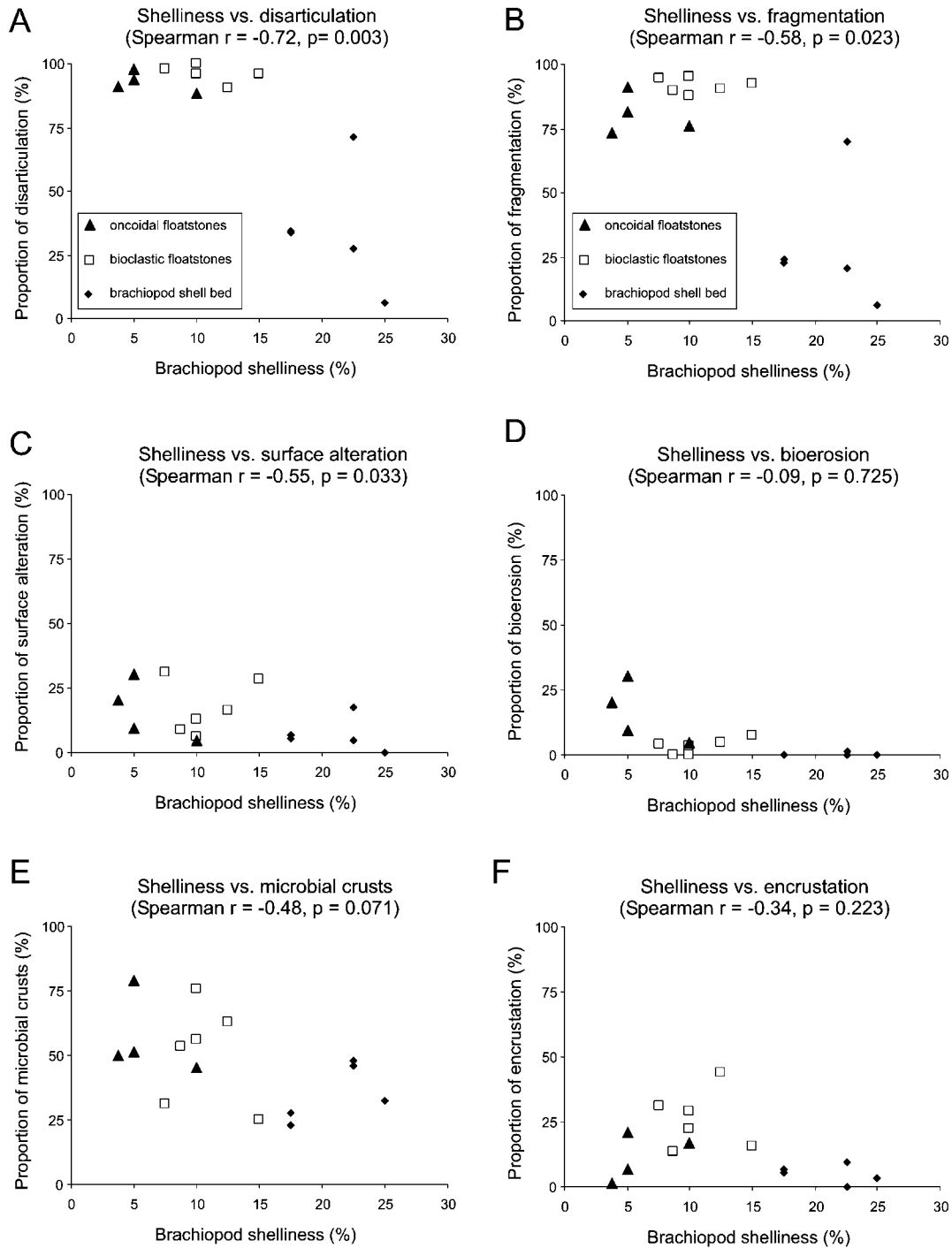
#### Positive Feedback between Hardpart Input and Sedimentation Rates

