VARIATION IN BRACHIOPOD PRESERVATION ALONG A CARBONATE SHELF-BASIN TRANSECT (RED SEA AND GULF OF ADEN): ENVIRONMENTAL SENSITIVITY OF TAPHOFACIES

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ABSTRACT

A bathymetric transect ranging from coral habitats down to a 1500-m-deep basin in the Red Sea and Gulf of Aden allows us to test the sensitivity of taphofacies to depth and sediment grain size in a tropical to subtropical carbonate basin, to partition variation in brachiopod preservation into extrinsic (environmental) and intrinsic (shell-specific) components, and to quantify residual variation that remains unexplained by such components. Factoring out environmental effects, thin-shelled, organic-poor rhynchonellids are more affected by fragmentation and fine-scale surface alteration and degrade rapidly compared to the more frequently bioeroded, organic-rich terebratulids. The negative role of shell organic content is overridden by shell thickness, and preservation rates of organic-rich brachiopods are enhanced by syndepositional cement precipitation. Environmental trends in preservation are confounded by shell-specific factors that account for 16% of variation in preservation: the amounts of multivariate variation explained by environment increase from 29% using combined brachiopod preservation to 46% using terebratulid preservation. Environmental sensitivity of taphofacies is driven by present-day variation in environment but also by past Pleistocene conditions. First, reduction in fragmentation, encrustation, and bioerosion is consistent with a decrease in light penetration and primary productivity. Second, brachiopods are coated with aragonite cement in basinal sites with lithified oozes and microbial carbonates that originated during the last glacial maximum when syndepositional aragonite cementation was favored by high temperature and salinity, and thus can be affected by millennial-scale time averaging. Skeletal preservation rates are thus not in steady state over the duration of time averaging, and the bathymetric reduction in alteration is partly related to past conditions amenable to cement precipitation.

INTRODUCTION

Nonrandom relationships between spatial variation in skeletal preservation and spatial variation in environment were recorded in several benthic groups and several types of modern marine settings, including siliciclastic and mixed carbonate-siliciclastic settings with mollusks (Fürsich and Flessa, 1987; Meldahl and Flessa, 1990; Kowalewski et al., 1994; Aguirre and Farinati, 1999; Best and Kidwell, 2000a, 2000b; Best et al., 2007; Schneider-Storz et al., 2008) and foraminifers (Goldstein and Harben, 1993; Berkeley et al., 2007; Perry et al., 2008), and carbonate settings with corals (Pandolfi and Greenstein, 1997; Perry, 2000), echinoderms (Meyer and Meyer, 1986; Nebelsick, 1999), and mollusks (Pilkey et al., 1979; Walker et al., 1998; von Rützen-Kositzkau, 1999; Powell et al., 2002; Parsons-Hubbard, 2005). In spite of such statistically significant relationships, however, the explanatory power of taphofacies analyses is frequently reduced because the actual amount of variation in skeletal preservation explained by environment can be low (Callender et al., 2002; Staff et al., 2002; Powell et al., 2008). Several factors contribute to high amounts of variation unexplained by environment. First, preservation patterns are affected not only by extrinsic (environmental) but also by intrinsic (shell-specific) factors. This has been shown experimentally (Chave, 1964; Henrich and Wefer, 1986; Smith et al., 1992; Glover and Kidwell, 1993), and by observational studies in natural systems (Best and Kidwell, 2000a, 2000b; Nielsen, 2004; James et al., 2005; Tomašových and Rothfus, 2005; Lockwood and Work, 2006). Most taphonomic studies factor out contributions of intrinsic factors by prior partitioning of datasets into subsets where intrinsic factors remain constant. This approach, however, does not allow quantifying individual contributions of these two factors to total spatial variation in preservation and, thus, evaluating whether these two types of factors covary positively, are independent of each other, or have confounding effects. Here, we use variation partitioning methods that quantify effects of these two types of factors on the total variation in preservation of death assemblages among sampling locations.

Second, the remaining variation in preservation unexplained by environmental and shell-specific factors can be related to a multitude of effects related to sampling effects, small-scale spatial stochasticity, and patchiness in preservation (Staff and Powell, 1990; Wilkinson et al., 1999; Rankey, 2004; Wilkinson and Drummond, 2004; Powell et al., 2008; Bosence, 2008), and vertical heterogeneity in preservation related to small-scale gradients in sediment pore-water chemistry (Aller, 1982, 2004; Cai et al., 2006). Of special interest are confounding effects of background and episodic processes that lead to interaction between residence time of shells in the taphonomically active zone and per capita skeletal alteration (i.e., a probability of being altered, bored, or encrusted) and destruction rates (i.e., a probability of being destroyed so that degraded individuals are not identifiable) (Davies et al., 1989; Parsons-Hubbard et al., 1999; Staff et al., 2002; Tomašových, 2004a; Brett et al., 2006; Hendy et al., 2006; Lazo, 2006; Bressan and Palma, 2008; Dattilo et al., 2008; Zaton et al., 2008). Finally, a tight link between spatial variation in preservation and spatial variation in environment also assumes that spatially variable skeletal input rates and preservation rates do not vary in time, and this assumption of steady state is likely to be violated under large-scale time averaging. In sum, all these effects can confound explanatory power of taphofacies.

In this study, in order to understand better the relationship between preservation and environmental gradients, (1) we evaluate contributions of intrinsic and extrinsic factors to spatial variation in brachiopod preservation among sites; (2) quantify how much of the spatial variation in preservation is explained by environmental factors and how much of the spatial variation remains unexplained; and (3) evaluate whether taphofacies correlate with biofacies and whether they capture environmental gradients to a similar degree (Meldahl and Flessa, 1990; Nebelsick, 1999; Parsons-Hubbard, 2005; Best, 2008). The amount of variation in skeletal preservation—defined either in

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univariate or multivariate terms—explained by environmental factors refers to environmental sensitivity of preservation features. For example, coral preservation can reveal subtle environmental gradients, whereas the species composition of the coral death assemblages is dominated by few species that do not discriminate environments owing to hurricane-induced spatial homogenization (Blanchon and Perry, 2004), and sensitivity of preservation to environment can exceed sensitivity of other sedimentary features (O'Brien et al., 1994; McLaughlin and Brett, 2007; Reolid et al., 2007; Reolid, 2008; Webster et al., 2008). Here, we address these aims by assessing preservation pathways that lead to preservation of brachiopod death assemblages along a bathymetric gradient that ranges from shallowest depths with coral fringing reefs in the Gulf of Aqaba down to about 1500-m-deep environments in the Red Sea and Gulf of Aden (Fig. 1). Studies that simultaneously evaluate preservation of organic-rich and organic-poor brachiopods along environmental gradients in tropical to subtropical carbonate settings are also lacking, and it is unclear whether their preservation rates vary along bathymetric gradients in carbonate environments.

STUDY AREA

The Red Sea is situated in an arid climate, with high mean annual sea surface temperature (25–29°C), low mean annual rainfall (<10–25 cm), and high evaporation (up to 2 m per year). It represents a marginal sea with antiestuarine circulation driven by high evaporation rates in the north, which results in surface inflow of open ocean waters and deep outflow of saline waters over the sill in the south (Eschel et al., 1994; Siddall et al., 2004). It has a high salinity (40.5‰) and a highly stable temperature (21.5°C) below 300 m (Sheppard, 2000). In contrast, a temperature gradient is developed in the Gulf of Aden, where temperature is reduced to 15°C at 200 m and to 3–4°C at 2000 m, and the salinity (36–36.5‰) is also lower than in the Red Sea (von Rützen-Kositzkau, 1999). The northern part of the Red Sea is nutrient poor; the southern part has higher nutrient levels and higher primary productivity owing to the input of ocean water from the Gulf of Aden. The influence of this water on the Red Sea water masses stops around 19°N (Weikert, 1987).

A narrow and shallow shelf (<100 m deep), a relatively flat and wide deep shelf (500–700 m deep), and an axial basin with 2900 m maximum water depth characterize the topography of the Red Sea. The Gulf of Aqaba is located in a narrow tectonic valley and fringed by a narrow, 1–2-km-wide shelf (Friedman, 1968). The Red Sea lies outside the major hurricane belts (Scoffin, 1993), and its relatively small spatial extent also limits intensity of storms. Intense storm events that form boulder-sized coral rubble near coral reefs occur rarely on a decadal scale (Friedman, 1968; Shaked et al., 2005) but in general are less frequent than in open-shelf areas. Sediment winnowing and transport is driven by wave energy, wind-driven nearshore currents and long-shore currents below wave base (Reiss and Hottinger, 1984).

Net sedimentation rates in the Red Sea are reduced on average from 60 cm/1000 years on the shallow shelf (at 100 m depth), to 7–30 cm/1000 years on the deep shelf, and to about 5–10 cm/1000 years in the basin (Hoffman et al., 1998; von Rützen-Kositzkau, 1999; Edelman-Furstenberg et al., 2009). The highest values of net sedimentation rates on the shallow shelf were, however, estimated from depressions near steep slopes where sediment can rapidly accumulate (von Rützen-Kositzkau, 1999). In the Gulf of Aden, sedimentation rates are also relatively low (9–14 cm/1000 years at 506 and 761 m water depth) (von Rützen-Kositzkau, 1999).

The Red Sea undergoes temporal changes in deep-sea water chemistry at glacial-interglacial time scales that are in phase with sea level changes: interglacial stages are characterized by precipitation of Mg calcite, whereas glacial stages by precipitation of aragonite
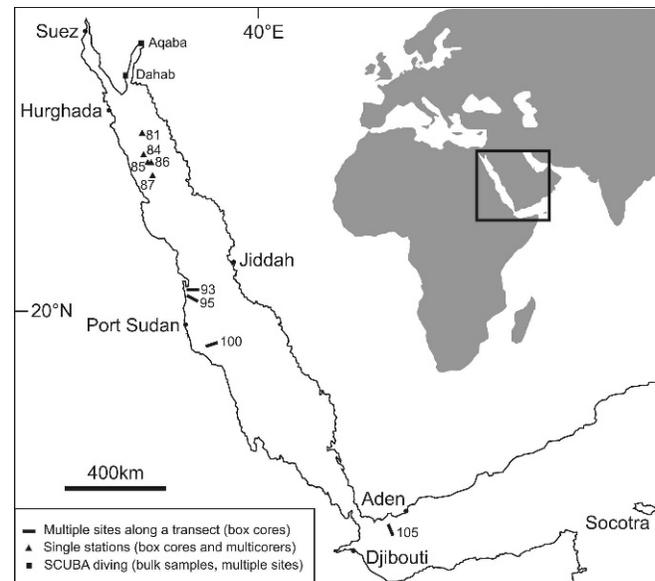
FIGURE 1—Location of sampled sites in the Red Sea and Gulf of Aden. The numbers 93, 95, 100, and 105 consist of several sites sampled along a bathymetric gradient. Offshore samples were collected during *Meteor 31/2* cruise in 1995.

(Almoghi-Labin et al., 1986). During the last glacial maximum, reduced flow of cold waters into the Red Sea led to high temperatures, high salinities (up to 50‰), and low oxygen content that limited neritic and pelagic carbonate production and triggered formation of hardgrounds, extensive precipitation of aragonite, and preservation of aragonitic pteropods in deep-sea sediments (Taviani, 1998; Arz et al., 2003). The so-called hard layer (regional terms used in Red Seas studies) formed by lithified carbonates—lithified pelagic oozes and microbial stromatolites and thrombolites—is a marker bed that is widespread in axial zones of the Red Sea between 500 and 2700 m (Gevirtz and Friedman, 1966; Milliman et al., 1969; Locke and Thunell, 1988; Almoghi-Labin et al., 1991). This layer is about 23–13 ky old, consists of alternation of lithified and nonlithified mudstone, stromatolithic, and thrombolitic layers, and is frequently coated by Mn-Fe crusts and encrusted by metazoans (Hoffman et al., 1998; Taviani, 1998; Brachert, 1999). At shelf depths, it is buried under sediment and only known from cores (Brachert, 1999). Several samples collected in basinal parts of the Red Sea are derived from portions of the sea floor where the Pleistocene hard layer is exposed.

METHODS

Sites

Bulk samples for taphofacies analyses were collected by giant box cores, dredges, and multicorers during *Meteor 31* cruise in the Red Sea and Gulf of Aden in 1995 (Oschmann et al., 1996; von Rützen-Kositzkau, 1999; Grill and Zuschin, 2001), and by SCUBA diving in the Gulf of Aqaba in 2002 and 2005 (Zuschin and Stachowitsch, 2007; Zuschin and Mayrhofer, 2009) (Fig. 1, and also see Supplementary Data 1–3[1]). Death assemblages in shallow-shelf habitats were collected by SCUBA diving from skeletal and muddy sands in cryptic habitats underneath coral colonies in Dahab and from sediments close to coral reefs near Aqaba (Domanski, 2006; Zuschin and Mayrhofer, 2009). Decapods, foraminifers, mollusks, scleractinians, and algae form the cryptic sands; brachiopods contribute <2% to assemblages (Zuschin and Mayrhofer, 2009). Bulk samples from Aqaba are bioclastic sands

and muddy sands (Domanski, 2006). Assemblages from shallow-shelf and deep-shelf soft-bottom habitats were collected by dredges and giant box cores in bioturbated sandy muds and muddy sands with mollusks and polychaetes (von Rützen-Kositzkau, 1999). Assemblages from basinal habitats collected with giant box cores, multicorers, and dredge are represented by pteropod-rich muds and by lithified pelagic mudstones and microbial carbonates that belong to the so-called Pleistocene hard layer (von Rützen-Kositzkau, 1999).

