January 1, 1992

Experimental analysis of abrasion and dissolution resistance of modern reef-dwelling Foraminifera: Implications for the preservation of biogenic carbonate

E. Kotler
R. E. Martin
W. D. Liddell, Utah State University
Experimental Analysis of Abrasion and Dissolution Resistance of Modern Reef-Dwelling Foraminifera: Implications for the Preservation of Biogenic Carbonate

ELAINE KOTLER and RONALD E. MARTIN
Department of Geology, University of Delaware, Newark, DE 19716
W. DAVID LIDDELL
Department of Geology, Utah State University, Logan, UT 84322

PALAIOS, 1992, V. 7, p. 244–276

Fringing coral reefs at Discovery Bay, Jamaica, exhibit a pronounced depth-related gradient in water turbulence and associated physicochemical taphonomic factors (abrasion, dissolution), and thus provide ideal settings for investigating the influence of taphonomic processes on the formation of fossil assemblages. Foraminifera are prominent constituents of bioclastic sediments at Discovery Bay, and exhibit a high diversity of test sizes, shapes, wall compositions, architectures, and microstructures which may potentially affect their post-mortem behavior. Herein, we develop a taphofacies model for Jamaican north coast fringing reefs and associated environments that has allowed us to generate hypotheses about the formation of foraminiferal sediment assemblages. Herein, we test the taphofacies model via laboratory and field experiments coupled with previous analyses of foraminiferal sediment assemblages. Based on laboratory and field investigations, dissolution and abrasion acting together are much more effective taphonomic agents than either agent acting alone. Most species tested are, however, resistant to both agents (acting alone or synergistically), although test surfaces may be severely altered (e.g., Amphistegina gibbosa). Only the most fragile species were totally destroyed (e.g., Planorbulina aceravis).

Foraminiferal preservation in carbonate sediments may, in some cases, mimic that of condensed intervals of siliciclastic environments, in which shell-rich layers create an environment favorable to their preservation by buffering pore waters of the surface mixed layer against dissolution. Conversely, carbonate and shell-poor terrigenous regimes are predicted to differ in the intensity of physicochemical processes affecting incipient fossil assemblages. Given that carbonate and terrigenous sedimentary regimes also differ in the continuity and rate of sedimentation, shelfal carbonate and shell-poor siliciclastic regimes may differ fundamentally in the taphonomic constraints they place on our interpretation of the paleoecology, biostratigraphy, and evolution of ancient microorganisms. Relative rates of test destruction in carbonate and terrigenous sediments may hold important implications for carbonate budgets and the global carbon cycle.

INTRODUCTION

Continental shelves display pronounced depth-related gradients in physical and biological parameters, all of which influence the ultimate transition from living to fossil communities. Ecological and preservational gradients have been exploited in the development of taphofacies models for macroinvertebrate assemblages formed in terrigenous shelf environments (Brett and Baird, 1986; Kidwell et al., 1986;
Speler and Brett, 1988; Fürsich and Flessa, 1987; Meldahl and Flessa, 1989). Because of the rapid decrease in water turbulence with depth, carbonate shelves also provide ideal settings for investigating the influence of taphonomic processes on the formation of subfossil assemblages. Like their terrigenous counterparts, carbonate shelves recur throughout the rock record and exhibit pronounced depth-related gradients in water turbulence, sedimentation rate, organic carbon content, water and pore fluid chemistry of sediments, bioerosion and bioturbation, community composition and structure, and corresponding taphonomic gradients in post-mortem abrasion, dissolution, and transport (Buxton and Pedley, 1989; Graus and MacIntyre, 1989).

Foraminifera are prominent constituents of biologic sediments and exhibit a high diversity of sizes, shapes, wall compositions, architectures, and microstructures (e.g., Table 1) which may affect their post-mortem behavior. Despite numerous distributional studies of foraminifera in modern carbonate environments, however, comparative taphonomic studies of benthic foraminiferal faunas are sorely lacking. Biological and physiographic reef zonations are well-documented for certain modern reef settings, such as the fringing reefs at Discovery Bay, Jamaica (Liddell et al., 1984, 1987; Martin and Liddell, 1988), and provide a means of assessing gradients in potential physicochemical factors affecting the formation of foraminiferal sediment assemblages. In turn, foraminiferal assemblages correspond to macroinvertebrate community zonations and reef geomorphology (Martin and Liddell, 1988, 1989), and therefore presumably also reflect the same physicochemical (and taphonomic) gradients as the macroinvertebrate assemblages.

JAMAICAN TAPHOFACIES MODEL

Based on previous studies at Discovery Bay, Jamaica (Fig. 1A; summarized in Liddell et al., 1984; see also Liddell et al., 1987; Martin and Liddell, 1988, 1989), and elsewhere (Martin, 1986; Martin and Wright, 1988), we developed a taphofacies model (Liddell and Martin, 1989; Fig. 1B; cf. Johnson, 1960) based upon the predicted degree of abrasion, dissolution, bioerosion, and transport of foraminiferal tests along taphonomic gradients. The model provides an initial theoretical framework for testing the influence of ecologic and taphonomic constraints on test morphology, evolution, and preservation through time (Wetmore, 1987), and has allowed us to develop and test hypotheses about the taphonomic behavior of foraminiferal tests via laboratory and field experiments (Kotler, 1990; Kotler et al., 1989; in press).

Taphofacies I (Fig. 1B) represents a low energy setting with low transport potential (i.e., sheltered lagoon or below wave base with a low slope angle). Assemblages consist of a diverse mixture of autochthonous abrasion-resistant and nonresistant tests of small to large miliolids, peneroploids, and foraminifers (Martin and Liddell, 1988; Martin and Wright, 1988), that represent differing shapes and sizes (different susceptibilities to transport or destruction). We predict that dissolution, resulting from oxidation (via bioirrigation and bioturbation) of abundant organic detritus, and, to a lesser extent, oxidation of sulfide particles, is important near shore (e.g., Walter and Burton, 1990), but decreases near the reef crest where waters are more agitated (Martin, 1986; Cottee and Hallcock, 1988; Martin and Wright, 1988), organic matter concentrations are lower and pore water pH is somewhat higher (Ginsburg, 1957, fig. 10).

We predict that abrasion increases in the outer back reef behind the reef crest. Outer back reef assemblages consist of mixtures of abrasion-resistant autochthonous and allochthonous terrace species transported over the reef crest by storms (taphofacies II). Outer back reef assemblages are enriched in resistant tests with a concomitant decrease in diversity (e.g., lag deposits of the resistant foraminifera Archaia angulatus and the rotaline Discorbis rosea; Martin, 1986; Martin and Wright, 1988).

Taphofacies III (lower terrace: 10–15 m; Fig. 1B) represents a relatively high energy setting with low transport potential (i.e., shallow water where wave surge is the main energy source and a low slope angle). Abrasion is predicted to modify residual assemblages, which are enriched in robust tests of Amphistegina gibbosa, and are therefore low in diversity.
TABLE 1—Foraminiferal species used in laboratory analyses. Species were selected on the basis of abundance, wall type, shape and size so as to utilize a diversity of forms. All species are benthic except for Globigerinoides quadrilobatus, which is planktonic.