Some authors already suggested the taphonomic consequences of biodeposition and trapping (Kid-

well 1991a), indicating that a biotically induced higher sedimentation rate related to biodeposition and trapping can significantly enhance preservation potential of fossil assemblages in low-energy habitats populated by abundant suspension feeders. This mechanism between an increase in hardpart-input and an increase in background sedimentation rate can be in fact the most likely pathway for how autochthonous or parautochthonous shell concentrations with low alteration levels can be preserved without rapid burial. On the one hand, an increase in population density of shell producers should lead to higher sediment input via biodeposition and sediment trapping. On the other hand, higher sediment input will lead to a decreased rate of shell destruction through suppression of predators, scavengers, or borers and stabilization and protection of the shell concentration. These processes thus result in a positive feedback between an increased hardpart-input rate and an increased biogenic sedimentation rate (fig. 12).

Although Thayer (1986) mentioned several pre-ingestion mechanisms of brachiopods that enable them to cope with turbidity, and some modern brachiopods live in highly turbid habitats (Rudwick 1962; Tunncliffe and Wilson 1988), it is assumed that brachiopods cannot tolerate very high rates of sedimentation (Rhodes and Thayer 1991; Rhodes and Thompson 1993). The higher abundance of brachiopods associated with higher sedimentation rates in the Fom Zidet shell bed thus contrasts with the observations that the abundance of brachiopods and sedimentation rates covaries negatively (Kidwell 1986a; Fürsich et al. 1991; Garcia and Dromart 1997; Brett 1998). This contrast follows because the higher sedimentation rates assumed in the Fom Zidet shell bed are directly related to the activity of shell producers and are a consequence rather than a cause of their ecologic success. In contrast, extrinsically driven variations in siliciclastic or carbonate sedimentation can cause a decrease in abundances of shell producers when an increase in sedimentation rate surpasses their ability to cope with high particle concentrations.

The positive feedback adds new details to solutions of the paradox that would arise if an increase in hardpart-input rate correlates with a decreased sedimentation rate (Kidwell 1986a, 1989; Davies et al. 1989). This paradox indicates that reduced sedimentation rates favoring higher brachiopod production rates also favor higher rates of shell destruction and make the formation of well-preserved brachiopods in growth positions improbable (Kidwell 1986a, 1989). In contrast, in the positive feedback scenario, the effects of high rates of produc-



**Figure 10.** Correlations between brachiopod shelliness and the proportion of taphonomic variables. *A*, Disarticulation. *B*, Fragmentation. *C*, Surface alteration. *D*, Bioerosion. *E*, Microbial crusts. *F*, Encrustation.

tion of dead shells are not canceled out by long exposure times (leading to high alteration), because they are associated with increased rather than decreased sedimentation rates.

One of the main explanations for the paradox of

preservation is that actual sedimentation rates may substantially differ from net sedimentation rates due to intermittent burial/exposure cycles via local bioturbation, bioerosion, or current winnowing (Kidwell and Aigner 1985; Flessa et al. 1993;

**Table 1.** Spearman Rank Correlation Shows Negative Coefficients between Observed Shelliness and Taphonomic Variables

Shelliness versus	Spearman $r$	$P$
Disarticulation	-.717	.0026
Fragmentation	-.582	.0228
Alteration	-.551	.0330
Bioerosion	-.090	.7247
Microbial crusts	-.478	.0715
Encrustation	-.334	.2234

Note. Shelliness defined as volumetric proportion of bioclasts in thin sections. If the Bonferroni correction would be used for correction of the multiple testing,  $\alpha$  will be lowered to 0.0083, and some significant results will be of borderline significance.