The sampling methods differ in penetration depth and spatial scale. A giant box core collected a sediment block with a surface area of 50 cm^2 and a maximum penetration of 40–50 cm. A multicorer consisted of 12 tubes with inner diameter of 6–7 cm, and penetration depths were 26 cm on average. Bulk sediment samples collected by SCUBA diving with a volume of about 1 dm^3 and penetration depth of about 10 cm were taken from cryptic reef habitats. On sediments next to coral reefs (Aqaba), a steel cylinder with a diameter of 35 cm was pushed into the seafloor and the uppermost 20 cm of sediment, accounting for a volume of 9.6 l, were removed. Differences in depth penetration, however, can have relatively small effects because (1) species composition at decimeter scales within giant box cores and bulk samples from steel cylinders remains constant, and overall preservation also does not show any tendency to increase or decrease with sediment depth (von Rützen-Kositzkau, 1999; M. Zuschin and H. Domanski, unpublished data, 2009); and (2) decimeter-scale burrows in several samples indicate that most assemblages capture the mixing zone (Oschmann et al., 1996). A dredge collected assemblages on a seafloor across several decameters, at a larger spatial scale than box cores and multicorers. The dredged assemblages, however, are derived from the basin only, and their species composition and preservation patterns do not consistently differ from multicorer and box core assemblages derived from the same habitat. Differences in penetration and spatial extent can cause the dredged assemblages to be less affected by small-scale spatial heterogeneity in preservation than the assemblages collected by other methods. Such differences, however, should not bias analyses toward higher environmental sensitivity of taphofacies but can rather represent one source of variation in preservation unexplained by environment. Standardization of taphonomic variables to proportions allows us to compare preservation of assemblages that differ in sample size.

All sediment samples were air dried and sieved through 1 mm mesh; 2094 specimens evaluated in this study represent all rhynchonellid and terebratulid brachiopods collected in these samples (Table 1). They belong to four species (Fig. 2): the rhynchonellid *Cryptopora curiosa* and terebratulids *Megerlia echinata*, *Argyrotheca* sp. A, and *Platidia anomioides*. To compare taphofacies with biofacies, we use species abundances of bivalves (167 species) and brachiopods (7 species) found in the corresponding samples used for taphofacies analyses and minimum sample size of 40 individuals (von Rützen-Kositzkau, 1999; Grill and Zuschin, 2001). Similarly as in analyses of preservation, sampling differences likely affect biofacies analyses to some degree in terms of differences in spatial scale, but we note that basinal assemblages sampled by dredge, box cores, and multicorers are similar in composition. Abundances are based on proportions of specimens sampled from surface death assemblages, because living mollusks and brachiopods are rare in level-bottom benthic communities of the Red Sea and Gulf of Aden at the spatial scales of several meters (Zuschin and Hohenegger, 1998; Domanski, 2006).

Data

We chose 10 individuals per site as the minimum sample size for conducting taphofacies analyses in this study. Thirty-three sites that fulfill this criterion are used in univariate and multivariate analyses (mean sample size = 62 specimens). With the exception of four sites in the Gulf of Aden that contain the rhynchonellid *Cryptopora*, other sites are situated in the central and northern parts of the Red Sea, north of 18°50′ N. The presence of eight taphonomic variables that capture

TABLE 1—The numbers of all specimens (valves and shells) of rhynchonellids and terebratulids in individual bathymetric and sediment categories in the Red Sea and Gulf of Aden.

	Rhynchonellids (N)	Terebratulids (N)
Shallow shelf	61	806
Deep shelf	842	211
Basin	20	154
Sands	127	347
Muds	776	698
Crusts	20	110

various aspects of mean site-level alteration in four species was evaluated under a light microscope magnification (25×). These variables include (1) disarticulation; (2) fragmentation; (3) external encrustation; (4) internal encrustation; (5) external nonpredatory bioerosion; (6) internal nonpredatory bioerosion; (7) internal fine-scale surface alteration; and (8) crystalline cement overgrowths on internal surface. Each variable is represented by a proportional value that is defined by the sum of altered specimens relative to the total sum of specimens at a given site. Fragments are defined as specimens with more than 10% of the valve lost. Internal fine-scale surface alteration represents any surface irregularities that damage the fine mosaic on the interior of the valve: this mosaic is formed by the spade-shaped ends of adjacent fibers of a secondary shell layer that were bounded by organic sheaths during life (Williams, 1968). Scanning electron microscopy (SEM) observations were used to reveal the sources of fine-scale surface alteration. Microscopic dissolution is rare and visible under 1000× magnification only.

The four brachiopods attain similar shell size: the length of the ventral valve does not exceed 5 mm (*Argyrotheca*: median = 1.7 mm, max = 3.2 mm; *Megerlia*: median = 2.1 mm, max = 4.3 mm; *Platidia*: median = 2.6 mm, max = 3.9 mm; *Cryptopora*: median = 2.5 mm, max = 4.8 mm). The small size can affect taphofacies signals (Kidwell et al., 2001), but this size range is comparable to the size range of mollusks from tropical carbonate environments where taphofacies signals correlate with environmental gradients (Hauser et al., 2008). Terebratulids have endopunctate (organic-rich) shells that are perforated with channels (punctae) occupied by caecal prolongations of outer mantle, and the rhynchonellid *Cryptopora* has an impunctate (organic-poor) shell. The valve thickness of *Cryptopora* ranges between 0.01–0.02 mm, the valves of *Platidia* attain 0.03–0.04 mm, and the valves of *Megerlia* and *Argyrotheca* are thicker (0.05–0.08 mm) and enforced by radial ribs. Pristine articulated shells of *Cryptopora* are transparent, whereas pristine shells of terebratulids are weakly to not transparent. They share such traits as calcitic mineralogy, fibrous shell microstructure, and epifaunal life habit. *Cryptopora* with winglike deltidial plates is attached to microscopic substrates with a thin, long pedicle (Curry, 1983). *Argyrotheca*, *Megerlia*, and *Platidia* have short pedicles and are firmly attached to hard media (Atkins, 1959, 1960, 1961; Cooper, 1973).

Analyses

Predictor Variables.—We partition the variation in skeletal preservation among sites into components that are explained by three (predictor) variables: one categorical intrinsic (shell-specific) variable related to shell structure and organic content (i.e., impunctate rhynchonellids versus punctate terebratulids) and two environmental variables. The latter include depth, either in continuous meters or in three categories: shallow shelf with 12 sites (a narrow rim of shelf shallower than 100 m), deep shelf with 13 sites, and basin with 8 sites (below the shelf break at around 600 m), and sediment-grain size in three categories: 16 sites with carbonate mud and sandy mud, 11 sites with carbonate sand and muddy sand, and 6 sites with lithified carbonates. Environmental gradients partly differ between the Red Sea
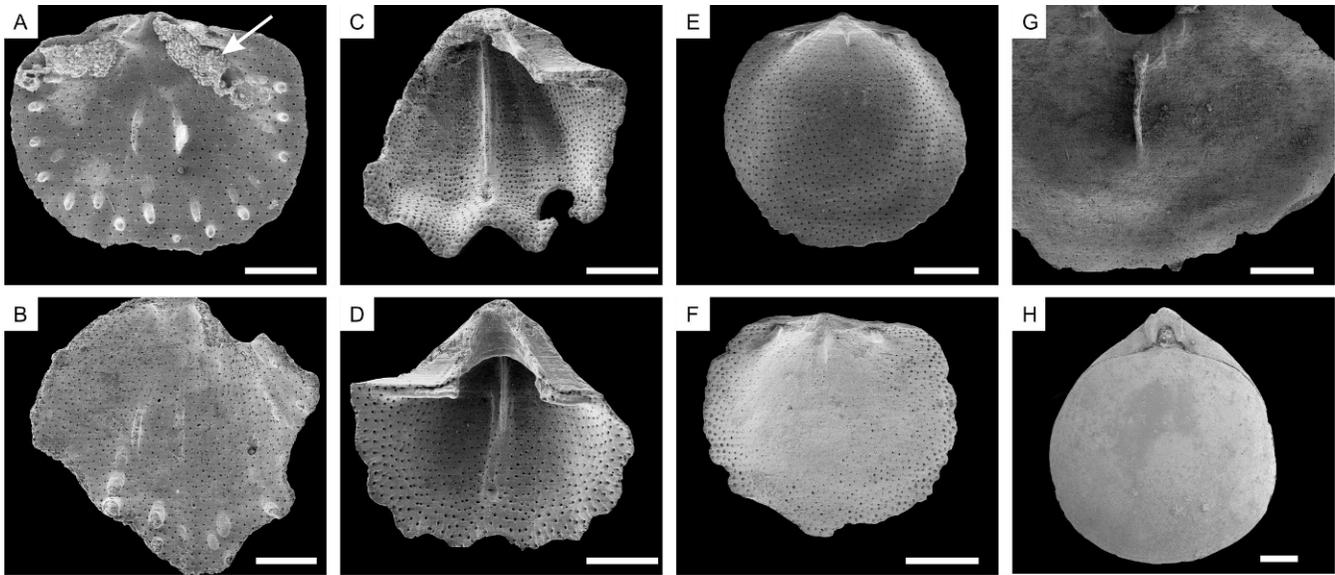
FIGURE 2—Brachiopod species in the Red Sea and Gulf of Aden analyzed in this study. A) Internal surface of complete dorsal valve of *Megerlia echinata* with encrusting agglutinated foraminifers (arrow) and pristine surface with well-preserved shell mosaic and punctae. Sample 100/8. B) Fragment of *M. echinata* affected by fine-scale surface alteration and bioerosion. Sample 100/8. C) Fragment of ventral valve of *Argyrotheca* sp. A without fine-scale surface alteration but partly affected by bioerosion and one drillhole. Sample 100/3. D) Pristine and complete ventral valve of *Argyrotheca* sp. A. Sample 100/3. E) Pristine and complete ventral valve of *Platidia anomioides*. Sample 93/6. F) Ventral valve of *P. anomioides* affected by fine-scale surface alteration and bioerosion. Sample 93/6. G) Internal surface of dorsal valve of *P. anomioides* with aragonite cement precipitations. Sample 81/2. H) Shell of *Cryptopora curiosa*. Sample 93/9. All scale bars = 0.5 mm.

and Gulf of Aden, but only four samples come from the Gulf of Aden, and these exclusively contain the rhynchonellid *Cryptopora*. The mixture of gradients, thus, might affect analyses of rhynchonellids. Preservation of the rhynchonellid *Cryptopora* is recorded in 11 sites, and terebratulid preservation in 22 sites—preservation features of *Megerlia*, *Argyrotheca*, and *Platidia* were pooled for analyses of shell-specific and environmental effects. Analyses comparing preservation of fragments and complete specimens are restricted to two species, *Cryptopora curiosa* and *Megerlia echinata*, and to shallow and deep shelf habitats, requiring more than 10 fragments and 10 complete individuals per site. The frequency of predatory drillholes is used to evaluate effects of predation pressure on assemblage-level alteration. The drilling frequency is estimated by dividing the number of drilled brachiopod specimens by the total number of shells (a number of valves divided by 2, Kowalewski, 2002). The F distribution is used to compute exact confidence intervals for individual samples on the basis of binomial cumulative distribution function.

Univariate Analyses.—Generalized linear models (GLM) evaluate effects of shell structure, depth, and sediment grain size on the eight taphonomic variables that define mean alteration levels within sites. In contrast to linear regression analyses, GLM can deal with residuals that do not conform to a normal distribution. The GLM coefficients and standard errors were estimated with the logit link function and the quasibinomial variance function because taphonomic variables are proportions and dispersion is frequently smaller than one. The logit link function is

$$g(\mu_i) = \ln \frac{\mu_i}{1 - \mu_i}$$

where μ_i is the expected value of response variable for a given value i of the predictor variable. It transforms the expectation of the response to the predictor variable so that the relationship between the mean of the taphonomic variable (μ) and the predictor variable becomes linear and the response variable is maintained in the interval [0, 1]. The variance function describes how the variance of the taphonomic variable depends on its mean μ. The variance is a product of the variance function $\mu(1-\mu)$ and the dispersion parameter c that corresponds to the

(weighted) sum of the squared Pearson residuals divided by the residual degrees of freedom (Venables and Ripley, 2002). With the binomial variance function, $c = 1$. With the quasibinomial variance function, c is estimated directly from the data. The dispersion parameter is used to scale up the standard error estimates of GLM slopes. We note that the amount of deviance explained by predictor variables in GLM is analogous to the amount of variance explained in linear regressions, but when c is estimated directly from the data, a model is no longer a true binomial and goodness-of-fit cannot be estimated. In order to compare the slopes of predictor variables that inherently differ in their measurement scale, depth and sediment grain size are standardized to Z-scores. In GLM with more than one predictor variable, the slopes measure the amount by which a taphonomic variable increases when the predictor variable increases and other predictor variables are held constant: they represent unique effects because contributions of other predictors to explained deviance are factored out.

Multivariate Analyses.—We use nonmetric multidimensional scaling (NMDS) based on the Manhattan distances to explore relationships among samples in terms of their preservation. In contrast to Euclidean distances, effects of outliers are diminished because between-sample differences in taphonomic variables are not squared. We use redundancy analysis (RDA) to quantify effects of the shell-specific and environmental factors on multivariate variation in preservation among sampling locations. NMDS configurations in two-dimensional plots are rotated so that the variation of samples is maximized along the first axis by principal component analysis and are rescaled so that ordination distances are comparable to underlying matrix distances (Oksanen et al., 2005).