<table>
<thead>
<tr>
<th>Species</th>
<th>Suborder</th>
<th>Wall structure</th>
<th>Shape</th>
<th>Wall thickness</th>
<th>Size (in natural habitat)</th>
<th>Reef zone habitat</th>
</tr>
</thead>
<tbody>
<tr>
<td>Amphistegina gibbosa</td>
<td>Rotaliina*</td>
<td>Calcareous, perforate</td>
<td>Lenticular</td>
<td>Thick</td>
<td>Small–large (0.5–2 mm)</td>
<td>Dominant on fore reef</td>
</tr>
<tr>
<td>Archaias angulatus</td>
<td>Miliolina</td>
<td>Calcareous, perforate</td>
<td>Lenticular</td>
<td>Thin, but reinforced by pillars</td>
<td>Small–large (0.5–2 mm)</td>
<td>Dominant in back reef</td>
</tr>
<tr>
<td>Asterigerina carinata</td>
<td>Rotaliina</td>
<td>Calcareous perforate</td>
<td>Conical</td>
<td>Thick, with heavy umbilical plug</td>
<td>Small (&lt;0.5 mm)</td>
<td>Common on reef reef terrace</td>
</tr>
<tr>
<td>Bigenerina irregularis</td>
<td>Textularina</td>
<td>Agglutinated</td>
<td>Curvilinear</td>
<td>Thick, but lightly cemented</td>
<td>Small–medium (0.5–1 mm)</td>
<td>Common on reef reef slope</td>
</tr>
<tr>
<td>Cyclorbiculina compressa</td>
<td>Miliolina</td>
<td>Calcareous, perforate</td>
<td>Discoidal</td>
<td>Thin, but reinforced by pillars</td>
<td>Small–large (0.5–2 mm)</td>
<td>Most abundant in back reef</td>
</tr>
<tr>
<td>Discorbis rosea</td>
<td>Rotaliina</td>
<td>Calcareous, perforate</td>
<td>Hemispherical</td>
<td>Thick</td>
<td>Small (&lt;0.5 mm)</td>
<td>Most abundant on fore reef terrace</td>
</tr>
<tr>
<td>Globigerinoides quadrilobatus</td>
<td>Rotaliina</td>
<td>Calcareous, perforate</td>
<td>Globular</td>
<td>Thin, fragile</td>
<td>Small (&lt;0.5 mm)</td>
<td>Most abundant on fore reef slope and island slope</td>
</tr>
<tr>
<td>Planorbulina acervalis</td>
<td>Rotaliina</td>
<td>Calcareous, perforate</td>
<td>Discoidal</td>
<td>Thin, fragile</td>
<td>Small–large (0.5–2 mm)</td>
<td>Common in back reef</td>
</tr>
<tr>
<td>Peneroplis proteus</td>
<td>Miliolina</td>
<td>Calcareous, perforate</td>
<td>Discoidal</td>
<td>Thin</td>
<td>Small–large (0.5–2 mm)</td>
<td>Common in back reef</td>
</tr>
<tr>
<td>Quinqueloculina lamarchiana</td>
<td>Miliolina</td>
<td>Calcareous perforate</td>
<td>Spindle</td>
<td>Thick</td>
<td>Small–medium (0.5–1 mm)</td>
<td>Ubiquitous in back reef and fore reef</td>
</tr>
<tr>
<td>Quinqueloculina tricarinata</td>
<td>Miliolina</td>
<td>Calcareous, perforate</td>
<td>Spindle</td>
<td>Thick</td>
<td>Medium (0.5–1 mm)</td>
<td>Fore reef terrace</td>
</tr>
<tr>
<td>Sortes marginalis</td>
<td>Miliolina</td>
<td>Calcareous, perforate</td>
<td>Discoidal</td>
<td>Thin, fragile</td>
<td>Medium–large (0.5–2 mm)</td>
<td>Common in back reef</td>
</tr>
</tbody>
</table>

* Suborder Miliolina—submicroscopic crystallites of test arranged in random or brick-like pattern; Suborder Rotaliina—crystallites usually arranged with c axis perpendicular to test surface; Suborder Textularina—sediment grains cemented together by a combination of organic and calcareous cements (Boersma, 1978).

Taphofacies IV (upper terrace: 5–10 m) and V (fore reef slope: 30–75 m) are similar to taphofacies III and I, respectively, but differ in that tests with high susceptibility to transport are winnowed from assemblages with a resultant decrease in diversity.

Taphofacies VI (island slope), located adjacent to a type III, IV, or V setting, is characterized by a diverse mixture of allochthonous and autochthonous species, including planktonic components; diversity is high due to mixing and low post-mortem alteration. This paper will consider only taphofacies I–V; separate studies of the island slope taphofacies are underway.

METHODS OF INVESTIGATION

Field Methods

Sediment samples were previously collected (Martin and Liddell, 1988, 1989) along traverses crossing the West Fore Reef of Discovery Bay (Fig. 1A). Sediment cores (approximately 5 cm diameter × 5 cm length; ~100 cm³ volume) were collected from each of the physiographic reef zones (Fig. 1B) in August, 1983, using SCUBA. Back reef samples were collected from sandy areas and fore reef samples were collected from reef buttresses and lobes in order to minimize mixing of faunal elements via downslope transport. Deep fore reef samples were collected from sediment trapped by ledges on the vertical escarpment (Fig. 1B). After collection, sediment samples were dried at low temperature (~28°C) in order to retain shell strength (Martin and Liddell, 1988).

Laboratory Methods

Specimen Selection

Species were chosen for experimental analysis based on their abundance in the modern Jamaican fauna (Martin
and Liddell, 1988) and on their test attributes (size, shape, thickness, composition, architecture) in order to provide a diverse array of morphotypes (Table 1). Admittedly, the exact test microstructure is not known for many foraminiferal species, but in our study the species utilized are assumed to be representative of the suborders to which they belong (see Table 1 bottom). All species selected were benthic foraminifera with the exception of Globigerinoideas quadrilibatus, which was planktonic. In addition, the calcareous green alga Halimeda was chosen for analysis as it is a major contributor to carbonate sediment at Discovery Bay. Foraminiferal species were identified to the species level primarily according to the taxonomy of Bock (1971).

Sediment samples were dry-sieved into 0.125–0.25, 0.25–0.5, 0.5–1 and >1 mm size fractions. With the exception of Halimeda (>1 mm) and Discorbis rosea and Asterigerina carinata (0.25–0.5 mm), all specimens were picked from the 0.5–1 mm size fraction. Specimen size was controlled in order to avoid bias that could result from differential rates of destruction related to test size (Cotney and Hallock, 1988). Specimens showing little or no evidence of worn ornamentation, shallow cracks, impact depressions or pitting, scalloping of margins, or breakage (i.e., taphonomic alteration) were picked from the sediment samples under a binocular microscope. In some cases, we were forced to use slightly imperfect specimens (i.e., minor surface alteration, pitting) at the outset of experiments.

Abrasion Experiment Protocol

Ten specimens of each species were picked from the sediment samples for use in abrasion analyses. Prior to experimentation (0 hour), all specimens were cleaned and photographed as detailed in the section on Scanning Electron Microscopy (SEM; see below). Specimens were then placed in containers with approximately 7 g of biogenic carbonate sediment (mollusc, algal, echinoid remains, etc.) that had been standardized to ~0.5 mm (approximate mean grain size of Jamaican fore reef sediments; Liddell et al., 1987), and that had been picked of all identifiable foraminifera and Halimeda platelets so that the specimens being tested could be differentiated from carbonate sediment. Containers were ~500 ml plastic containers with airtight lids (to prevent evaporation) with rubber stoppers secured to their centers to prevent buildup of sediment as it rotated in a circular motion during rotation of the shaker. Two containers were used: one with six species of foraminifera and the second with the six remaining species of foraminifera and Halimeda platelets. Sediment and specimens were submerged in 20 ml of Instant Ocean® Synthetic Sea Salts (Aquarium Systems, Mentor, Ohio), a buffered solution that has been shown to retain a pH of ~8.0 when combined with carbonate sediment. Water volume was sufficient to immerse the sediment and specimens in solution. The solution remained at room temperature (~20–24°C) throughout the abrasion experiments. The pH of artificial seawater was checked periodically during the experiment to ensure that it remained stable.

The entire container (with foraminiferal specimens, Halimeda platelets, carbonate sediment and artificial seawater) was evacuated of air prior to experimentation in order to permit filling of test chambers and voids with seawater to prevent flotation. The containers were then secured on a Lab-Line (Melrose Park, IL) Orbit Shaker and rotated at 150 rpm to simulate shifting bottom sediments of the turbulent reef environment. This speed had been determined through previous experimentation to maximize grain-to-grain contact while minimizing suspension of sediment grains. Experimental specimens were picked from the sediment at pre-selected intervals of 125, 250, 500, and 1000 hours (based on preliminary experiments), mounted on SEM specimen stubs, photographed, and cleaned as described below. The duration of abrasion was cumulative; e.g., 250 hours of abrasion was the next 125 hours following the previous 125 hour interval. Using the same specimens continually throughout experimentation allowed for accurate descriptions of the changes encountered during the abrasion runs. In many instances, individual specimens of different species remained sufficiently distinctive that they could be identified throughout the experiment.

Those specimens that were not retrieved from the sediment at the end of a designated time interval were presumed to have been destroyed beyond recognition by abrasion, and were labelled as being "lost due to taphonomic processes" (i.e., obliteration). Some of these specimens may have been sufficiently degraded to be overlooked while we picked through sediment, however. Picking through carbonate sediment for experimental foraminiferal specimens was laborious and time-consuming, but necessary. The alternative method of staining experimental specimens for ease of retrieval was not employed because staining etched test surface features and outer test layers, thereby weakening the test. Inevitably, some specimens were also lost during experimental procedures (i.e., picking, SEM mounting and coating) before the SEM photography stage, and were labelled as "lost due to operator error." Also, after commencement of the experiment, some specimens were identified as being nonrepresentative of the species at 0 hour. These specimens (four of Discorbis rosea and one of Quinqueloculina lamarkiana) seemed intact under the binocular microscope, but upon closer scrutiny with the scanning electron microscope the tests appeared taphonomically altered (cf. Lewis et al., 1990): the ornamentation on specimens of D. rosea was polished, and the specimen of Q. lamarkiana appeared to have been damaged by microorganisms. These specimens were therefore eliminated from further analysis. Despite these caveats, most species were represented by a sample size of eight to ten specimens at the conclusion of the experiment (Table 2, Column B).