Simões and Kowalewski 1998; Olszewski 1999; Parsons-Hubbard et al. 1999; Carroll et al. 2003). However, the intermittent burial scenario alone cannot lead to the negative correlation between shelliness and assemblage-level alteration. When net sedimentation rate decreases but shells are still covered with some sediment (i.e., sediment input is constant but sediment output increases), lower dilution increases shelliness but assemblage-level alteration remains constant. Therefore, if the intermittent burial scenario is supposed to be responsible for higher shelliness and lower alteration, it needs to be associated with increased hardpart-input rate.

### Implications

**Understanding the Dynamics of Shell Concentrations.** The positive feedback between high shell density and increased background sedimentation rate was already assumed in several studies of shell concentrations. Wilson (1982) explained preservation of in situ brachiopods due to a combination of sediment trapping by living organisms and current activity. Samankassou and West (2002) suggested that the preservation of the Carboniferous phylloid algal mounds reflects the growth of a densely packed skeletal framework, stabilized by encrus-

ters and peloidal sediment. Similar biogenic deposition may have played a role in the preservation of autochthonous shell concentrations with rudists in life position (Gili et al. 1995; Simone et al. 2003). In these examples, either sediment trapping and/or increased biodeposition might have been important in enhancing the preservation potential of in situ organisms.

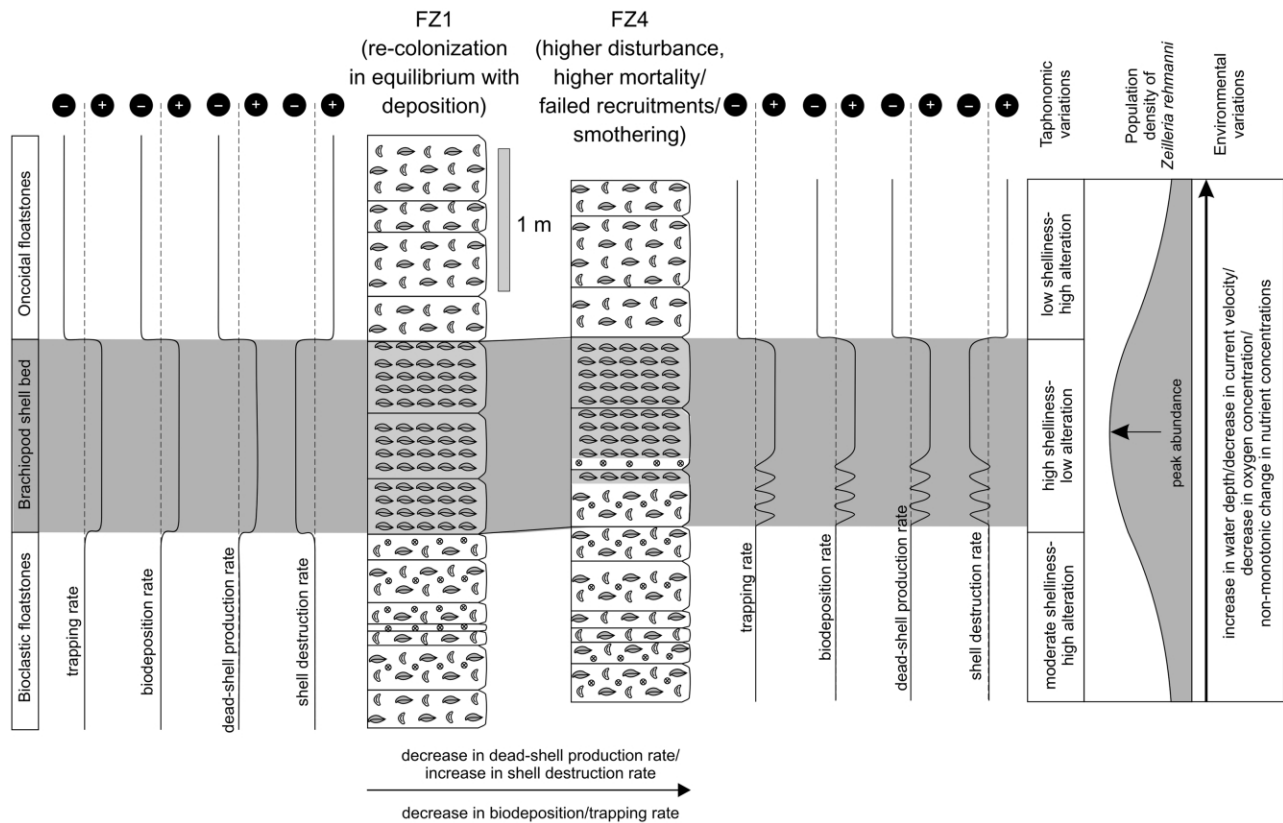
Thick Paleozoic and Mesozoic brachiopod shell concentrations typically have a complex origin due to multiple colonization-burial events, commonly of storm origin (Johnson 1989; Brett 1991; Kidwell and Brenchley 1994, 1996; Li and Droser 1999). However, some autochthonous shell concentrations and in situ preserved brachiopod clusters can be reinterpreted in terms of the described mechanism (Middlemiss 1962; Brookfield 1973; West 1977; Fürsich and Hurst 1981; Hagdorn and Mundlos 1982). Pentamerid brachiopods commonly form densely packed shell concentrations with brachiopods still in growth positions (Johnson 1977). Although their preservation is explained by rapid sediment smothering during storm events, it is possible that dense shell concentrations of live brachiopods led to rapid biodeposition rates or sediment trapping, thus enhancing their preservation potential. Webby and Percival (1983) described several-decimeters-thick, densely packed Ordovician shell concentrations formed by trimerelloid brachiopods in growth positions. Although they lived semi-infaunally and were thus partly stabilized in the sediment, superposition of at least four generations indicates that this had to be coupled with relatively high background sedimentation rates.