RDA is a multivariate linear regression that models effects of one or more predictors on several response variables and is an extension of principal component analysis. It displays a part of multivariate variation in preservation that is explained by predictors (Legendre and Legendre, 1998) and is used to decompose the total between-sample variation in the preservation into components explained by shell-specific and environmental factors (Borcard et al., 1992). The amount of variance explained by individual components (R^2) in RDA is adjusted by the number of degrees of freedom (Peres-Neto et al., 2006).
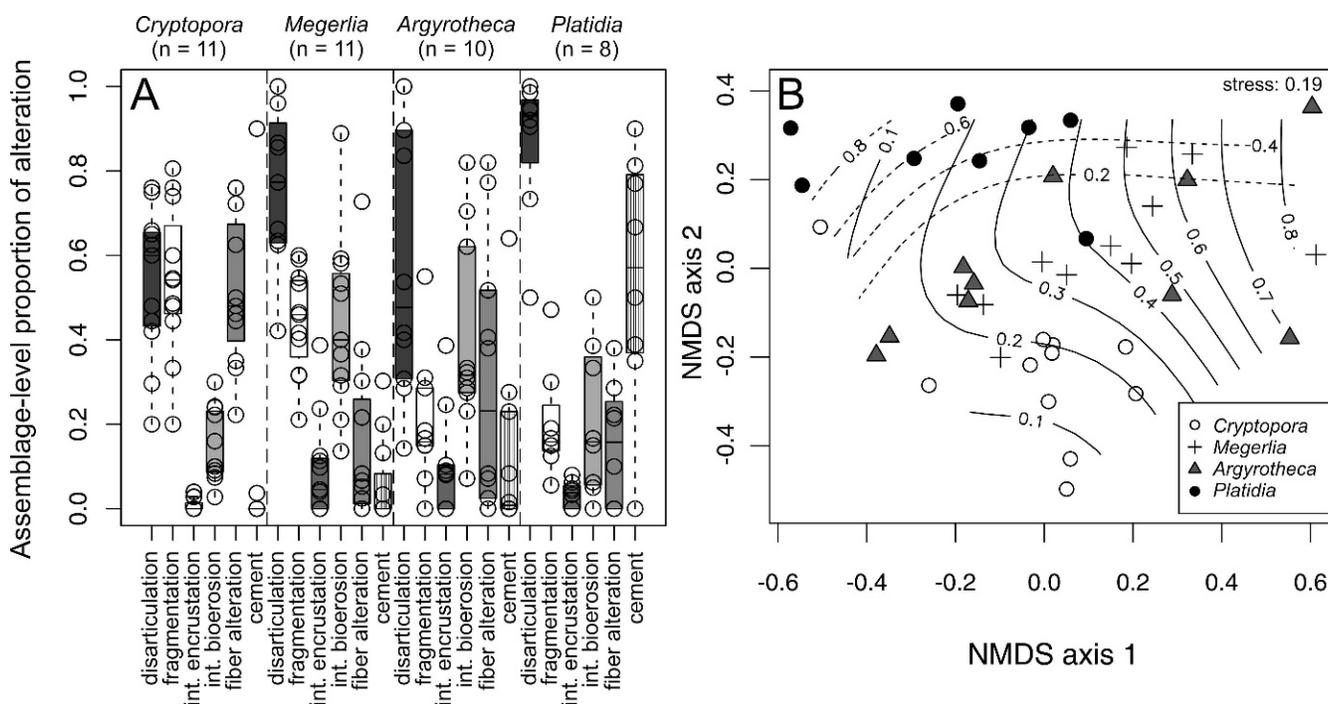
FIGURE 3—Preservation differences among *Argyrotheca*, *Cryptopora*, *Megerlia*, and *Platidia*. A) Boxplots showing differences in preservation among four genera (all sites combined). *Cryptopora* is characterized by high fine-scale surface alteration, *Megerlia* and *Argyrotheca* by high bioerosion, and *Platidia* by high proportions of cement precipitation. Boxplots display median and 25 and 75 quartile values. External encrustation and bioerosion positively correlate with their internal encrustation and bioerosion and are omitted for the sake of plot brevity. B) NMDS plot shows that *Platidia* is segregated from *Megerlia* and *Argyrotheca*, and also from *Cryptopora*. Contours depicting changes in taphonomic alteration, fitted by generalized additive models, show that differences in preservation are mainly determined by differences in proportions of cement (dashed contours) and internal bioerosion (solid contours). This analysis is based on 40 genus-level assemblages collected from 33 sites; several sites contain more than one genus, and such assemblages are analyzed separately.

We note that RDA assumes a linear relationship between the environmental variables and the response variables. We, therefore, also transform depth and sediment-grain size variables to their quadratic and cubic functions to allow for nonlinear relationship between environment and preservation (Jones et al., 2008). Final predictor variables used in RDA were selected with forward selection in the R package packfor (Blanchet et al., 2008). Several components contributing to the variation in the preservation are measured with RDA: (1) the variation explained by environmental factors, i.e., simultaneously by depth and sediment grain size [E]; (2) by depth alone [D]; (3) by sediment grain size alone [S]; (4) the variation explained by intrinsic (shell-specific) factors [I]; (5) variation explained by depth without a component related to sediment grain size [D|S]; and (6) variation in sediment grain size without a component related to depth [S|D]. The significance of these components is evaluated with a permutation test (permutest.cca in the vegan package, Oksanen et al., 2005), with 1000 permutations.

To display quantitative changes in taphonomic variables (or changes in environmental variables) in NMDS and RDA plots, changes in taphonomic alteration in ordination plots are fitted with generalized additive models, using thin-plate splines in two dimensions and selecting the degree of smoothing by generalized cross-validation (ordisurf in the vegan package, Oksanen et al., 2005). These surfaces are either plotted as two-dimensional contours in ordination plots or as three-dimensional surfaces where the third axis gives the expected estimate of the taphonomic or environmental variable.

We use permutational multivariate analysis of variance (PERMA-NOVA, Anderson, 2001) to evaluate differences in preservation between two brachiopod orders and among three sediment-grain size types. PERMANOVA is similar to analysis of similarities (Clarke and

Green, 1988), but it is based on raw rather than on rank-order distances, and it is less sensitive to among-group differences in variances (Anderson, 2001). PERMANOVA partitions sums of squared distances within and among groups on the basis of distance matrices (Anderson, 2001). The total sum of squares (SS_T) corresponds to the sum of all distances among all samples divided by the total number of samples (N), and the within-group sum of squares (SS_W) corresponds to the sum of within-group between-sample distances divided by the number of samples per group. The among-group sum of squares is $SS_A = SS_T - SS_W$, and the approximate F-ratio for M groups is computed as:

$$F = \frac{SS_A/(M-1)}{SS_W/(N-M)}$$

The approximate F-ratio is comparable to the F-ratio statistic in one-factorial ANOVA models. In Euclidean space, SS_W corresponds to the sum of the squared distances between individual samples and their centroid, and SS_A is the sum of squared distances from group centroids to the overall centroid. To test the null hypothesis of no differences between groups, p values are obtained by permutations so that group labels are randomly reshuffled. We measure the compositional segregation as the proportion of total sum of squares explained by between-group differences ($R^2 = SS_A/SS_T$), and adjusted by the number of degrees of freedom.

Relationship between Distance Matrices.—In previous studies, several methods were used to link taphofacies patterns to biofacies patterns, such as comparative treatments of two types of data with cluster analyses and such indirect ordinations as NMDS followed by demonstrations that categorical (environmental) groupings are (or not) preserved in both types of analyses (Parsons-Hubbard, 2005; Best, 2008). Here, we use the Mantel test that evaluates whether Spearman
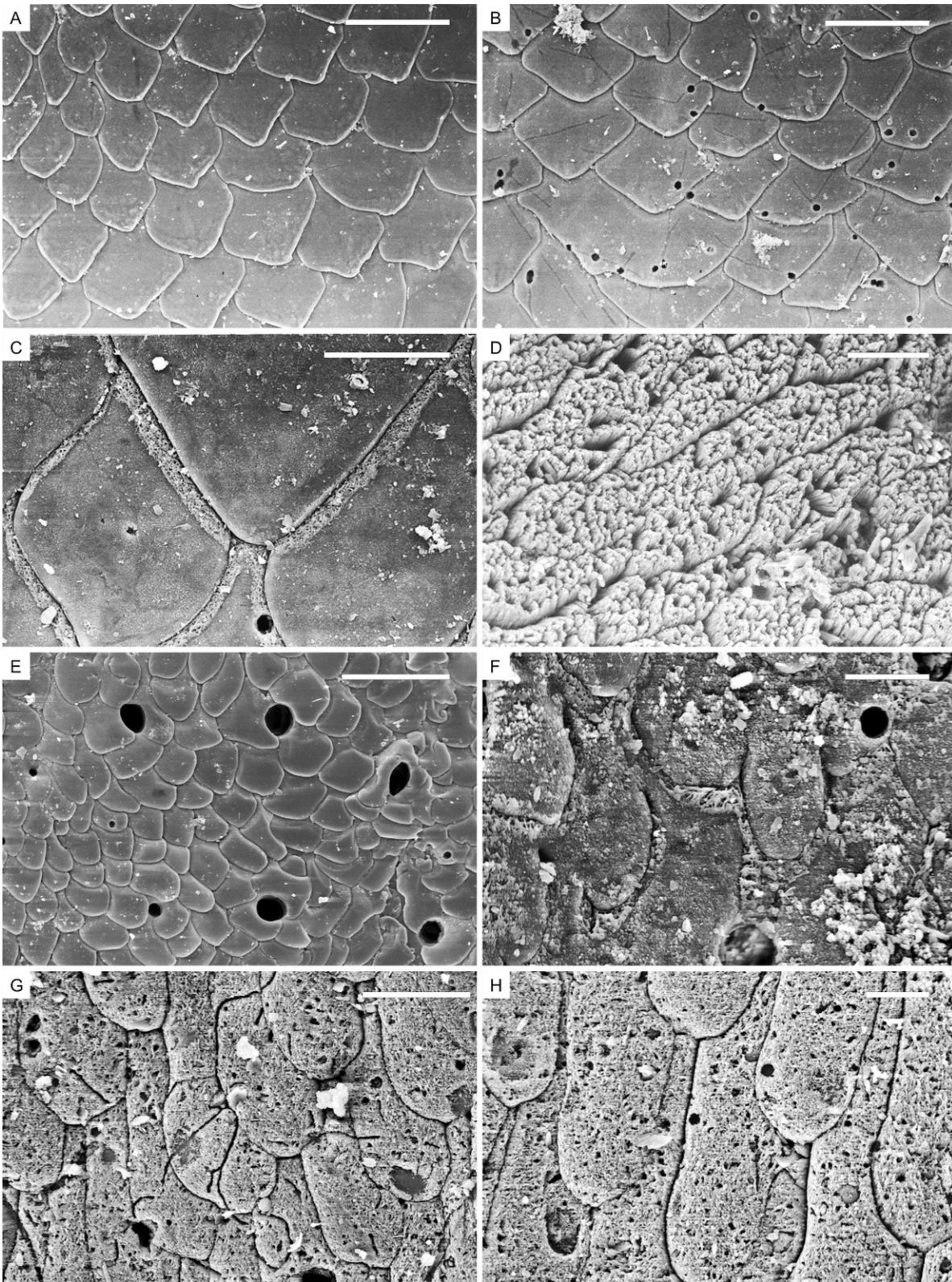
FIGURE 4—Preservation of internal surfaces in *Cryptopora* and *Platidia*. A) Pristine internal surface of *Cryptopora curiosa*. Sample 93/9. Scale = 50 μm. B) Pristine internal surface with dispersed microborings: this is the highest boring density generally observed in *C. curiosa*. Sample 93/9. Scale = 50 μm. C) Cement formed by aragonitic needle meshworks in grooves along fiber boundaries in *C. curiosa*. Sample 84. Scale = 20 μm. D) Internal surface of *C. curiosa* completely covered by syntaxial fibrous cement formed by 10–20-μm-long, densely packed, and regularly arranged aragonite needles. Sample 81/2. Scale = 20 μm. E) Pristine internal surface of *Platidia anomioides*. Sample 93/6. Scale = 50 μm. F) Internal surface of *P. anomioides* covered by initial needles and polyhedral crystals. Sample 93/6. Scale = 10 μm. G) Cement coatings with microborings in *P. anomioides*. Sample 87/1. Scale = 20 μm. H) Several microns-thick rim of cement formed by needle meshwork on internal surface of *P. anomioides*. Sample 87/1. Scale = 10 μm.
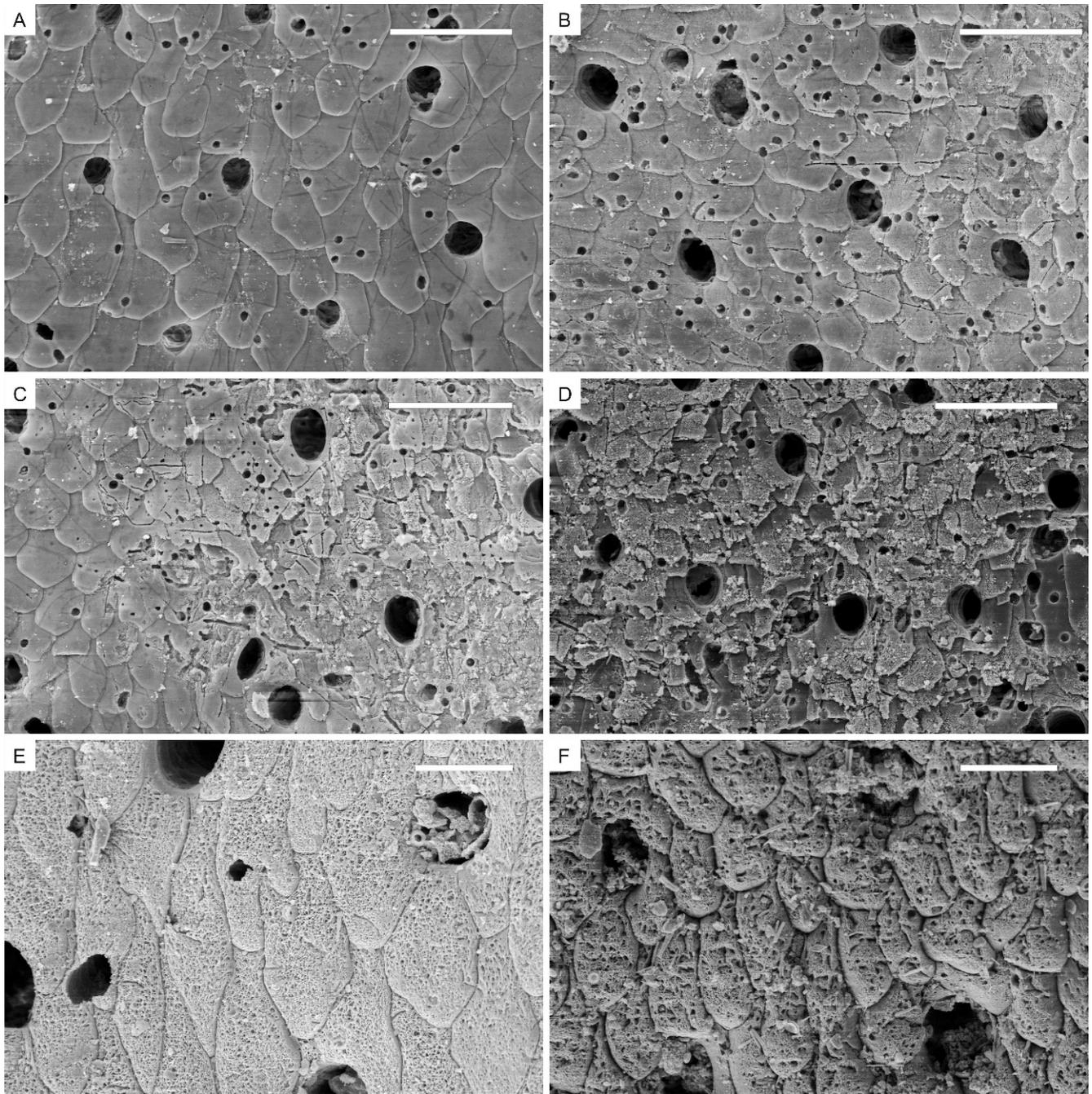
FIGURE 5—Preservation of internal surfaces in *Megerlia* and *Argyrotheca*. A) Pristine internal surface of *Megerlia echinata* with dispersed microborings. Sample 100/8. Scale = 50 μm. B) Pristine internal surface of *Megerlia echinata* with abundant microborings. Sample 100/8. Scale = 50 μm. C) Internal surface with bioerosion and fine-scale alteration in *Megerlia echinata*. Sample 100/8. Scale = 50 μm. D) Internal surface with intense fine-scale surface alteration in *Megerlia echinata* caused by bioerosion. Sample 100/8. Scale = 50 μm. E) Internal surface of *Megerlia echinata* with fibrous cement. Sample 100/3. Scale = 20 μm. F) Cement on internal surface of *Argyrotheca* sp. A formed by bladelike crystals. Sample 93/9. Scale = 20 μm.