In an attempt to quantify the degree of taphonomic exposure (Kidwell, 1986) during the abrasion experiment, one specimen each of Amphistegina gibbosa, Sorites marginalis, and Discorbis rosea, and Halimeda (chosen so as to vary test shape and therefore hydraulic properties; Table 1) was monitored on the shaker table at 150 rpm for three different runs, and the number of rotations of each specimen around the container (circumference 15 cm) was
TABLE 2—Abrasion rankings of species tested. The higher the rank of the species, the greater its susceptibility to abrasion. Column A shows the average percent specimen area affected by 1000 hours of abrasion. Column B shows the number of specimens of each species presumably destroyed by abrasion out of specimens not lost to operator error or eliminated from analysis (see "Methods" for further discussion). Column C is the abrasion index (rank of A × rank of B) for each species.

<table>
<thead>
<tr>
<th>Species</th>
<th>Column A Average % area affected by abrasion after 1000 hours (±std. dev.)</th>
<th>Rank of Column A</th>
<th>Column B Proportion of initial population presumably destroyed by abrasion</th>
<th>Rank of Column B</th>
<th>Column C Abrasion index (A × B)</th>
<th>Rank of Column C</th>
</tr>
</thead>
<tbody>
<tr>
<td>Archaias angulatus (M)*</td>
<td>15 ± 8</td>
<td>4.5</td>
<td>0/10</td>
<td>3</td>
<td>13.5</td>
<td>2</td>
</tr>
<tr>
<td>Amphistegina gibbosa (R)</td>
<td>81 ± 34</td>
<td>11</td>
<td>0/10</td>
<td>3</td>
<td>33</td>
<td>6</td>
</tr>
<tr>
<td>Asterigerina carinata (R)</td>
<td>100 ± 0</td>
<td>13</td>
<td>4/8</td>
<td>11</td>
<td>143</td>
<td>13</td>
</tr>
<tr>
<td>Bigenerina irregularis (T)</td>
<td>16 ± 18</td>
<td>4.5</td>
<td>1/8</td>
<td>6</td>
<td>27</td>
<td>4</td>
</tr>
<tr>
<td>Cyclorbiculina compressa (M)</td>
<td>83 ± 28</td>
<td>11</td>
<td>0/10</td>
<td>3</td>
<td>33</td>
<td>6</td>
</tr>
<tr>
<td>Discorbis rosea (R)</td>
<td>38 ± 48</td>
<td>7.5</td>
<td>1/6</td>
<td>7</td>
<td>52.2</td>
<td>10</td>
</tr>
<tr>
<td>Globigerinoides quadrilobatus (R)</td>
<td>11 ± 22</td>
<td>4.5</td>
<td>3/9</td>
<td>10</td>
<td>45</td>
<td>9</td>
</tr>
<tr>
<td>Planorbulina acervata (R)</td>
<td>5 ± n/a**</td>
<td>1.5</td>
<td>10/10</td>
<td>13</td>
<td>19.5</td>
<td>3</td>
</tr>
<tr>
<td>Peneroplis proteus (M)</td>
<td>10 ± 3</td>
<td>4.5</td>
<td>2/7</td>
<td>9</td>
<td>40.5</td>
<td>8</td>
</tr>
<tr>
<td>Quinqueloculina lamarkiana (M)</td>
<td>60 ± 44</td>
<td>9</td>
<td>2/9</td>
<td>8</td>
<td>72</td>
<td>11</td>
</tr>
<tr>
<td>Quinqueloculina tricolorata (M)</td>
<td>3 ± 6</td>
<td>1.5</td>
<td>0/10</td>
<td>3</td>
<td>4.5</td>
<td>1</td>
</tr>
<tr>
<td>Sartes marginalis (M)</td>
<td>45 ± 42</td>
<td>7.5</td>
<td>8/10</td>
<td>12</td>
<td>90</td>
<td>12</td>
</tr>
<tr>
<td>Halimeda (algae)</td>
<td>70 ± 45</td>
<td>11</td>
<td>0/10</td>
<td>3</td>
<td>33</td>
<td>6</td>
</tr>
</tbody>
</table>

* M = Suborder Miliolina (calcareous imperforate test wall); R = Suborder Rotellina (calcareous perforate test wall); T = Suborder Textulariina (agglutinated wall). See also Table 1.

** Only fragments remained; standard deviation not calculated.

counted for each run (duration one minute). The average distance travelled was then calculated for each species. Distances travelled by particles in the experimental container were based on the particles moving in seawater only (for reasons of visibility). A similar experiment using foraminifera, seawater, and pure quartz beach sand (0.5–1 mm) demonstrated that foraminifera alternately move over and under the surface of the sediment layer, and travel between ½ and ⅔ of the distances calculated using only water. Therefore, distances calculated in Table 2 must be considered as maximum distances travelled.

Test Surface Analysis

In order to quantify the degree of test surface alteration, all photographs from the abrasion experiments were digitized, with the exception of 125 hours (little or no evidence of abrasion). Taphonomic features of abrasion (Fig. 2) were categorized into 1) deep pits—rounded impact depressions that breach the test wall to expose inner chambers; 2) shallow pits—rounded impact depressions that do not breach the test wall; 3) breakage—irregular portions of the specimen that are missing; 4) scalloping (of the margins of the test); and 5) cracks—fractures on the test surface. A final category ("other") was used for abrasion features which were relatively indistinct at the binocular microscope level (shallow surface degradation). Only one side of each specimen was photographed, but because individual specimens often remained recognizable throughout the experiment, the same surface of each specimen was usually photographed, and was therefore considered to be representative of the whole test. All features, with the exception

![FIGURE 2—TAPHONOMIC FEATURES PRODUCED BY ABRASION. See text for explanation of features. 1) Deep pits, shallow pits, and scalloping in Peneroplis proteus. A) Initial specimen (0 hour); B) 1000 hour specimen; a = deep pit; b = shallow pit; c = scalloping. 2) Breakage in Globigerinoides quadrilobatus. A) Initial specimen (0 hour); B) 1000 hour specimen (a = breakage). 3) Cracks in Quinqueloculina lamarkiana. A) Specimen after 125 hours of abrasion showing fractures (a, b) of the test wall. B) Enlargement of cracks (b) shown in A. 4) Shallow test surface degradation in Amphistegina gibbosa. A) Initial specimen (0 hour); B) 250 hour specimen. Note relatively coarse texture of test surface in B compared with relatively smooth surface in A. 5) Obliteration of aperture in Amphistegina gibbosa. A) Initial specimen (0 hour); B) 1000 hour specimen with obliterated aperture (a). B) Exposure of chambers in Quinqueloculina lamarkiana. A) Initial specimen (0 hour); B) 250 hour specimen. Outer test wall has been removed to expose inner chambers of the specimen. 7) Loss of detail of sutures in Asterigerina carinata. A) Initial specimen (0 hour); B) 250 hour specimen showing loss of sutural detail (a).](image-url)
TAPHONOMIC FEATURES OF ABRASION
of shallow cracks, were calculated as a percentage of the test surface area. Cracks were measured using a line intersection method detailed by Mark (1974) for calculating drainage density of streams.

**Dissolution Experiment Protocol**

A preliminary experiment to determine the relative resistance of foraminifera to dissolution was conducted using a fluidized bed reactor (Chou and Wollast, 1984). Five specimens each of *Amphistegina gibbosa*, *Archaia insula*, *Bigenerina irregularis*, *Discorbis rosea*, and *Quinqueloculina tricolorata* were dissolved in a calcium-free artificial seawater solution (salinity ~35%, temperature ~19°C, pH ~8; 30 g NaCl, 10 g MgSO₄·7H₂O, 2 mmol/L NaHCO₃). NaOH was added to adjust pH. A pumping rate (2 ml/min) was maintained to keep the specimens in suspension and to avoid grain-to-grain contact. The rate of addition of fresh solution (6 ml/hr) kept the solution undersaturated in calcium carbonate. Dissolution rates were calculated based on the amount of Ca²⁺ released during the experiment as measured by Flame Atomic Absorption Spectrophotometry on a Varian Spectra AA-20. Rates of dissolution were normalized to the initial foraminiferal weight (of each group of five specimens of each species) measured before dissolution. Measurements were taken over a period of 84 hours, with samples taken ~every 2 hours in the first 8-hour period and less frequently (every 6–18 hours) thereafter.

**Combined Dissolution and Abrasion Experiment**

Another experiment was conducted to determine the taphonomic features produced by the interaction of dissolution and abrasion. Four sets (for four different time intervals) of five taphonomically unaltered specimens of each species were each placed in a pouch sewn of chiffon. This material was found to be of a mesh size small enough (~0.125–0.250 mm) to contain specimens of most species, yet large enough to allow an aqueous solution to flow through freely. The pouches were placed in a recirculating seawater table (pH 7.7; ~3°C) located at the College of Marine Studies, University of Delaware, Lewes, Delaware. The pH of this seawater is somewhat more acidic than that of open-marine regimes (pH 8.1–8.3); we feel that this protocol more accurately simulates test dissolution in pore waters of lowered pH (Ginsburg, 1957; Walter and Burton, 1990) than does treatment of test surfaces with acids for short periods of time (Cottee and Hallock, 1988; Peebles and Lewis, 1991).