The mechanism of autochthonous shell bed formation presented here may be generally applicable to other well-preserved shell concentrations. It is important to note that the scenario of positive feedback between hardpart-input rates and biogenic sedimentation rates might apply not only for such exceptional cases as the Fom Zidet shell bed but

**Table 2.** Wilcoxon Rank Sum Test Evaluates Differences in Median Proportions of Taphonomic Variables between Shell-Rich and Shell-Poor Beds

Taphonomic variable	$Z$	$P$	Median proportion	
			Shell bed	Shell-poor bed
Disarticulation	-3.062	.0022	34.3	94.8
Fragmentation	-3.062	.0022	22.9	90.2
Microbial crusts	-1.959	.05	32.2	52.3
Surface alteration	-1.959	.05	5.7	14.6
Bioerosion	-1.224	.167	0	1.5
Encrustation	-2.449	.0143	5.7	18.9

Note. Note that the  $P$  values can be the same because the sums of ranks for the shell-rich and shell-poor beds are equivalent in some tests.



**Figure 11.** Interpreted temporal and spatial changes in biogenic sedimentation rates and hardpart-input rates between shell-rich and shell-poor beds in the Fom Zidet section. Biodeposition, trapping, and hardpart-input rates are supposed to be slightly higher in bioclastic floatstones than in oncoidal floatstones because of the higher brachiopod shelliness observed in bioclastic floatstones. For legend, see figure 3.