rank correlation between intersample taphonomic distances (Manhattan distances) and species compositional similarities (Bray-Curtis dissimilarities) is positive. The significance is computed by permuting rows and columns of one of the distance or dissimilarity matrices (Legendre and Legendre, 1998). We also compare taphofacies and biofacies sensitivity to two environmental variables with the adjusted R^2 values estimated by RDA. All analyses were performed using the R-language (R Development Core Team, 2007).

RESULTS

Brachiopod Preservation

Across all samples (Fig. 3A), the four species significantly differ in multivariate preservation (PERMANOVA $R^2 = 0.42$, $p < 0.001$). In multivariate space defined by preservation, samples with *Cryptopora* and *Platidia* are segregated and samples with *Megerlia* and *Argyrotheca*

TABLE 2—Generalized linear models using logit link function and quasibinomial variance function show that differences between punctate and impunctate brachiopods have significant effects on several taphonomic variables. The p-values in bold represent the significant results after the sequential Bonferroni correction.

	Slope	St. error	t-test	p-value
Disarticulation	0.55	0.18	2.99	**0.005**
Fragmentation	−0.43	0.14	−2.98	**0.005**
External encrustation	0.98	0.37	2.66	**0.012**
Internal encrustation	0.99	0.49	2.02	0.051
External bioerosion	0.31	0.19	1.58	0.12
Internal bioerosion	0.54	0.19	2.9	**0.007**
Internal alteration	−0.67	0.19	−3.5	**0.0014**
Cement	0.67	0.44	1.53	0.14

overlap (Fig. 3B). *Cryptopora* is characterized by moderately high proportions of fragments (54%), high proportions of internal fine-scale surface alteration (48%), and very low internal bioerosion (10%); *Platidia* is characterized by high proportions of cement (54%); and *Megerlia* and *Argyrotheca* are characterized by moderate levels of fragmentation (44% and 20%) and moderately high proportions of internal bioerosion (44% and 40%, Fig. 3A).

Similarly as in the Southeast Brazilian Bight (Rodland et al., 2004), brachiopod encrusters in the Red Sea consist of serpulids, bryozoans, and agglutinated foraminifers. Agglutinated foraminifers (89.5%) dominate in encrusting communities along the whole bathymetric gradient; serpulids (7.8%) and bryozoans (2.6%) are rare. Pristine internal surface represented by a fine mosaic formed by adjacent fibers of secondary shell layer is visible in *Cryptopora* (Fig. 4), *Platidia* (Fig. 4), and *Megerlia* (Fig. 5). In *Cryptopora*, borings are either absent or dispersed on pristine surfaces (Figs. 4A–B), density of borings is rarely high, and fine-scale surface alteration is not associated with borings, but corresponds to surface delamination and fragmentation of fibers. In *Megerlia* (Fig. 5B), *Argyrotheca*, and *Platidia*, bioerosion achieves high density, and fine-scale surface alteration is represented by a dense network of microborings rather than by delamination of fibers from the internal surface (Figs. 5C–D). Microborings in deep-shelf and basinal sites, represented mainly by bulbous swellings 2–4 µm in diameter that are connected by unbranching, straight, or sinuous channels (<1 µm in diameter) of uniform diameter that cross fiber boundaries without interruptions, were probably produced by fungi (Golubic et al., 2005). Microborings on specimens sampled in shallow sites near coral colonies vary in size, diameter, and branching patterns and probably correspond to a mixture of algal and heterotrophic borings (see Radtke and Golubic, 2005).

Cement is represented by mesh of micron-sized needles along fiber boundaries (Fig. 4C) and by 10–20-µm-long fibrous needle-shaped crystals that grow syntaxially on internal ends of calcitic fibers (Fig. 4D). The crystals are either dispersed and patchily distributed (Fig. 4F) or form fringes and continuous rims with densely packed and regularly arranged needles (Figs. 4G–H, 5E). The longest crystal axes are frequently parallel with longitudinal morphological axes of calcitic fibers. Meshlike and fibrous cements occur on brachiopods in basinal environments and are typical of aragonite (see Milliman et al., 1969, and Brachert, 1999, for diffraction and microprobe analyses). Brachiopods from deep-shelf sites are also covered locally by bladed and peloidal cements (Fig. 5F). Bioerosion can postdate the cement formation (Fig. 4G).

Differences in Preservation Between Terebratulids and Rhynchonellids

Univariate Patterns.—Light-microscope and SEM observations show that terebratulids accrue more bioerosion than rhynchonellids, and rhynchonellids are less bioeroded but are affected by physical disintegration of the valve surface into individual fibers. The shell-specific factor has significant effects on disarticulation, fragmentation, external encrustation, internal bioerosion, and fine-scale surface alteration in GLM; i.e., rhynchonellids are more fragmented and terebratulids are more bioeroded and encrusted (Table 2). Rhynchonellids in mud and sands (Figs. 6A–B) and on shallow and deep shelfs (Figs. 6C–D) are characterized by higher proportions of fine-scale surface alteration and lower proportions of internal bioerosion and internal encrustation than terebratulids. Fragmentation is positively correlated with external (Spearman r = 0.58, p = 0.004) and internal bioerosion (Spearman r = 0.64, p = 0.0014) and uncorrelated with fine-scale surface alteration (Spearman r = 0.18, p = 0.42) in terebratulids. In contrast, fragmentation is positively related to fine-scale surface alteration in rhynchonellids (Spearman r = 0.85, p = 0.0009) and is unrelated to bioerosion.

Multivariate Patterns.—Differences in preservation between terebratulids and rhynchonellids in multivariate space are related to differences in internal bioerosion and fine-scale surface alteration (Figs. 6E–F). The shell-specific component (adjusted R^2 = 0.16) explains a significant proportion of multivariate variation in the preservation in RDA (Table 3). Partialling out effects of sediment grain size and water depth, terebratulids and rhynchonellids significantly differ in preservation in muds and sands (PERMANOVA R^2 [muds] = 0.44, p < 0.001; R^2 [sands] = 0.41, p < 0.001), and in shallow-shelf and deep-shelf environments (PERMANOVA R^2 [shallow shelf] = 0.23, p = 0.01; R^2 [deep shelf] = 0.42, p = 0.001).

Environmental Effects on Preservation

Univariate Patterns.—Means of alteration variables are significantly affected by depth (Fig. 7) and sediment-grain size (Fig. 8), and the effects of environment expressed by the GLM slopes increase and their standard errors decrease when terebratulids are treated separately (Table 4–5). In terebratulids, proportions of fragmentation, external bioerosion, and external encrustation significantly decrease with depth in simple GLM. Proportions of internal bioerosion and internal encrustations are reduced with depth but the slopes do not differ from zero in multiple GLM (Table 5, Fig. 7). Disarticulation, however, significantly increases with depth in multiple GLM where effects of sediment grain size are factored out. Rhynchonellid preservation is weakly related to depth (Tables 4–5, Figs. 7–8) and does not differ between muds and sands (Fig. 8A). Terebratulids are more disarticulated and bioeroded in muds than in sands and lithified carbonates (Fig. 8B). The proportion of cement significantly increases with depth in both groups. Rhynchonellids in basin are represented by one sample only, but rhynchonellids in small-sized basinal assemblages are also coated by cement.