The pouches were retrieved at 150, 300, 600, and 2000 hours and viewed under binocular microscope. Since no major changes in the specimens were noted after early retrieval, only the 2000-hour specimens were photographed with the Scanning Electronic Microscope. After being photographed, the specimens were placed in the shaker containers and subjected to abrasion as previously detailed. Specimens were removed after 250 hours and photographed to determine the effect of dissolution on the relative rates of abrasion.

**Scanning Electron Microscopy**

All specimens were photographed with a Cambridge 150 Model Stereoscans 90B Electron Microscope. Samples were mounted an aluminum stub with a thin (400 Å) silver paint and coated in a vacuum evaporator with a gold-palladium-carbon coating. The coating served to reduce charging of the samples while they were being photographed.

After photography, the coating and paint were removed with a minimal amount of acetone as quickly as possible. This step was necessary to clean the specimen and to remove it from the aluminum stub to which it was mounted, and to prevent the silver paint and coating from having a protective effect on the specimen. The effect, if any, of acetone on shell strength was assumed to be uniform (and minimal) within each species group, and must be regarded as systematic error in the experimental procedure.

**RESULTS**

**Abrasion Experiment**

**Test Surface Features**

Foraminiferal species and *Halimeda* platelets examined in this study display varying susceptibilities to abrasion. The percent specimen area of each species affected by abrasion (deep pits, shallow pits, etc.) tended to increase through time (Fig. 3), but no significant change in the rank susceptibility of species to abrasion occurred (Mann-Whitney U for tied ranks, α < 0.05); i.e., the species most affected after 250 hours of abrasion were also the most affected after 500 and 1000 hours. Percent surface area affected by abrasion varied considerably, however, among specimens of the same species (Table 2, Column A).

Abrasion features varied according to species. Fitting, both deep and shallow, was among the most common features produced by experimental abrasion (Figs. 2–16). Deep pits were most abundant on the surfaces of *Archaia insula*, *Cyclorubiculina compressa*, and *Peneroplis peales*, all three of which have thin outer test walls as an adaptation for housing algal symbionts (Figs. 3A, E, I, 4, 8, 12). Shallow test surface degradation ("other") was also identified on all species in the study, but was especially prominent on *Amphistegina gibbosa*, *Asterigerina carinata*, *Bigenerina irregularis*, *Cyclorubiculina compressa*, *Discorbis rosea*, *Quinqueloculina tricolorata*, *Sorites marginalis*, and *Halimeda* (Figs. 3B–F, K–M, 5–9, 14–16). In some cases, removal of the outermost test layer apparently exposed fresh test surfaces underneath (decrease in "other" category with time for *Discorbis rosea*, *Peneroplis peales*; Fig. 3F, I). In other cases, removal of the outermost test layer was accompanied by increased roughening at the ultrastructural level (e.g., *Asterigerina*; Fig. 6). The tests of *Bigenerina irregularis* (Figs. 3D, 7), *Globigeri-
FIGURE 3—Percent surface area of specimens of each species affected by abrasion. Categories represent abrasion-induced textural features recognized during digitizing of SEM photographs. A) Archaias angulatus; B) Amphistegina gibbosa; C) Asterigerina carinata; D) Bigenerina irregularis; E) Cyclorbulina compressa; F) Discorbis rosea; G) Globigerinoids quadriloculatus; H) Peneroplis aceris; I) Discorbis proteus; J) Quinquilocula lamarkiana; K) Quinquilocula tricolorina; L) Sorites marginalis; M) Halimeda (calcaceous green alga). See "Methods" for discussion of abrasion categories and Table 2 (Column B) for number of specimens used to calculate percent surface area affected by abrasion.
Globigerinoides quadrilobatus (Figs. 3G, 10), Planorbulina acervalis (Figs. 3H, 11), and Quinqueloculina lamarkiana (Figs. 3J, 13), all of which are relatively thin-walled, experienced a large amount (up to 15% test area) of breakage. Scalloping was most frequent on tests of *Archaia angulatus* and *Peneroplis proteus* (Figs. 3A, I, 4, 12). Cracks covered up to about 5 and 10% of test area on *Amphis-

tegina gibbosa* (Figs. 3B, 5) and *Quinqueloculina lamarkiana* (Figs. 3J, 13), respectively. There was no apparent relation between test surface alteration and ultrastructural detail (Figs. 4–16).

Also, there was no consistent relationship between the percent test surface area affected by abrasion and complete loss of tests during the experiment. In some cases (*Am-

---

**FIGURE 3—Continued.**
TABLE 3—Average distance travelled by selected carbonate particles on shaker table at 150 rpm. Distances are based on the average of three runs for each particle around experimental container (in seawater only). Each run lasted for one minute. Distances should be considered the maximum distances travelled by particles (see text for further discussion).

<table>
<thead>
<tr>
<th>Species</th>
<th>Rotations/minute</th>
<th>Average distance travelled (cm) in seawater</th>
<th>Distance (calculated) travelled (km)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Run 1</td>
<td>Run 2</td>
<td>Run 3</td>
</tr>
<tr>
<td><em>Halimeda</em></td>
<td>44</td>
<td>47</td>
<td>50</td>
</tr>
<tr>
<td><em>Amphistegina gibbosa</em></td>
<td>37</td>
<td>51</td>
<td>45</td>
</tr>
<tr>
<td><em>Sortes marginalis</em></td>
<td>36</td>
<td>45</td>
<td>28</td>
</tr>
<tr>
<td><em>Discorbis rosea</em></td>
<td>24</td>
<td>32</td>
<td>26</td>
</tr>
</tbody>
</table>

**FIGURE 3—Continued.**

*Halimeda*, a species underwent surface degradation but persisted in easily recognizable form (Table 2, Column A). On the other hand, some specimens of *Asterigerina* were apparently so greatly affected by surface degradation that they were degraded beyond the point of recognition (Table 2, Column B; Fig. 6). Still other genera (*Planorbulina*) were sufficiently frag- le that they were easily broken and destroyed before extensive surface alteration could occur. This experimental finding is in agreement with field observations on the low abundance of this species in sediment (as opposed to living populations on plants) at Discovery Bay (Martin and Liddell, 1988) and the Florida Keys (Martin, 1986; Martin and Wright, 1988), and therefore the predictions of the taphofacies model.

Species were ranked according to abrasion resistance utilizing an abrasion index (Table 2, Column C). Because a species could undergo extensive degradation and still persist essentially intact (e.g., *Archatias angulatus*), or, conversely, some specimens of a species could apparently be severely altered by abrasion while others were not (e.g., *Asterigerina carinata*; Table 2), the index was calculated by multiplying rank percent surface area affected (Table 2, Column A) by rank specimen loss (Table 2, Column B). In the case of *Planorbulina*, calculation of percent area affected was based on the relatively few fragments that remained for the species. Recovered fragments were small, with not much surface area affected (5%), hence the anomalously low ranking of this species (Table 2), although 100% of the specimens were considered to have been destroyed. Mann-Whitney U for tied ranks (α < 0.05) of rank percent surface area affected (Table 2, Column A) vs. rank specimen loss (Table 2, Column B), rank surface area vs. abrasion index (Column C), and rank specimen loss vs. abrasion index indicated that no one suborder was more susceptible to abrasion than another.