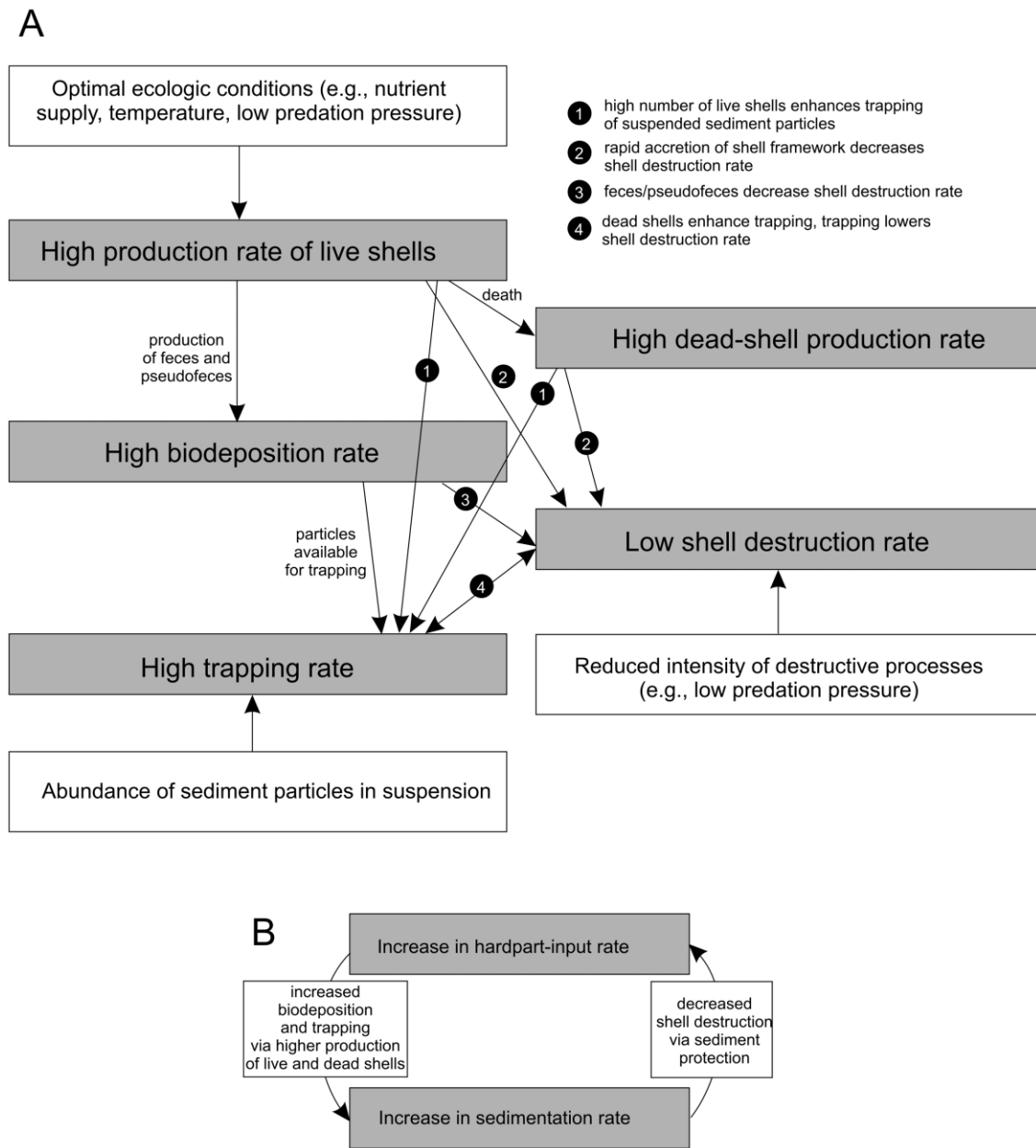
also for any autochthonous or parautochthonous nonevent shell beds that show lower alteration levels than surrounding shell-poor concentrations and thus cannot be explained by variations in sedimentation rates alone. This option is supported by the lateral equivalents of the shell bed where thin, less spectacular shell concentrations alternate with shell-poor layers. It is probable that the positive feedback also played an important role in the formation of those thin shell concentrations, but because of higher environmental instability and disturbance, they did not develop into thick shell beds.