Multivariate Patterns.—The environmental component explains a significant proportion of multivariate variation in the brachiopod preservation in RDA (adjusted R^2 = 0.29), and both depth (adjusted R^2 = 0.21) and sediment types (adjusted R^2 = 0.29) have significant effects on their preservation (Table 3). The multivariate variation in preservation explained by environment is higher for terebratulids: variations in depth explain 35% and variations in sediment grain size explain 45% of variation in the terebratulid preservation in RDA (Table 3). Shell-specific factors, therefore, confound environmental effects, and a large part of multivariate variation in preservation still remains unexplained by environmental and shell-specific factors. Depth and sediment grain size covary (i.e., sands do not occur and lithified carbonates are restricted to basinal sites), and when factoring out the effect of the second environmental variable, the unique contributions of depth and sediment grain size to variation in the preservation are substantially reduced (Table 3). RDA shows that fragmentation, bioerosion, and encrustation are reduced and disarticulation and cement precipitation increase along RDA axis 1, i.e., with depth—this axis explains 33% of total variation in preservation—and internal bioerosion increases along
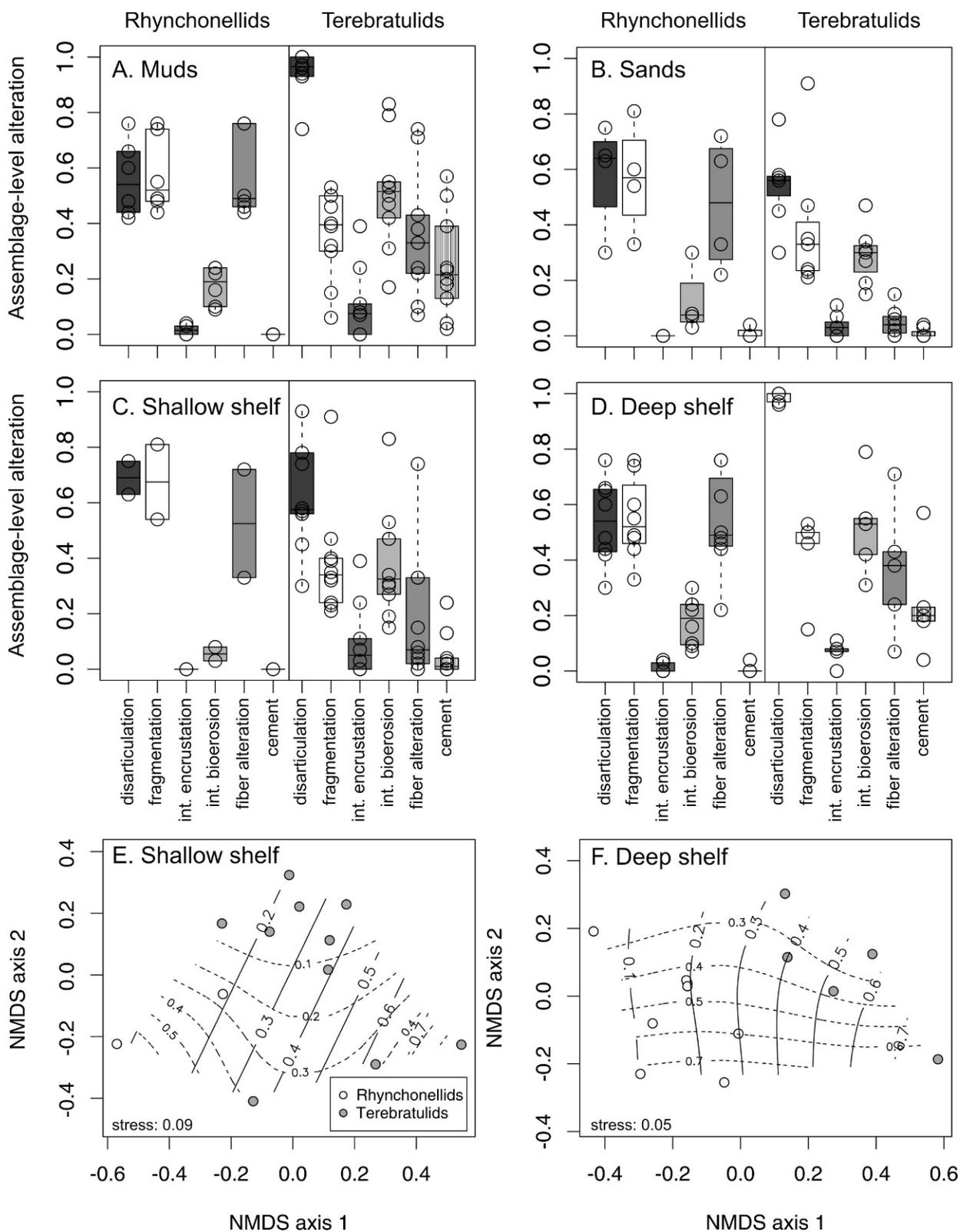
FIGURE 6—Rhynchonellids have higher fine-scale surface alteration and lower internal bioerosion than terebratulids, partitioned by sediment grain size (A–B) and by depth (C–D). Boxplots display median and 25 and 75 quartile values. NMDS plots for (E) shallow-shelf and (F) deep-shelf environments show that gradients in internal bioerosion (dashed contours) and fine-scale surface alteration (solid contours) discriminate preservation of rhynchonellids and terebratulids.

TABLE 3—Partitioning of spatial variation in the preservation using redundancy analysis shows that (1) both extrinsic (water depth and sediment grain size) and intrinsic (shell-specific) factors account for significant amounts of variation in preservation, and (2) intrinsic factors confound taphofacies sensitivity to environmental gradients because the adjusted R^2 increases when terebratulids and rhynchonellids are treated separately. Simple environment is represented by a dataset formed by the depth and sediment type. Polynomial environment corresponds to an environmental dataset consisting of the original depth and sediment type and their quadratic and cubic functions. Note: Depth|sediment refers to the effect of depth, factoring out the effect of sediment grain size, sediment|depth refers to the effect of sediment grain size, factoring out the effect of depth.

	Simple environment - adjusted R^2	p-value	Polynomial environment - adjusted R^2	p-value
Terebratulids and rhynchonellids (n = 33)				
Depth	0.2	**<0.001**	0.21	**<0.001**
Sediment	0.16	**<0.001**	0.29	**<0.001**
Extrinsic factor (depth+sediment)	0.29	**<0.001**	0.29	**<0.001**
Depth|sediment	0.16	**<0.001**	0	**0.36**
Sediment|depth	0.09	**<0.001**	0.09	**0.006**
Intrinsic factor (punctate vs impunctate)	0.16	**<0.001**	0.16	**<0.001**
Total (intrinsic + extrinsic)	0.46	**<0.001**	0.47	**<0.001**
Terebratulids (n = 22)				
Depth	0.29	**<0.001**	0.35	**<0.001**
Sediment	0.21	**<0.001**	0.45	**<0.001**
Depth+sediment	0.44	**<0.001**	0.46	**<0.001**
Depth|sediment	0.23	**<0.001**	0.02	0.23
Sediment|depth	0.15	**<0.001**	0.11	0.009
Rhynchonellids (n = 11)				
Depth	−0.05	0.69	−0.05	0.7
Sediment|depth	0.02	0.29	0.02	0.29
Depth+sediment	−0.05	0.34	−0.05	0.55
Depth|sediment	−0.06	0.78	−0.06	0.76
Sediment|depth	0	0.36	0	0.35

RDA axis 2 (16%), i.e., toward smaller grain size (Fig. 9). Multivariate variation in preservation of rhynchonellids is weakly related to environmental variables (Table 3).

Preservation of Fragments

Complete individuals of *Cryptopora* show low proportions and fragments show high proportions of fine-scale surface alteration (6% versus 92%; Fig. 10A). In contrast, complete (<1%) and fragmented individuals (20%) of *Megerlia* do not strongly differ in fine-scale surface alteration (Fig. 10B). Internal bioerosion of fragments of *Megerlia* reaches higher levels than in *Cryptopora* fragments, and fragments of *Megerlia* are less affected by fine-scale surface alteration than fragments of *Cryptopora* (Figs. 10–11). Fragments and complete specimens of *Cryptopora* are well segregated in the NMDS plot and significantly differ in preservation (PERMANOVA R^2 = 0.55, p < 0.001), whereas fragments and complete specimens of *Megerlia* do not differ in preservation (PERMANOVA R^2 = 0.08, p = 0.12, Fig. 11).

Linking Taphofacies to Biofacies

Rank correlation between variation in brachiopod preservation (taphofacies) and variation in species composition (biofacies) is significantly positive but low (Fig. 12A, Mantel test r = 0.28, p < 0.001). Rank correlation between variation in terebratulid preservation and variation in species composition (on the basis of bivalves and brachiopods), however, is moderately high (Fig. 12B, Mantel test r = 0.43, p < 0.001). Rank correlation between variation in terebratulid preservation and variation in brachiopod species composition is slightly larger (Mantel test r = 0.45, p < 0.001). Grill and Zuschin (2001) and Logan et al. (2008) also showed that

bivalves and brachiopods occur in well-defined, depth-related biofacies in the Red Sea and Gulf of Aden. In accord with this, environmental variables explain 66% of variation in species composition of brachiopod assemblages and 42% of variation in species composition of bivalve-brachiopod assemblages in RDA. Environmental variables explain 29% (using rhynchonellids and terebratulids) and 46% (using terebratulids only) of multivariate variation in preservation in RDA. Biofacies and taphofacies, therefore, show comparable levels of explanatory power in paleoenvironmental reconstructions.

DISCUSSION

Under steady state input and loss of shells, signals of preservation depend on the ratio of alteration rate to destruction rate, rather than on their absolute values (Tomašových et al., 2006). This ratio can be substantially larger than one when alteration counteracts weight loss (e.g., cement precipitation) and overall destruction rate is minor (Alexandersson, 1972; Reid and Macintyre, 2000; Nebelsick, 2008), or equal to or smaller than one when alteration positively contributes to overall destruction rate. One of the main paradoxes associated with analyses of taphonomic biases is that the relationship between alteration and destruction rates can result in highly altered assemblages that signify either (1) highly destructive conditions, or (2) low-destructive conditions under which accrual of weakly destructive or constructive alteration is allowed. Higher levels of taphonomic alteration, thus, do not necessarily equate to higher probability of skeletal weight loss. Here, we use assemblage-level fragmentation as a proxy for intensity of skeletal destruction that should positively correlate with skeletal destruction rates and against which other patterns of taphonomic alteration can be compared because fragmentation is inevitably coupled with disintegration of specimens into nonidentifiable debris (Zuschin et al., 2003). For example, assemblage-level fragmentation can predict dissolution rates of foraminifers and pteropods (Bé et al., 1975; Thunell, 1976; Kucera et al., 1997; Gerhardt et al., 2000; Conan et al., 2002; Mekik and Francois, 2006). Positive relationships (or concordance in Powell et al., 2008) between fragmentation and other alteration variables, therefore, indicate that an increase in assemblage-level alteration correlates with increased rather than with decreased destruction rates.

Differential Preservation of Rhynchonellids and Terebratulids

Shell-specific factors do affect preservation pathways, but contrary to expectations, high shell organic content covaries positively with preservation rate. Fragmentation and fine-scale surface alteration are higher in organic-poor but thin-shelled *Cryptopora* than in organic-rich but thicker terebratulids. Terebratulids are characterized by higher bioerosion, which is positively related to fragmentation, rather than fine-scale surface alteration. These results show that terebratulids and the rhynchonellid *Cryptopora* inherently differ in preservation pathways, but the results do not demonstrate that their net destruction rates differ. It is possible that colonization rates by borers are higher in terebratulids because endolithic fungi can proliferate in shells with high organic content, and rates of physical fragmentation can be higher in rhynchonellids, keeping their destruction rates constant.

Cryptopora fragments, however, are significantly more physically damaged than complete individuals (Fig. 11A). Terebratulid fragments are also more frequently bioeroded than complete terebratulids, but differences in overall damage between complete and fragmented shells are insignificant (Fig. 11B). With increasing postmortem age of shells in the taphonomically active zone, complete and fragmented individuals represent consecutive stages of shell disintegration, and fragments can be expected to be more altered than complete specimens. Low difference in preservation between complete specimens and fragments, however, can arise under high destruction rates and low alteration rates when complete specimens and fragments are weakly altered because
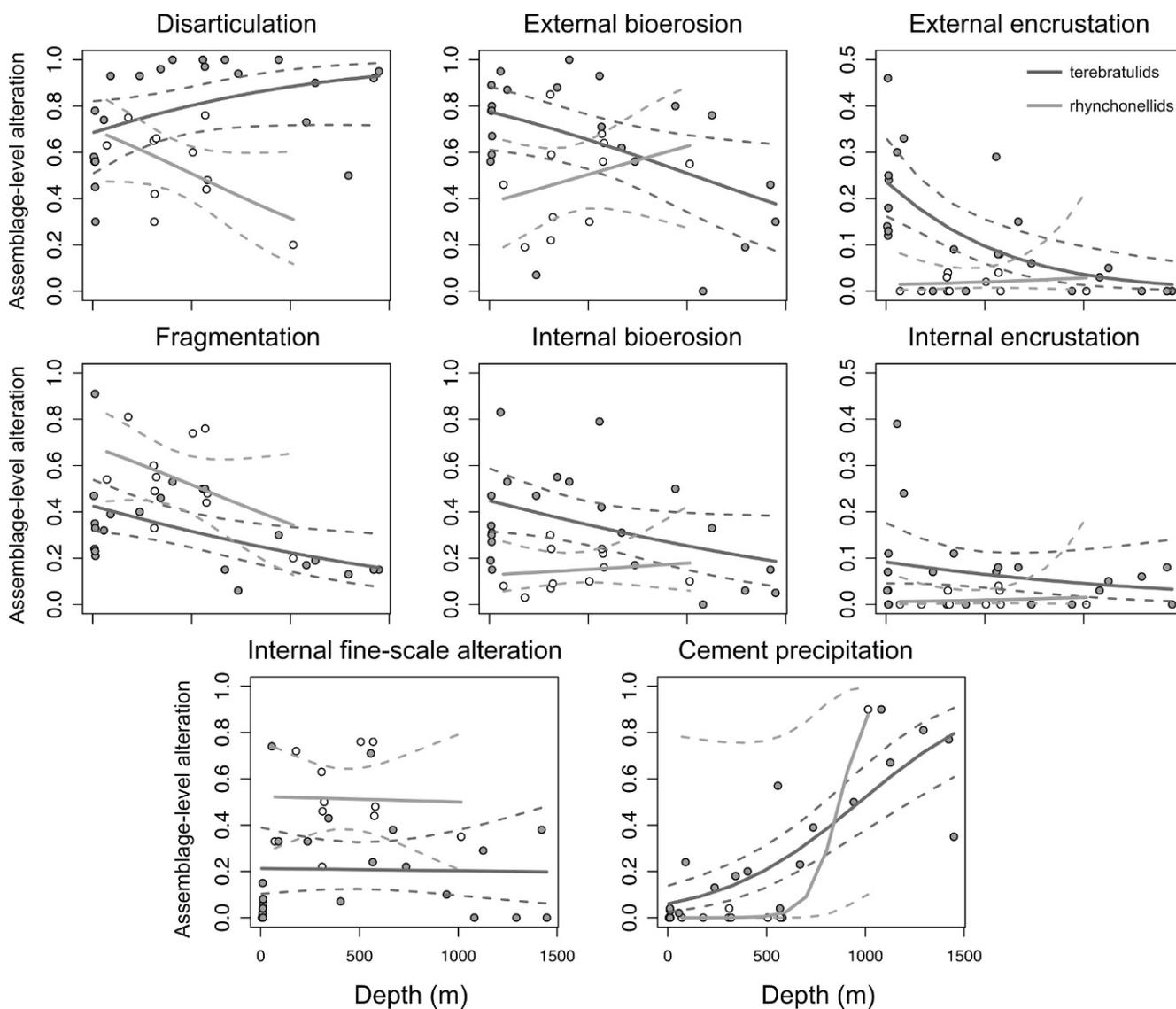
FIGURE 7—Bathymetric trends in assemblage-level alteration of terebratulids (dark grey lines and circles) and rhynchonellids (light grey lines and white circles). In terebratulids, disarticulation correlates positively, and fragmentation, external encrustation, and external bioerosion correlate negatively with depth. Proportions of aragonitic cement increase with depth in both terebratulids and rhynchonellids. We note that rhynchonellids in basin are represented by one sample only, but rhynchonellids in small-sized assemblages are also coated by cement at basinal sites. The slopes (solid lines) and 95% confidence intervals (dashed lines) were estimated with generalized linear models using logit link function and quasibinomial variance function.

destruction rates substantially exceed alteration rates. Reversely, under low destruction and high alteration rates, complete specimens and fragments are highly altered because alteration rates substantially exceed destruction rates. In the latter case, fragments do not accrue any further alteration because most of the damage signal is already captured by relatively durable complete specimens. This case is likely for terebratulids because they are not pristine but rather moderately altered. Complete specimens of terebratulids are equally altered as fragments because they can endure damage for long periods of time before they disintegrate into fragments, in contrast to rhynchonellids. Higher destruction rates of *Cryptopora* can be related to highly reduced shell thickness and lack of ribs when compared to terebratulids.