**Taphonomic Exposure**

We attempted to quantify the degree of exposure of foraminifera to abrasion on the shaker table operating at 150 rpm (Table 3). The range of sizes and shapes of experimental particles tested (Table 1) gave a range of 243–425 km maximum distance travelled during 1000 hours on the shaker table (Table 3). Based on observations, a particle moving in bidirectional surge currents at 15 m depth (turbulent fore reef) at Discovery Bay travels—on average—0.125 m onshore and 0.125 m offshore, for a total distance of 0.250 m per wave. Assuming a wave period of 30 seconds, and 7 hr/day of wave activity (Discovery Bay Marine Lab wind records indicate strongest wave activity at Jamaica occurs from approximately 10–11 A.M. to 5–6 P.M.), 0.5 m of travel per minute = 76.6 km of travel per year. According to these calculations (based on 347 km average distance travelled for the four particle types; Table 3), 1000 hours on the shaker table corresponds to about 5 years at 15 m depth at Discovery Bay. This time estimate is undoubtedly high because the rate of particle travel on the shaker table was calculated for particles in water only (for reasons of visibility), and movement of experimental particles was slowed by sediment present during the abra-
<table>
<thead>
<tr>
<th>FULL VIEW</th>
<th>2000 X</th>
<th>5000 X</th>
</tr>
</thead>
<tbody>
<tr>
<td>0 HOUR</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1. A</td>
<td>B</td>
<td>C</td>
</tr>
<tr>
<td>250 HOUR</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2. A</td>
<td>B</td>
<td>C</td>
</tr>
<tr>
<td>500 HOUR</td>
<td></td>
<td></td>
</tr>
<tr>
<td>3. A</td>
<td>B</td>
<td>C</td>
</tr>
<tr>
<td>1000 HOUR</td>
<td></td>
<td></td>
</tr>
<tr>
<td>4. A</td>
<td>B</td>
<td>C</td>
</tr>
</tbody>
</table>

**FIGURE 4—*Archaia angulatus*. Column A) Full view (scale = 500 μm); Column B) scale = 10 μm; Column C) scale = 5 μm. 1) 0 hour: specimen displays some pitting (see "Methods" for further discussion). 2) 250 hours: note increased number of pits. 3) 500 hours: number and diameter of pits has increased from 250 hours. 4) 1000 hours: specimen still intact and nearly same size as at 0 hours. Note apparent lack of ultrastructural alteration by abrasion.
sion experiment. Assuming an order of magnitude decrease in average distance travelled during the abrasion experiment (to ~35 km/1000 hours), we calculate that 1000 hours on the shaker table corresponds to ~0.5 years at 15 m depth at Discovery Bay. The degree of taphonomic exposure produced by the constant agitation of experimental particles in sediment may actually be higher, however, than that produced by the more intermittent abrasion on the fore reef terrace that results from bidirectional wave surge.

Our calculations of distance travelled on a shaker table are comparable to those of Peebles and Lewis (1989, 1991) for distance travelled in a tumbler. They cite a range of 34–100 km of movement in 2000 hours of tumbling, which is equivalent to 17–50 km of movement in 1000 hours. Both the force and frequency of grain-to-grain collisions in their tumbler experiments were, however, probably maximized relative to those produced on our shaker table (see “Discussion”).

Dissolution Experiments

Seawater Table Experiment

Natural seawater used in this experiment had slightly lower pH (~7.7) than that of open marine water (pH ~8.1–8.3). Because no major changes were observed in specimens under the binocular microscope (e.g., slight etching of test surfaces with coarsened textures) after 150, 300, and 600 hours of dissolution in natural seawater, exposure of specimens to natural seawater was continued to 2000 hours. After 2000 hours in the seawater table, recovered specimens were still recognizable to the species level and largely remained intact (Figs. 17–18). Out of five original specimens per species, one specimen each of Globigerinoides quadrilobatus, Planorbulina acervais and Quinqueloculina lamarkiana, two of Bigenerina irregularis, and three of Discorsis rosea were not recovered. All unrecovered specimens were either broken into small pieces or apparently dissolved sufficiently to pass through the chiffon mesh. All five specimens of the other species survived the 2000 hours of dissolution in the seawater table (Table 4, Column A).

Dissolution features seen at 150, 300, and 600 hours tended to be more pronounced at 2000 hours (Figs. 17–18). In Discorsis rosea and Globigerinoides quadrilobatus, diameter of pores increased due to preferential dissolution in these regions. In these species and in Peneroplis proteus and Quinqueloculina lamarkiana, surface textures were coarser and more etched, and ornamentation, when present, removed. In the case of the testulariid Bigenerina irregularis, the test cement was apparently more susceptible to dissolution than the agglutinated calcareous particles that make up the test, as test grains were accentuated by dissolution of the surrounding cement (Fig. 17). On the other hand, Archaias angulatus, Amphistegina gibbosa, Cyclorubicina compressa, Planorbilina acervais, Quinqueloculina tricarina, Sorites marginalis, and Hali- meda displayed relatively little evidence of dissolution.

Fluidized Bed Reactor Experiment

Relative dissolution rates of species in the reactor are in accord with results of the seawater table experiment (Table 4). But dissolution in the fluidized bed reactor occurred much more rapidly than in the seawater table because the fluid used was essentially calcium carbonate-free. Normalized rates of dissolution peaked early and then levelled off to a steady rate (Fig. 19). Initial (0–12 hr) weight loss

<table>
<thead>
<tr>
<th>Species</th>
<th>A) Number of specimens lost after 2000 hours of dissolution only</th>
<th>B) Number of specimens destroyed by 250 hours of abrasion after 2000 hours of dissolution</th>
</tr>
</thead>
<tbody>
<tr>
<td>Archaias angulatus (M)*</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>Amphistegina gibbosa (R)</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Bigenerina irregularis (T)</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td>Cyclorubicina compressa (M)</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Discorsis rosea (R)</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>Globigerinoides quadrilobatus (R)</td>
<td>1</td>
<td>4</td>
</tr>
<tr>
<td>Peneroplis proteus (M)</td>
<td>0</td>
<td>5</td>
</tr>
<tr>
<td>Planorbilina acervais (R)</td>
<td>1</td>
<td>4</td>
</tr>
<tr>
<td>Quinqueloculina lamarkiana (M)</td>
<td>1</td>
<td>4</td>
</tr>
<tr>
<td>Quinqueloculina tricarina (M)</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Sorites marginalis (M)</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Hali meda (alg)</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

* M = Suborder Milolina, R = Suborder Rotaliina, T = Suborder Textulariina; see also Table 1.

FIGURES 4–16—EFFECTS OF ABRASION. Abrasion-induced test surface features of representative specimens of each species at 0, 250, 500, and 1000 hours. In all cases, view B is a magnification of view A, and view C is a magnification of view B. In most cases, the same specimen is shown in each figure of each plate.
<table>
<thead>
<tr>
<th>FULL VIEW</th>
<th>2000 X</th>
<th>5000 X</th>
</tr>
</thead>
<tbody>
<tr>
<td>0 HOUR</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1. A</td>
<td>B</td>
<td>C</td>
</tr>
<tr>
<td>250 HOUR</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2. A</td>
<td>B</td>
<td>C</td>
</tr>
<tr>
<td>500 HOUR</td>
<td></td>
<td></td>
</tr>
<tr>
<td>3. A</td>
<td>B</td>
<td>C</td>
</tr>
<tr>
<td>1000 HOUR</td>
<td></td>
<td></td>
</tr>
<tr>
<td>4. A</td>
<td>B</td>
<td>C</td>
</tr>
</tbody>
</table>

**FIGURE 5**—Amphistegina gibbosa. Column A) Full view (scale = 500 µm); Column B) scale = 10 µm; Column C) scale = 5 µm. 1) 0 hour: note nearly smooth test surface. 2) 250 hours: impact features and scalloping of test periphery have occurred. 3) 500 hours: note microborings in full view; pores appear to increase in size and cracks begin to occur. 4) 1000 hours: outermost test layer has been removed and test surface appears polished.
recorded in the reactor experiment was primarily due to rapid reduction of thin outer test layers and delicate surface ornamentation. After that, more gradual dissolution of the foraminiferal tests occurred as the surface area available for dissolution was reduced. This trend is probable under natural conditions, though the solution in the reactor was extremely undersaturated in calcium carbonate, a condition not readily encountered in most carbonate sediments (Walter and Burton, 1990).

All five species analyzed followed the same pattern (peaking at 6 hours and levelling off after 12 hours) though the rates varied. *Archaia angulatus* and *Discorbis rosea* (suborders Milolina and Rotaliina, respectively) had higher maximum normalized rates of dissolution (Rate\textsubscript{max} = 0.0098 and 0.0071 mg/hr/mg, respectively) than did the miliolid *Quinqueloculina tricarinata* (Rate\textsubscript{max} = 0.0048 mg/hr/mg), the rotaliine *Amphistegina gibbosa* (Rate\textsubscript{max} = 0.0031 mg/hr/mg) and the textulariid *Bigerinella irregularis* (Rate\textsubscript{max} = 0.0027 mg/hr/mg). After 84 hours of dissolution in the fluidized bed reactor most specimens had dissolved. The remaining specimens (five of *Amphistegina gibbosa* and two of *Quinqueloculina tricarinata*) were badly corroded (Fig. 18).

**Dissolution and Abrasion Combined**

Subjecting tests to only 250 hours abrasion after 2000 hours of dissolution in the seawater table produced results different from those when either process was the solitary destructive agent (Table 4, Column B). In some cases, chemical degradation by dissolution apparently caused higher susceptibility to abrasion in otherwise abrasion-resistant species: tests of *Bigerinella irregularis*, *Globigerinoides quadrilobatus*, *Peneroplis proteus*, and *Quinqueloculina lamarchiana* largely survived 100 hours of abrasion (no dissolution; Table 2), yet 60% (3 out of 5) to 100% (5 out of 5) specimens were completely obliterated after 250 hours of abrasion subsequent to 2000 hours of dissolution in the seawater table (Table 4, Column B). Other species (i.e., *Amphistegina gibbosa*, *Cyclorbiculina compressa*, *Quinqueloculina tricarinata*, *Halimeda*) were little affected by dissolution (Table 4, Column A), and were no more susceptible to abrasion coupled with dissolution than without. Remaining species were intermediate between these groups in resistance to combined dissolution and abrasion.