**Environmental Significance.** Because sedimentation rate is one of the main factors that govern changes in accommodation space, an explicit estimation of the role of sedimentation and hardpart-input rates in shell concentration genesis through comparison of shelliness with assemblage-level alteration should be of high importance in sequence stratigraphic studies (Holland 2000). Most of the studies that found that the variations in sedimentation rates can largely explain shell bed formation

are derived from mixed carbonate-siliciclastic or pure siliciclastic habitats, where extrinsically driven variations in siliciclastic sedimentation rates exert a strong control on dilution and abundance of shell producers (see review by Kidwell [1991a] and references above). In shallow, carbonate-dominated habitats, there is mostly a combined effect of sedimentation and hardpart-input rates on shell bed preservation (Kidwell 1991a; Sanders and Pons 1999; Carannante et al. 2000; Monaco and Giannetti 2002). Obviously, the variations in hardpart-input rates can be most easily recognizable in habitats where extrinsically driven sedimentation rates are more or less constant. This situation seems to be reflected by the Fom Zidet Formation, where siliciclastic input was minimal and carbonate sediment was mostly produced in situ.

Recognizing the positive feedback in shell concentrations also has environmental implications. The positive feedback is most likely driven by ecology of shell producers: under optimal conditions, they can form high-density populations that modify





**Figure 12.** Concept of positive feedback between increased hardpart-input rates and increased biogenic sedimentation that provides possible pathway for preservation of autochthonous shell concentrations. *A*, Detailed relationship between particular components of hardpart-input rates and sedimentation rates. *B*, Simplified positive feedback between hardpart-input rate and biogenic sedimentation rate.

their habitat and influence its sedimentary regime. Because of the hydrodynamics of micritic grains or pellets and low high-energy resistance of shell concentrations, nondisturbed shell concentrations can be preserved only in relatively low-energy habitats (e.g., protected lagoons or deep habitats). The preservation of such shell concentrations can thus indicate intense biodeposition-related carbonate pro-

duction taking place in protected shallow habitats or in deep habitats below storm wave base. Although shell concentrations can trap sediment from suspension that is derived from extrinsic sources, pellet abundance correlating with shell producers would imply that carbonate is produced largely in situ and as a response to higher production of shell producers or other organisms that share environmental pref-

erences with shell producers. Taphonomic analyses of shell concentrations that are preserved through the positive feedback could thus recognize whether the pellet-rich sediment in such deep-water deposits is produced in situ or derived from platform habitats.

### Conclusions

A negative correlation between shelliness and assemblage-level alteration in the Foum Zidet shell bed from Lower Jurassic carbonates of Morocco indicates that the concentration was generated primarily by an increase in hardpart-input rates rather than by a decrease in sedimentation rates. The increase in net hardpart-input rates was triggered by increased population density of the brachiopod *Zeilleria rehmanni*. Stratigraphic and sedimentologic data indicate that the shell bed grew in equilibrium with the sediment-water interface of the neighboring areas. An increase in the hardpart-input rates was associated with increased sedimentation rates, in contrast to the usual negative relationship that is inferred between hardpart-input and sedimentation rates. The suggestion that brachiopods grew in equilibrium with a positive sedimentation rate and that concentrated assemblage formed by attritional mortality of numerous generations can be preserved in the fossil record may be provocative, but it follows if an increase in hardpart-input rate increased the sedimentation rate due to biodeposition and sediment trapping. This led to increased stabilization and protection of the densely packed shell bed, leading to a decrease in

shell destruction rates. Therefore, there was a positive feedback between increased hardpart-input rate and increased biodeposition and sediment trapping. Recognizing the role of biodeposition in the formation of shell concentrations has some environmental significance because it implies that carbonate sediment is produced largely in situ in deep-water habitats and is directly or indirectly related to the activity of benthic fauna.

The Foum Zidet shell bed is very exceptional because it is very thick and densely packed with epifaunal brachiopods commonly still in growth position. However, we suggest that the mechanism of the positive feedback can be the important factor in the preservation of many shell beds that are less spectacular at first sight. This possibility is demonstrated by the lateral equivalents of the shell bed that show less peculiar, thin shell concentrations that alternate with shell-poor layers.

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