High shell organic content and porous architecture of punctate shells do not reduce preservation rates in tropical to subtropical environments of the Red Sea because organic-poor rhynchonellids suffer more rapid destruction than organic-rich terebratulids. In contrast, terebratulids accrue minor bioerosion levels and degrade more rapidly than rhynchonellids owing to degradation of shell organic content in cool-temperate environments (Collins, 1986; Emig, 1990; Tomašových,

2004b; Kidwell, 2005; Tomašových and Rothfus, 2005). First, the effect of shell organic content is counteracted by effects of shell thickness. Preservation rates of thick-shelled terebratulids (e.g., Simões et al., 2007a) are also relatively high in tropical environments of the southern Brazilian shelf where they are affected by centennial to millennial scales of time averaging (Carroll et al., 2003) and can undergo intense abrasion (Simões et al., 2007b). Second, the effect of thickness can account for relative differences in preservation between *Cryptopora* and terebratulids in tropical to subtropical environments of the Red Sea, but it is not sufficient to explain differences in preservation between large-sized, 0.5–1-mm-thick cool-temperate terebratulids and small-sized, 0.03–0.08-mm-thick tropical to subtropical terebratulids. In spite of their small size and small thickness that can reduce preservation potential (Cummins et al., 1986; Cooper et al., 2006), preservation potential of the Red Sea terebratulids is rather enhanced by constructive pathways such as cement precipitation, whereas preservation of brachiopods in cool-temperate environments is characterized by the lack of cements (Tomašových and Rothfus, 2005). Although constructive pathways frequently characterize preservation in tropical

A. Rhynchonellids
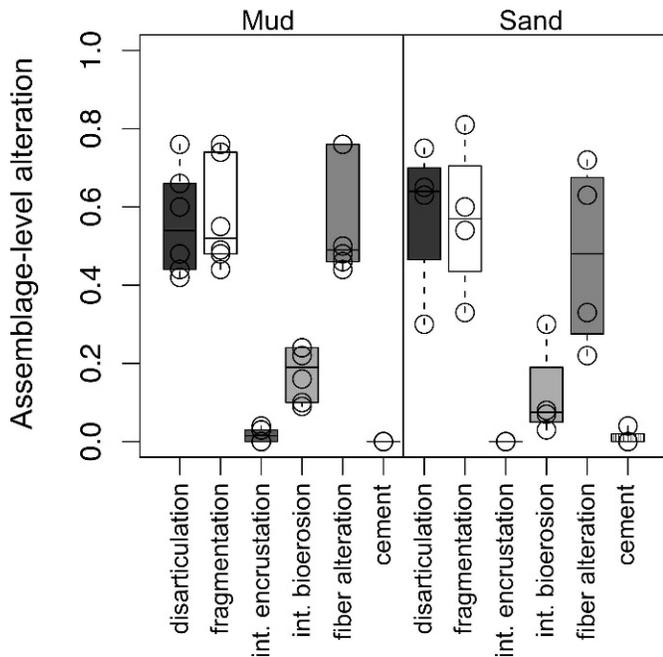
B. Terebratulids
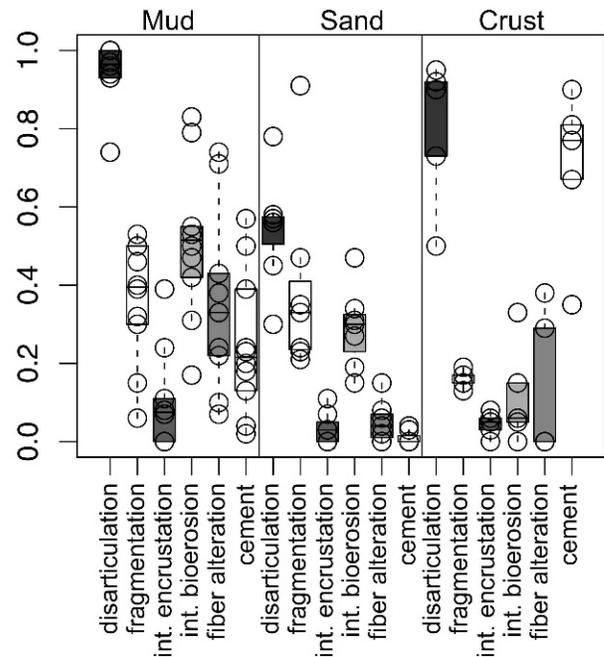
FIGURE 8—Differences in preservation of rhynchonellids (A) and terebratulids (B) among three sediment-grain size types. Rhynchonellid preservation does not differ between mud and sands, but terebratulids are more bored and fragmented in muds than in sands and microbial carbonate crusts. Boxplots display median and 25 and 75 quartile values. External encrustation and external bioerosion positively correlate with their internal counterparts and are omitted for the sake of plot brevity.

reef and slope carbonate environments (Perry and Hepburn, 2008), they can also actively enhance preservation rates in tropical siliciclastic environments (Kidwell et al., 2005). Syndepositional cementation processes occur also in some cool-water environments (Nelson and James, 2000; Caron et al., 2005), but in contrast to tropical and subtropical environments, they are less widespread and their rates are slow (Smith and Nelson, 2003).

The role of cementation is visible in basinal environments at sites with lithified carbonates where inorganic and microbially mediated cement precipitation was favored during the last glacial maximum owing to high salinity, low oxygen content, and reduced shallow-water and pelagic carbonate production (Taviani, 1998; Brachert, 1999). Carbonate preservation in basinal environments of the Red Sea oscillated between glacial and interglacial stages: aragonitic cements formed on pteropod shells during glacial maxima, whereas Mg calcite cements formed during interglacial stages (Almoghi-Labin et al., 1986). Brachiopod preservation at sites with lithified carbonates and the simultaneous presence of extensive aragonite cements on their shells therefore indicate that they can represent relics of glacial maxima and underwent extensive millennial-scale time averaging. Cementation pathways, however, are not restricted to pre-Holocene intervals because cement is present on brachiopods preserved at deep-shelf sites without exposed lithified carbonates, and primary cements are actively formed on reef slopes in the Red Sea (Friedman et al., 1974; Reiss and Hottinger, 1984; Brachert and Dullo, 1991).

Effects of Environmental Factors on Preservation

In terebratulids, the decrease in fragmentation, encrustation, and bioerosion levels with increasing depth is consistent with scenarios that predict reduced destruction rates owing to (1) reduced light penetration that negatively affects light-dependent borers (Budd and Perkins, 1980; Vogel et al., 2005); and (2) reduced primary productivity that negatively affects rates of bioerosion and encrustation by heterotrophic borers and encrusters (Hallock, 1988; Lescinsky, 2002; Mutti and Hallock, 2003) and intensity of predation and predation-induced fragmentation

TABLE 4—Generalized linear models using logit link function and quasibinomial variance function show that depth has significant effects on univariate taphonomic alteration patterns. The p-values in bold represent the significant results after the sequential Bonferroni correction. The p-values in italics represent the results insignificant after the sequential Bonferroni correction.

Brachiopods	Slope	St. error	t-test	p-value
Disarticulation	0.31	0.22	1.44	0.16
Fragmentation	−0.44	0.16	−2.81	**0.008**
External encrustation	−1.09	0.33	−3.26	**0.0027**
Internal encrustation	−0.35	0.32	−1.07	0.29
External bioerosion	−0.37	0.19	−1.93	0.06
Internal bioerosion	−0.34	0.19	−1.73	0.09
Internal alteration	−0.08	0.21	−0.36	0.72
Cement	1.6	0.28	5.73	**<0.0001**

Terebratulids	Slope	St. error	t-test	p-value
Disarticulation	0.64	0.34	1.88	0.075
Fragmentation	−0.48	0.18	−2.64	*0.016*
External encrustation	−1.09	0.3	−3.59	**0.002**
Internal encrustation	−0.39	0.33	−1.18	0.25
External bioerosion	−0.62	0.26	−2.42	*0.025*
Internal bioerosion	−0.45	0.22	−2.05	0.054
Internal alteration	−0.03	0.3	−0.11	0.92
Cement	1.46	0.26	5.55	**<0.0001**

Rhynchonellids	Slope	St. error	t-test	p-value
Disarticulation	−0.41	0.22	−1.9	0.09
Fragmentation	−0.36	0.23	−1.55	0.16
External encrustation	0.19	0.42	0.46	0.660
Internal encrustation	0.25	0.52	0.47	0.65
External bioerosion	0.26	0.27	0.94	0.37
Internal bioerosion	0.1	0.22	0.45	0.66
Internal alteration	−0.02	0.24	−0.1	0.92
Cement	3.5	1.7	2.05	0.07

TABLE 5—Generalized linear models using logit link function and quasibinomial variance function show that unique effects of depth and sediment grain size on taphonomic alteration patterns (i.e., independent contributions of one predictor variable to total variation in taphonomic alteration after variation accounted by the second predictor variable is removed) differ between terebratulids and rhynchonellids. The p-values in bold represent the significant results after the sequential Bonferroni correction for 8 tests per predictor variable. The p-values in italics represent the results insignificant after the sequential Bonferroni correction.

Terebratulids		Slope	St. error	t-test	p-value
Disarticulation	depth	1.291	0.24	5.39	**<0.0001**
	sediment	−1.511	0.32	−4.75	**0.00014**
Fragmentation	depth	−0.421	0.2	−2.11	*0.048*
	sediment	−0.179	0.2	−0.91	0.38
External encrustation	depth	−1.118	0.33	−3.39	**0.0031**
	sediment	−0.179	0.28	−0.63	0.54
Internal encrustation	depth	−0.296	0.36	−0.82	0.42
	sediment	−0.46	0.35	−1.32	0.2
External bioerosion	depth	−0.392	0.3	−1.3	0.21
	sediment	−0.433	0.3	−1.43	0.17
Internal bioerosion	depth	−0.226	0.21	−1.08	0.29
	sediment	−0.765	0.2	−3.75	**0.0014**
Internal surface alteration	depth	0.344	0.36	0.97	0.35
	sediment	−0.88	0.34	−2.59	*0.018*
Cement	depth	1.596	0.36	4.47	**0.00026**
	sediment	−0.172	0.28	−0.62	0.54

Rhynchonellids		Slope	St. error	t-test	p-value
Disarticulation	depth	−0.393	0.23	−1.74	0.12
	sediment	−0.245	0.22	−1.1	0.31
Fragmentation	depth	−0.326	0.23	−1.4	0.2
	sediment	−0.299	0.23	−1.29	0.23
External encrustation	depth	0.378	0.65	0.58	0.58
	sediment	−0.953	0.66	−1.44	0.19
Internal encrustation	depth	0.339	0.85	0.4	0.7
	sediment	−12.78	2348	−0.005	0.99
External bioerosion	depth	0.273	0.29	0.94	0.37
	sediment	−0.109	0.29	−0.38	0.72
Internal bioerosion	depth	0.158	0.26	0.6	0.57
	sediment	−0.275	0.25	−1.08	0.31
Internal surface alteration	depth	0.024	0.25	0.1	0.93
	sediment	−0.288	0.25	−1.16	0.28
Cement	depth	0.939	0.59	1.58	0.15
	sediment	2.81	1.1	2.57	*0.033*

(Walker et al., 2002). First, in spite of the fact that light penetration is relatively deep and can reach to depth of ~130 m in the Gulf of Aqaba (Reiss and Hottinger, 1984), nonpredatory boring patterns on brachiopods in deep-shelf and basinal environments are restricted to heterotrophic endoliths represented by fungal forms with bulbous swellings, similar to other dysphotic and aphotic zones (Zeff and Perkins, 1979; Golubic et al., 2005). Shallow-water brachiopods occur in cryptic spaces underneath coral colonies, and their boring traces can be less frequent in shaded than in exposed habitats (e.g., Perry and MacDonald, 2002; Radtke and Golubic, 2005; Gektidis et al., 2007). Second, a bathymetric reduction in encrustation of mollusks (von Rützen-Kositzkau, 1999) and brachiopods (this study) by agglutinated foraminifers is consistent with primary productivity that peaks in the upper 200 m of the water column in the Red Sea and then declines with depth (Reiss and Hottinger, 1984). Rhynchonellid preservation can be less sensitive to bathymetric effects than that of terebratulids because (1) their high degradation rate preempts the development of an environment-specific signature; (2) their bathymetric range is shorter than the range of terebratulids; and (3) *Cryptopora* was collected also in the Gulf of Aden, which is characterized by different environmental gradients than the Red Sea.