**DISCUSSION**

**Abrasion**

Previous studies on abrasive shell reduction in macroinvertebrates (Chave, 1964; Driscoll, 1967, 1970; Driscoll and Weitman, 1973; Michel, 1986; Cutler, 1987; Davies et al., 1990b) and foraminifera (Moberly, 1968; Miller and Ellis, 1982; Cottey and Hallock, 1988) have demonstrated the effects of shell size, shape, thickness, surface-area-to-volume (weight), and microstructure and architecture on preservation potential. Despite our use of a variety of species which differ in test size, shape, composition, and structure (Table 1), most species examined in the present study differed only slightly in their relative resistance to abrasion (Fig. 3). Some species were progressively destroyed by abrasive processes in our experiments (e.g., breakage and cracks in *Bigerinella irregularis*, *Globigerinoides quadrilobatus*, *Planorbulina acervalis*, and *Quinqueloculina lamarchiana*), but even after 1000 hours of abrasion in medium-sized (~0.5 mm) carbonate sand, specimens of most species were still easily recognizable to the species level (Figs. 4–16). Despite the high degradation of platelet surfaces of *Halimeda* by abrasion (Table 2; Fig. 16), platelets too were easily recognizable at the termination of the experiment.

Various methods of achieving an overall ranking of abrasion-resistance gave similar results (Table 2), and no taxonomic bias was evident; i.e., species of one suborder were not destroyed preferentially over those of another. Fragile tests were, however, most easily destroyed by abrasion (e.g., *Planorbulina acervalis*, *Sortes marginalis*). This is in agreement with previous observations of foraminiferal assemblages of the outer back reef (high energy environment; taphofacies II; Fig. 1B) of the Florida Keys: in the transition from relatively large living populations on *Thalassia* to death assemblages in sediment off Key Largo, Florida, *Planorbulina* and *Sortes* are greatly reduced in number (Martin, 1986; Martin and Wright, 1988).

The results of our abrasion experiments differ somewhat from those of Peebles and Lewis (1991). They found that foraminiferal specimens underwent rapid weight loss and that large specimens (e.g., *Cyclorbiculina compressa*) were more resistant to abrasion than small ones (e.g., *Discorbis rosea*). Increased size no doubt confers increased abrasion-resistance (except in the case of fragile forms such as *Planorbulina*). The protocol of Peebles and Lewis (1991) would appear to maximize the frequency and force of grain-to-grain impacts, however, and may only be representative of high-energy events (storms). Our protocol, on the other hand, would appear to simulate normal background conditions associated with fair-weather wave surge. Peebles and Lewis (1991) tumbled (in buffered seawater of pH 7.45) their specimens and allowed the specimens themselves to serve as the abrasive, whereas we placed our specimens in carbonate sediment (0.5 mm mean grain size) on a shaker table (seawater pH 8.0). Although fairly representative of pore-water pH of carbonate sediments (Ginsburg, 1957; Walter and Burton, 1990), the slightly lower seawater pH in the Peebles and Lewis abrasion experiments may also have accelerated abrasion, based on our experiment on combined dissolution and abrasion (Table 4). If our inferences regarding the relationship between experimental protocol and energy regime (and therefore time scales of sediment accumulation) are correct, then the differing results of the two abrasion studies beg the question (and testable hypotheses) as to which depositional regime, fair-weather or storm, produces the most abrasion (cf. Davies et al., 1990b).

Variation in abrasion-resistance of foraminiferal species (Table 2, Column A) no doubt also depends on their hy-
FIGURE 6—Asterigerina carinata. Column A) Full view (scale = 200 μm); Column B) scale = 5 μm; Column C) scale = 5 μm. 1) 0 hour. 2) 250 hours: apertural region has been destroyed and shallow test surface degradation has occurred. Surface is uneven and coarser than in 0 hour specimens. A large impact depression is present in upper center of the specimen. Note loss of detail on the foraminiferal test surface. 3) 500 hours: pattern of alteration continues. 4) 1000 hours: this specimen is near the point of nonrecognition after 1000 hours of abrasion.
draulic behavior (dependent on size, shape, and test density; Maitl, 1968). Martin and Liddell (1991, fig. 8.5) have found that although some large, robust species are put into suspension relatively easily (i.e., low traction velocities), they settle to the bottom rapidly. Such species are likely to remain emplaced in sediment for long periods of time and therefore undergo relatively rapid abrasion [e.g., Amphistegina; Table 2; Peebles and Lewis (1981) also found this form to be susceptible to abrasion]. This may explain the much higher rates of abrasion of Cyclorbiculina compressa (Table 2) in our study compared to theirs. Test shape may counteract increased likelihood of emplacement (and abrasion) in sediment, however. *Archaia angulatus* approximates Cyclorbiculina compressa in size, but is lenticular, whereas adult tests of Cyclorbiculina are flattened. Thus, abrasive wear is decreased on *Archaia* (mean surface affected: 15%; Table 2) and is concentrated on the central and peripheral portions of the test; by contrast, abrasion occurs over much of the test surface of Cyclorbiculina (mean surface area affected: 83%).

Smaller species with relatively robust tests (e.g., *Discorbis rosea*) are less easily put into suspension (Martin and Liddell, 1991, fig. 8.5), but once entrainment in bottom currents occurs, they settle somewhat more slowly than larger species, and so would remain in suspension or at the sediments-water interface (rather than below it), and would therefore be less likely to abrade. More delicate, small, slow-settling species such as *Asterigerina* (Martin and Liddell, 1991, fig. 8.5) are also likely to remain at or above the sediment-water interface, but once embedded in sediment they could degrade rapidly. (Interestingly, the cone shape of *Asterigerina* approximates that of the planktonic foraminifer *Globorotalia truncatulina*.) The hydraulic behavior of *Asterigerina* may explain the great variation in surface degradation and test destruction of this species (Table 2; compare Columns A and B).

Decreased size itself may actually enhance abrasion-resistance in some cases. Although whole tests of Planorbilina are easily broken, the fragments of this species recovered in our experiments were only slightly affected by abrasion (mean surface area affected: 5%). This, because of their small size (which decreases settling velocity and minimizes target area for impacts) and the surrounding cushion of water, small species may actually be less likely to be rapidly abraded (and completely destroyed) than larger specimens under normal abrasive regimes.

Our experimental results confirm previous analyses of natural assemblages (Martin, 1986; Martin and Liddell, 1988; Martin and Wright, 1988). Although abrasion no doubt characterizes taphofacies II and IV at Discovery Bay, once produced, most carbonate particles tested in this study appear to resist abrasion and would be expected to persist in natural assemblages. Although abrasion-induced taphonomic exposure produced by our experiments (Table 2) is probably minimal compared to that in natural environments (Kotler et al., 1991), abrasion alone appears to be a relatively unimportant agent of test destruction in natural carbonate settings, even in high-energy environments such as the outer back reef and shallow fore reef (taphofacies II and IV, respectively; Fig. 1B). For example, *Discorbis rosea* is prominent in outer back reef and shallow fore reef sediment assemblages of Discovery Bay and the Florida Keys (Martin, 1986; Martin and Lid-

![FIGURE 7—Bigenerina irregularis. Column A] Full view (scale = 500 μm). Column B] scale = 20 μm. 1) 0 hour: typical appearance of this textularid; the surface is rough and hummicky as a result of the agglutination of grains. 2) 250 hours: a part of the early biserial portion of the test has been removed. 3) 500 hours: test grains have been abraded and some removed. 4) 1000 hours: overall test surface has been somewhat smoothed.

The test is greatly reduced in size due to breakage and removal of outer test layer. There is some indication of test roughening at the ultrastructural level.
FIGURE 8—Cyclorbiculina compressa. Column A) Full view (scale = 500 μm); Column B) scale = 10 μm; Column C) scale = 5 μm. 1) 0 hour: initial specimen already has some pits on outer test surface (see “Methods” for further discussion). 2) 250 hours: pitting continues. 3) 500 hours: test surface has become very rough. 4) 1000 hours: portions of the outermost chamber (lower left) have been broken off. Test surface appears polished, apparently as a result of removal of outer test wall.
**FIGURE 9**—*Discorbis rosea*. Column A) Full view (scale = 500 μm); Column B) scale = 20 μm; Column C) scale = 10 μm. 1) 0 hour. 2) 250 hours: little surface alteration has occurred. 3) 500 hours: numerous impact features are now present and surface ornamentation has been worn down. 4) 1000 hours: specimen is still intact and easily recognizable, although test surface has been highly roughened.
**Figure 10.** *Globigerinoides quadrilobatus.* Column A) Full view (scale = 500 μm); Column B) scale = 20 μm; Column C) scale = 10 μm. 1) 0 hour, 2) 250 hours: pitting has occurred. 3) 500 hours: test is probably not the same as that shown for 0 and 250 hours and is virtually intact. 4) 1000 hours: outermost chamber has been broken.
**FIGURE 11**—Planorbilina acervalis. Column A) Full view (scale = 500 μm); Column B) scale = 20 μm; Column C) scale = 10 μm. 1) 0 hour: initial specimen shows a few signs of alteration (see “Methods” for further discussion). 2) 250 hours: portions of test margin have been removed and large pits have appeared. 3) 500 hours: pitting and fragmentation of the test continues. 4) 1000 hours: the test has been greatly reduced in size as it nears the point of total obliteration. Pitting is the major feature that appears on the remaining fragments of Planorbilina acervalis.
**FIGURE 12**—*Peneroplis proteus*. Column A) Full view (scale = 500 μm); Column B) scale = 10 μm; Column C) scale = 10 μm. 1) 0 hour: initial specimen displays several shallow pits (see "Methods" for further discussion). 2) 250 hours: portions of the outer chamber have been broken. The margin is scalloped and deep, and shallow pits appear on the test surface. 3) 500 hours: remaining portion of the outer chamber has been lost, and pitting and shallow test surface degradation continue. 4) 1000 hours: test surface has been polished. Note change from shallow pits in 3A to deep pits in 4A.
Figure 13—Quinqueloculina lamarckiana. Column A) Full view (scale = 500 μm); Column B) scale = 10 μm. 1) 0 hour: initial test surface is very smooth. 2) 250 hours: cracks begin to appear and surface texture has coarsened. 3) 500 hours: large cracks have appeared (lower left of test). 4) 1000 hours: test surface has been polished.

Figure 14—Quinqueloculina tricarinata. Column A) Full view (scale = 500 μm); Column B) scale = 20 μm. 1) 0 hour: the corrugated appearance of the test is characteristic of this species. 2) 250 hours: tip of the apertural neck has been broken. 3) 500 hours: little apparent change has occurred from 250 hours. 4) 1000 hours: further removal of apertural neck has occurred and surface corrugations have been smoothed.

dell, 1988; Martin and Wright, 1988) and specimens are frequently highly abraded and exhibit deep pits and breakage, suggesting a much higher degree of taphonomic exposure than that produced experimentally. Similarly, Amphistegina and Archaeaia are prominent lag deposits of abraded tests in fore reef terrace and outer back reef environments, respectively (taphofacies III and I; Fig. 1B; Martin, 1986; Martin and Liddell, 1988; Martin and Wright, 1988; Triffleman et al., 1991). Thus, results of both laboratory and field studies negate our model-based predictions for abrasion alone as a short-term agent of destruction. Abrasion features may eventually prove useful, however, in determining relative taphonomic exposure and rates of burial (Peebles and Lewis, 1989, 1991; Peebles et al., 1990). Both the percent of specimen surface affected and the features produced should be taken into consideration (studies underway).

Our results utilizing carbonate sediments are in marked contrast to experimental studies conducted on calcareous shell abrasion in terrigenous sediments. Driscoll and Weitl (1973) found that bivalves and gastropods were most rapidly abraded in very coarse quartz sand, less so in very fine sand, and least in medium sand. Moberly (1968) found that smaller foraminifera undergo a more rapid percent weight loss than larger specimens when abraded in a mix-
erably more attention than has abrasive test reduction (see references cited in Martin and Liddell, 1991). Benthic foraminifera are, however, typically more resistant to dissolution than are planktonic species (Berger, 1973), and benthic/planktonic ratios are commonly used as indicators of CO$_2$-rich bottom waters (Thunell, 1976; see also Berger and Diester-Haass, 1988). But shallow (e.g., Amphistegina) and deep-dwelling (e.g., Gyroidinoides spp.; Nutbulides spp.) benthic species can differ substantially in dissolution resistance (Douglas et al., 1980; Corliss and Honjo, 1981; Tkalcsna and Lohmann, 1983). Specimens used by Corliss and Honjo (1981) in their deep-sea dissolution experiment were all of approximately the same size (0.250–0.500 μm), so surface-to-volume ratio can be ruled out in determining dissolution resistance in this instance. Relative dissolution resistance in this case is apparently a result of differences in test microstructure and architecture between species (Corliss and Honjo, 1981; see also Walter and Morse, 1984; Walter, 1985; Henrich and Wefer, 1986).

Based on the results of the dissolution reactor experiment, shallow-dwelling foraminiferal species also differ considerably in their relative dissolution resistance (Fig. 19) but for more complex reasons. Discorbis rosea (suborder Rotalinina) had one of the highest rates of dissolution in the reactor and three out of five specimens of this species were lost in the seawater table experiment (Table 4, Column A). Archaias angulatus had an even higher rate of dissolution in the reactor than did Discorbis, but persisted in natural seawater, possibly as a result of its much larger size (lower surface-to-volume ratio; Table 1). Bigenerina irregularis (suborder Textulariiina) had the lowest rate of dissolution in the reactor experiment, but rapid breakdown of test cement no doubt enhanced test friability and destruction (Table 4). Although they belong to different suborders (Table 1), Amphistegina gibbosa and Quinqueloculina tricarinata exhibited intermediate dissolution rates in the reactor. Both are relatively large (low surface-to-volume ratio) and thick-walled forms. In the case of these two species, dissolution rate appears to reflect a greater influence of wall thickness and surface area over test ultrastructure (see Table 1).

At the end of the reactor run (84 hr), only two specimens of Quinqueloculina tricarinata and five of Amphistegina gibbosa were retrieved; all others had dissolved. Although specimens of A. gibbosa with portions of the outer test layers removed have been observed in surface sediment assemblages, the highly etched surfaces observed on specimens retrieved from the reactor (Fig. 18) have rarely been observed on any of the tens-of-thousands of specimens from Discovery Bay examined by us over an 8-year period (Martin and Liddell, 1988, 1989), nor on specimens from the Florida Keys (Martin, 1986; Martin and Wright, 1988). By suspending specimens of Amphistegina sp. for two months in carbonate-undersaturated waters (~5600 m depth; below the CCD) of the central North Pacific, Corliss and Honjo (1981, their plate 1, figs. 10–11, 14, 15) produced surface textures similar to ours, which testifies to the extreme degree of corrosiveness produced in the reactor. In contrast to the results of the reactor experiment, surface

**FIGURE 15—Sorites marginalis. Column A) Full view (scale = 500 μm); Column B) scale = 20 μm. 1) 0 hour: note deep pit in the center of the test. 2) 250 hours: deep pits (penetrations of test chamberlets) cover a large percentage of test surface area. 3) 500 hours: pits have increased in size and a large portion of the test has been removed. 4) 1000 hours: deepening of pits continues.**

ture of carbonate and detrital grains, Miller and Ellison (1982) demonstrated that certain agglutinated foraminifera are destroyed much more quickly than a calcareous species when agitated with glass beads, and Cott and Hallock (1988) found that the outer window-like test layer of Archaias angulatus was more rapidly abraded in quartz sand than in carbonate sediment.

**Dissolution**

Dissolution of foraminiferal tests, especially planktonic species found in deep-sea sediments, has received consid-
FIGURE 16—Halimeda. Column A) Full view (scale = 1 mm); Column B) scale = 50 μm; Column C) scale = 10 μm. 1) 0 hour. 2) 250 hours: surface of specimen has been coarsened by the removal of outermost layers of crystallites. 3) 500 hours: appearance similar to 250 hours. 4) 1000 hours: specimen surface has been polished by removal of outer layer of crystallites, but platelet size has not been diminished significantly.
features associated with dissolution produced in the seawater table much more strongly resembled the dull surface lusters and coarsened textures commonly observed on specimens of many species in surface sediments of Discovery Bay. But, as with abrasion, dissolution in natural seawater alone was insufficient to destroy most foraminiferal tests or algal platelets (Table 4).

Some species that completely dissolved in the reactor experiment apparently persist in natural sediment assemblages. For example, in low-energy (high organic matter) environments (taphofacies I; Fig. 1B), Archaiaus angulatus, which had the highest rate of dissolution in the reactor, is often represented by badly corroded specimens, in which the thin, outer window-like layer has been removed (Cushman, 1930, plates 16–17; see also Cottee and Hallock, 1988). Indeed, chemically degraded tests may be indicative of quiet-water sediments with high organic carbon content (e.g., back reef and deep fore reef; taphofacies I and V) where microbial decomposition and biogenic reworking create microenvironments that are at least intermittently undersaturated with calcium carbonate (see also Cottee and Hallock, 1988). Quiet-water environments are characterized by abundant burrowing infauna, which both rework organic matter and sulfide particles (especially in siliciclastic sediments; Walter and Burton, 1990) to the surface mixed layer and irrigate subsurface layers. Organic matter and sulfide are thereby oxidized to produce acids, which lower pore water pH (Aller, 1982; see also Walter and Burton, 1990) and etch foraminiferal test surfaces (Murray and Wright, 1970; Cottee and Hallock, 1988; Murray, 1989).