In the Red Sea, the frequency of drilled gastropods (von Rützen-Kositzkau, 1999) and the frequency of terebratulids with circular *Oichnus*-like boreholes also decline with depth (Spearman r = −0.53, p

= 0.01, Fig. 13). Such bathymetric decline can reduce the likelihood of fragmentation, because predatory borings can directly affect the susceptibility of shells to damage (Roy et al., 1994; Zuschin and Stanton, 2001). In terebratulids, however, the decrease in the drilling frequency is of borderline significance in generalized linear model (p = 0.069), 95% confidence intervals are too broad owing to small sample sizes (Fig. 13), and the relationship between the drilling frequency and fragmentation is positive but insignificant (Spearman r = 0.33, p = 0.14). In addition, the relationship is not significant for rhynchonellids (Spearman r = −0.29, p = 0.39), and the frequency of drilled bivalves and the proportion of gastropods with crustacean-induced breakage remain constant with depth (von Rützen-Kositzkau, 1999). A similar absence of correlation between alteration levels and drilling frequency on shallow-water echinoderms in the Red Sea was observed by Nebelsick and Kowalewski (1999). The relationship between depth and drilling frequency in the Red Sea remains unclear, and the support for the scenario where the bathymetric decline in fragmentation is caused by drilling predation is weak.

It is possible that some reduction in alteration with depth can be related to the presence of aragonite cement that can enhance resistance against degradation in basinal samples. In addition, differences in terebratulid preservation among sediment types are mainly driven by higher internal bioerosion and higher fine-scale surface alteration in muds than in microbial carbonate crusts. These effects can arise because (1) cement coatings overlie the shell surface that is perforated with borings; or (2) cement formation reduces the likelihood of surface degradation. It is likely, however, that the increase in the proportion of cemented shells and, thus, in the importance of constructive pathways, is related to past conditions amenable to cement precipitation rather than to present-day bathymetric variation in precipitation rate. The temporal decrease in the importance of constructive pathways is demonstrated by the fact that lithified carbonates of the Pleistocene hard layer are buried under muds and sapropels in shallower depths of the deep shelf (Brachert, 1999). Changes in proportions of cement rather correspond to the past conditions of aragonite precipitation during the last glacial maximum when cementation was favored by high salinity, low oxygen content, and reduced shallow-water carbonate production (Taviani, 1998; Brachert, 1999). This indicates that skeletal preservation rates are not in steady state during the formation of surface death assemblages with brachiopods, and taphofacies patterns are partly driven by past environmental conditions.

As an alternative to bathymetric changes in rates of skeletal destruction, changes in burial rate alone can affect preservation because the length of exposure time in the taphonomically active zone determines the cumulative probability of shells being altered (Olszewski, 1999). The bathymetric reduction in assemblage-level alteration, however, is unlikely related to changes in residence time because sedimentation rate decreases, rather than increases, toward deeper environments. The absence of residence time effects can arise when death assemblages are represented by untruncated postmortem age-frequency distributions—when burial rates are substantially slower than rates of skeletal destruction (Tomašových et al., 2006)—so that an increase in residence time does not increase assemblage-level alteration.

Environmental Sensitivity and Explanatory Power of Taphofacies

Shallow-water brachiopods of the Red Sea and Gulf of Aden occur in cryptic coral-associated habitats (Logan et al., 2008; Zuschin and Mayrhofer, 2009) but do not occur on high-energy beaches, in seagrass beds, or in extensively bioturbated sands, environments that are characterized by distinctive taphonomic signals (Perry, 1999; Bradshaw and Scoffin, 2001; Parsons-Hubbard, 2005). In spite of the narrow environmental range of brachiopods, their preservation captures changes in depth and sediment grain size in carbonate environments. In contrast to findings of Parsons-Hubbard (2005) and Powell et al.
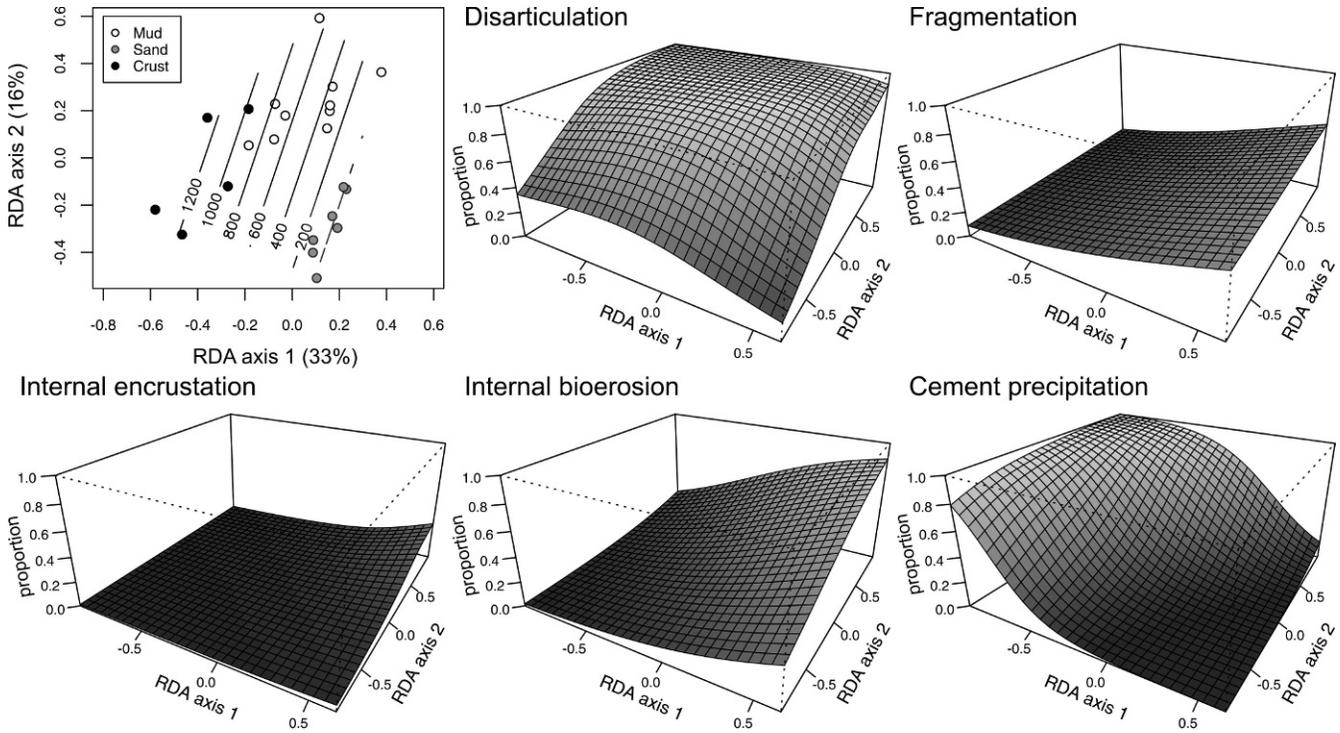
FIGURE 9—Relationships between environmental variables (expressed by axes of redundancy analysis) and taphonomic gradients in terebratulid preservation. RDA axis 1 increases with decreasing depth and RDA axis 2 increases with decreasing sediment grain size (contours show bathymetric position of samples in meters). Surfaces depicting changes in individual taphonomic variables were fitted with generalized additive models: fragmentation, internal bioerosion, and internal encrustation are reduced with depth, internal bioerosion increases toward smaller grain size, and disarticulation and cement precipitation increase with depth.
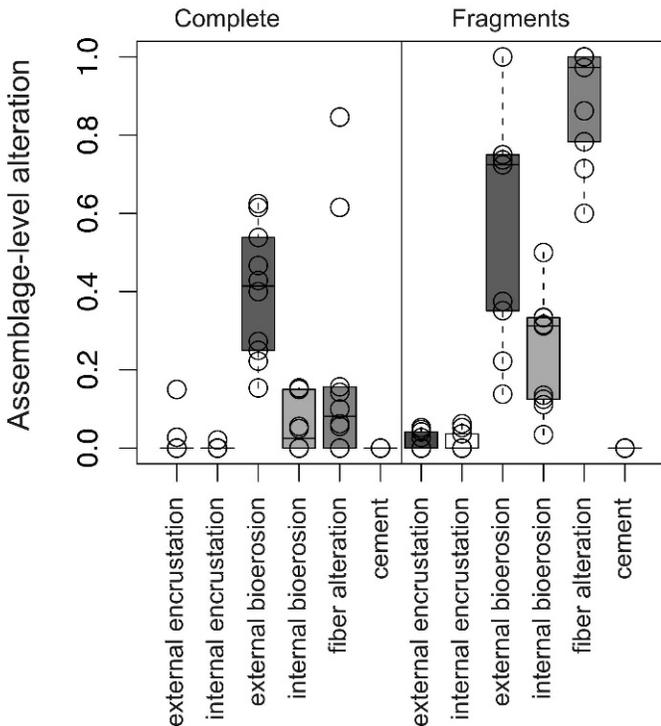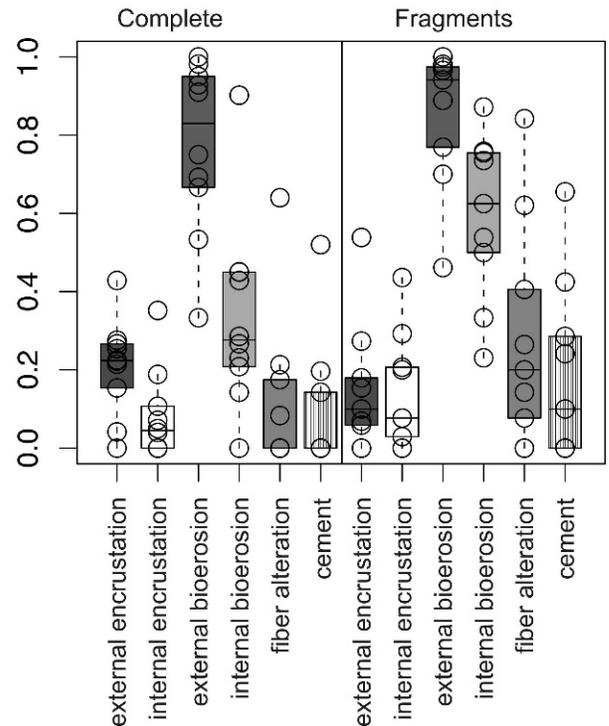
FIGURE 10—Differences in preservation of fragments and complete specimens in (A) rhynchonellids (*Cryptopora*) and (B) terebratulids (*Megerlia*). Fragments of *Cryptopora* are more altered than complete specimens, whereas fragments of *Megerlia* do not differ in preservation from complete specimens. *Megerlia* fragments, however, are more bored than fragments of *Cryptopora*. Boxplots display median and 25 and 75 quartile values.
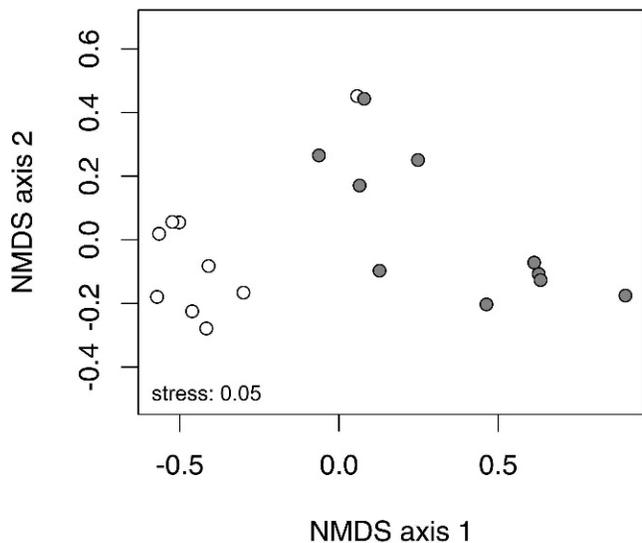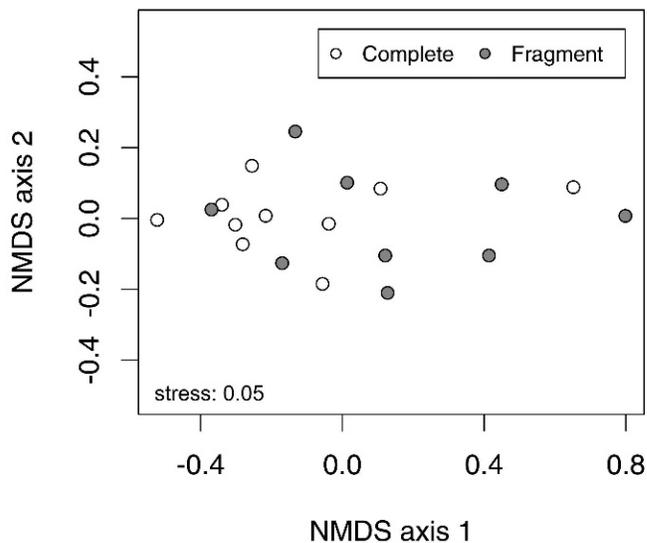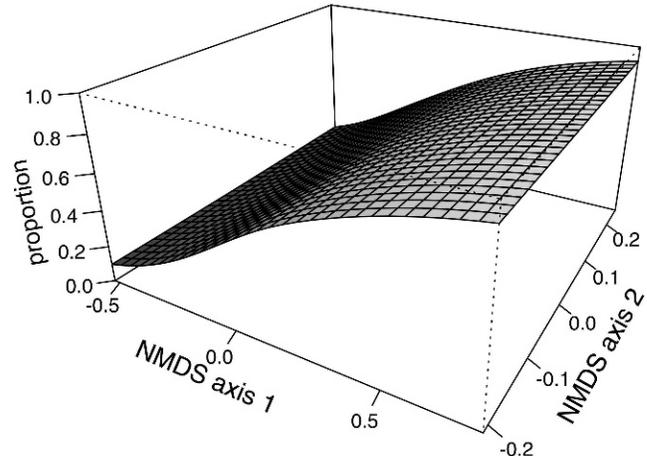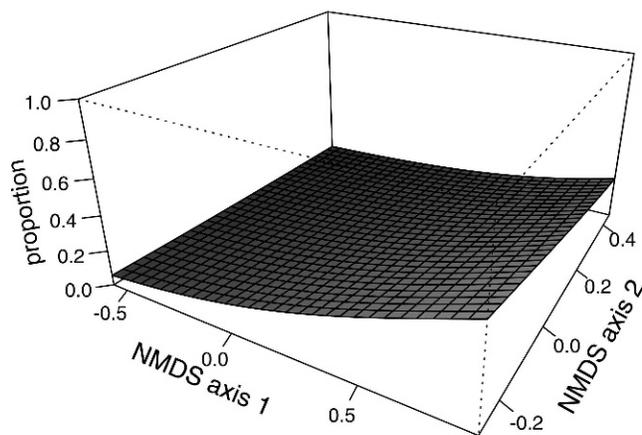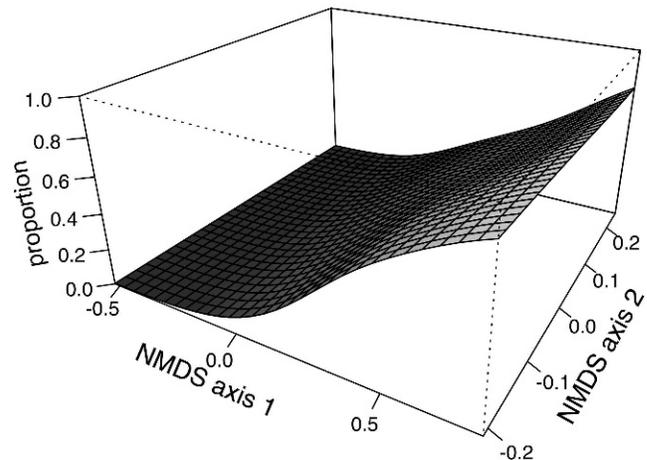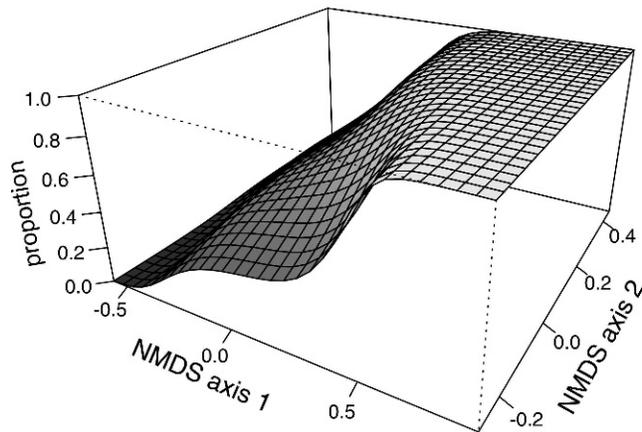
FIGURE 11—Differences in multivariate preservation of fragments and complete specimens in (A) rhynchonellids (*Cryptopora*) and (B) terebratulids (*Megerlia*) visualized by NMDS plots. The surfaces fitted by generalized additive models visualize changes in taphonomic alteration and show that internal bioerosion and fine-scale surface alteration is higher in fragmented than in complete specimens of *Cryptopora*, whereas complete and fragmented specimens of *Megerlia* do not differ in these variables. Internal bioerosion in *Megerlia* reaches higher levels than in *Cryptopora*, whereas *Megerlia* is less affected by fine-scale surface alteration than *Cryptopora*. Analyses are restricted to shelf environments and mud and sands.
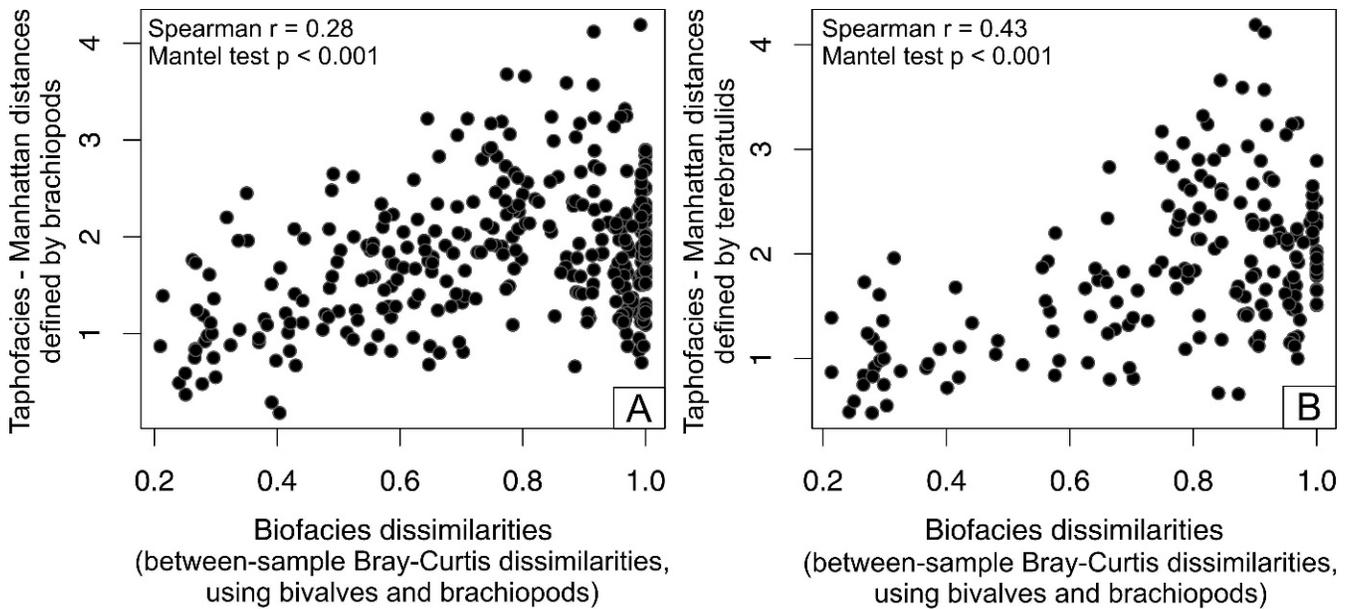
FIGURE 12—Significantly positive rank correlations between dissimilarities in species composition and distances in brachiopod preservation (Mantel test). This relationship is lower using (A) preservation of rhynchonellids and terebratulids than using (B) preservation of terebratulids only.

(2008), several taphonomic variables are intercorrelated and correlate with environment: this difference is partly related to the effects of shell-specific traits that confound environmental sensitivity of taphofacies. First, shell-specific traits of rhynchonelliform brachiopods are more uniform in terms of their size, shell structure, mineralogy, and life habit relative to more diverse skeletal groups. Second, shell-specific traits that differentiate organic-rich and organic-poor brachiopods are factored out in this study. The part of the multivariate variation in preservation that remains unexplained by environmental and shell-specific variations, however, is still 53%. In this study, this residual variation can be likely to be related to sampling effects related to limited sample size and differences among sampling gears but also to variation in preservation

within environments owing to small-scale patchiness in preservation. For example, dispersion of samples around the predicted slopes in univariate analyses is larger in shelf environments than in basin (Fig. 7): shelf sites are generally characterized by higher spatial heterogeneity in distribution of coral and bryozoan reefs than deep-shelf and basinal sites with soft-bottom communities (Reiss and Hottinger, 1984).

Relationship Between Taphofacies and Biofacies

Variation in preservation related to such shell-specific factors as thickness, shell porosity, or shell organic content can cause changes in taphonomic alteration that imply changes in species composition along environmental gradients, rather than changes in skeletal destruction rates or changes in residence time in the taphonomically active zone. The rank correlation between taphonomic distances and biofacies dissimilarities, however, increases when shell-specific factors related to shell structure are removed—when variation in preservation of terebratulids is compared against variation in composition of bivalve and brachiopod assemblages. The relationship between taphofacies and biofacies is, therefore, not related to this type of dependency in our study. We note that the size of bivalves collected in the individual samples and used in biofacies analyses is on average larger than the size of micromorphic brachiopods (e.g., median of maximum shell sizes = 25 mm in reef habitats, Zuschin and Oliver, 2005), although many bivalve species have maximum shell sizes that are also smaller than 5 mm and most specimens from larger species are also small. Such a difference in size can lead to differences in the scale of environmental processes to which brachiopod preservation and bivalve distribution patterns respond. It is possible that small-scale environmental gradients can affect preservation of small-sized species, whereas composition of assemblages with larger bivalve species is driven by environmental variability at larger spatial scales. Such differences can be expected to minimize concordance between taphofacies and biofacies. The positive relationship between taphonomic and compositional distances, however, indicates that similar environmental factors can still affect distribution and preservation of skeletal groups, although this correlation is not perfect and can be also related to the differences in scale of processes that control species abundance and species preservation rates.
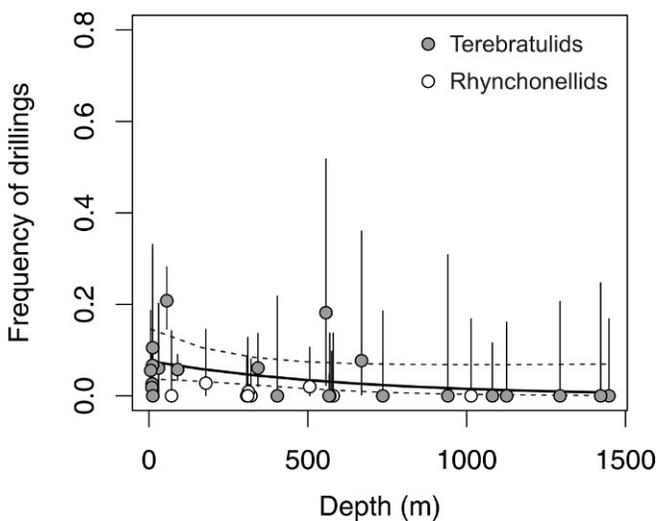
FIGURE 13—The relationship between proportions of terebratulid valves with predatory boreholes and depth. The relationship is significantly positive (Spearman r = −0.53, p = 0.01), but the GLM slope is of borderline significance (p = 0.069). The expected slope (solid line) and 95% confidence intervals around the slope (dashed lines) are computed for terebratulid samples using the logit-link function and the quasibinomial variance function.

CONCLUSIONS

The high shell-organic content and porosity that reduce preservation rates of terebratulids in cool-temperate environments do not play a large role in preservation in tropical and subtropical environments because the rhynchonellid *Cryptopora* degrades more rapidly than similar-sized organic-rich terebratulids, probably owing to reduced shell thickness and lack of ornamentation. Importantly, constructive pathways that lead to cementation of skeletal particles in present-day reef and slope environments, or pathways that led to cementation in deep-shelf and basinal environments during the Pleistocene, enhance overall preservation rates of small-sized brachiopods in tropical and subtropical environments of the Red Sea.

We find that shell-specific effects confound environmental sensitivity of skeletal preservation: the amounts of variation in preservation explained by environment increase from 29% using combined brachiopod preservation to 46% using terebratulid preservation only. On one hand, alteration patterns show that destruction rates decrease with depth in terebratulids, probably owing to depth-dependent changes in productivity affecting rates of predation, encrustation, and bioerosion. On the other hand, brachiopod structural elements are extensively cemented with aragonite in basinal environments. The increase in the proportion of shells with aragonite cement does not reflect bathymetric changes in rate of cement precipitation but rather correspond to past conditions amenable to aragonite precipitation during the last glacial maximum. Brachiopod preservation rates are not in steady state over the duration of time averaging: environmental sensitivity of taphofacies is not only driven by present-day bathymetric variation in primary productivity and light penetration, but also partly by past Pleistocene conditions that favored aragonite precipitation.

Although taphofacies capture environmental gradients to a similar degree as biofacies, the amounts of variation in preservation unexplained by environmental and shell-specific factors attain 53% and, thus, limit explanatory power of taphofacies in environmental reconstructions. Some portions of residual variation, however, can be minimized by increasing sample sizes and their spatial extent so that small-scale patchiness effects are reduced.

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