The agglutinated Bigenerina irregularis exhibited the lowest rate of dissolution of the five species employed in the experiment (Fig. 19). Apparently the individual calcareous grains comprising the test were much less soluble than the test cement itself. The abundance of agglutinated foraminifera in sediment can be accentuated by different dissolution rate of calcareous species (Murray and Wright, 1970; Goldstein, 1988; Goldstein et al., 1989; Murray, 1989; see also Greiner, 1969, 1970), although this is highly variable between environments (Smith, 1987) and is probably dependent on both the particular environmental conditions and the species involved. The increased abundance of agglutinated foraminifera on the fore reef slope (taphofacies V; Martin and Liddell, 1988) would seem to indicate increased dissolution of calcareous tests in fore reef slope sediments (higher organic matter concentrations), but increased abundance of intact dissolution-susceptible planktonic foraminifera here is a contraindication of dissolution. Indeed, Pigott and Land (1986) found active submarine cementation to occur in fore reef sediments at Discovery Bay. In the case of Discovery Bay, increased abundance of agglutinated taxa on the fore reef slope (taphofacies V, Fig. 1B) may indicate populations which live infaunally (Goldstein, 1988; Tappan and Loeblich, 1988) on bacteria associated with abundant organic matter.

Dissolution is undoubtedly accelerated in taphofacies I and V at Discovery Bay. But the results of our dissolution studies suggest that, like abrasion, foraminiferal tests and algal platelets are remarkably persistent in carbonate sediments once produced. This is in marked contrast to reports of rapid skeletal dissolution in surficial layers of modern siliciclastic environments (e.g., Fitzgerald et al., 1979). Aller (1982) and Davies et al. (1989a; see also Alexander-son, 1979) maintain that in terrigenous sediments (Long Island Sound and shallow Texas bays, respectively) rapid transfer of calcareous shells from the surface dissolution zone (Aller, 1982; “taphonomically active zone” of Davies et al., 1989a) into the preservation zone (Aller, 1982) is necessary for the preservation of assemblages. Pore waters of the terrigenous preservation zone are characterized by alkalinity buildup and are presumably saturated with cal-

---

**FIGURE 17** — EFFECTS OF DISSOLUTION. Effects of 2000 hours of dissolution alone in seawater table and effects of 2000 hours of dissolution followed by 250 hours of abrasion. 1-2) Archaiaus angulatus. A) Full view (scale = 500 μm); B) scale = 10 μm. 1) Specimen after 2000 hours of dissolution. Surface is highly etched, coarse, and uneven. Compare to Figure 4 (0 hours abrasion). 2) Same specimen as in Figure 1, but after 250 hours of abrasion following 2000 hours of dissolution. Solution pits at 0 hours have been enlarged by abrasion. Compare to Figure 4 (250 hours abrasion alone). 3-4) Amphistegina gibbosa. A) Full view (scale = 500 μm); B) scale = 10 μm. 3) Specimen after 2000 hours of dissolution. Test surface has been little affected. Compare to Figure 5 (0 hours abrasion). 4) Same specimen as in number 3, but after 250 hours of abrasion following 2000 hours of dissolution. Features seen here are about the same as when abrasion was the sole process affecting the species. Compare to Figure 5 (250 hours abrasion alone). 5) Bigenerina irregularis. A) Full view (scale = 1 mm); B) scale = 20 μm. The cement of this textuariid has been preferentially dissolved, but agglutinated grains also show signs of dissolution (solution pits shown in B). This species was completely obliterated after 250 hours of abrasion following 2000 hours of dissolution (Table 4), whereas the species survived 1000 hours of the sole process of abrasion. 6) Cyclococculina compressa. A) and B) Full view (scale = 500 μm). A) Specimen after 2000 hours of dissolution. Compare to Figure 8 (0 hours abrasion). B) Same specimen as in A, but after 250 hours of abrasion following 2000 hours of dissolution. Compare to Figure 8 (250 hours abrasion alone). 7) Discorsis rosea. A) and B) Full view (scale = 200 μm). A) Specimen after 2000 hours of dissolution. Compare to Figure 9 (0 hours abrasion). B) Same specimen in A, but after 250 hours of abrasion following 2000 hours of dissolution. Compare to Figure 9 (250 hours abrasion). Both dissolution and abrasion coupled with abrasion have greater effect on degradation of this species than abrasion alone. 8) Globoconicoides quadratibatus. A) Full view (scale = 200 μm); B) scale = 20 μm. This planktonic foraminifer is highly susceptible to dissolution. Pore regions were preferentially dissolved (see in B; compare to Figure 10, 0 hours abrasion). This species was completely obliterated after 250 hours of abrasion following 2000 hours of dissolution (Table 4), whereas the species survived 1000 hours of abrasion alone. 9) Planorbulina acervata. A) Specimen after 2000 hours of dissolution. Full view (scale = 500 μm); B) scale = 20 μm. C) Fragments of Planorbulina acervata remaining after 250 hours of abrasion following 2000 hours of dissolution. Scale = 2 mm. Compare with Figure 11 (0 hours abrasion). Results after 250 hours of abrasion following 2000 hours of dissolution were the same as for the abrasion process alone; this species may be easily broken by abrasion before significant weakening by dissolution can occur.
FIGURE 18.—EFFECTS OF DISSOLUTION. 1–6) effects of 2000 hours of dissolution alone in seawater table and effects of 2000 hours of dissolution followed by 250 hours of abrasion. 7–8) effects of dissolution in fluidized bed reactor. 1) *Peneroplis proteus*. A) Full view (scale = 500 μm); B) scale = 20 μm. Tests of this species were highly affected by 2000 hours of dissolution in natural seawater. Large portions of the test were removed and test surface was severely etched. Compare to Figure 12 (0 hours of abrasion). No specimens of this species survived 250 hours of abrasion after being subjected to 2000 hours of dissolution (Table 4). 2) *Quinqueloculina lamarckiana*. A) Full view (scale = 500 μm); B) scale = 10 μm. Tests of this species were highly affected by 2000 hours of dissolution. Test surface was severely etched. Compare to Figure 13 (0 hours of abrasion). No specimens of this species survived 250 hours of abrasion after being subjected to 2000 hours of dissolution (Table 4). 3) *Quinqueloculina tricarinata*. A and B) Full view (scale = 500 μm). A) Specimen after 2000 hours of dissolution. B) Same specimen as in A, but after 250 hours of abrasion following 2000 hours of dissolution. This thick-walled species shows preferential resistance to both dissolution and abrasion. Compare with Figure 14 (0 and 250 hours of abrasion alone). 4) *Sorites marginalis*. A) and B) Full view (scale
Cium carbonate (Berner et al., 1970) which should enhance preservation (Aller, 1982).

Dissolution and Abrasion Combined

Based on our laboratory studies, it appears that dissolution and abrasion coupled together are often much more effective than either agent alone as a taphonomic process (Table 4): dissolution presumably weakens the test of many species to abrasion and, conversely, abrasion may accelerate dissolution by surface roughening (thereby increasing surface area). Indeed, specimens from sediment assemblages frequently exhibit surface features produced by both processes.

Given the known energy distribution at Discovery Bay, and presumably the accompanying taphonomic regimes (Fig. 1B), it would appear that abrasion and dissolution have the greatest synergistic effect in environments transitional between the inner (low energy) and outer (high energy) reef tracts. For example, although *Discorbis rosea* is resistant to abrasion alone, and persists in sediment of the outer back reef and shallow fore reef (taphofacies II and IV; Fig. 1B), this species is apparently easily destroyed by 250 hours of abrasion following 2000 hours of dissolution (Table 4). Sediments of taphofacies II and IV are characterized by relatively low organic matter content (cf. Ginsburg, 1957), and, therefore, presumably low relative rates of dissolution. Thus, *D. rosea*, which maintains its largest living populations in the outer back reef and shallow fore reef (Martin and Liddell, 1988; Martin and Wright, 1988), may not normally experience significant dissolution before incorporation into subfossil assemblages. Similarly, based on our experiments, *Archaia angulatus* is less resistant to abrasion and dissolution when they act synergistically (Table 4). *Archaia angulatus* dominates inner and outer back reef foraminiferal assemblages (Martin, 1986; Martin and Liddell, 1988), and undergoes significant abrasion in outer reef tract sediments (taphofacies II), but is presumably most severely affected by dissolution in inner reef tract (taphofacies I) environments (Cottee and Hallock, 1988; see also Walter and Burton, 1990).

![NORMALIZED DISSOLUTION RATE VS TIME](image)

**FIGURE 19**—Normalized dissolution rates vs. time. Graph represents dissolution rates of five specimens of each species normalized to the initial weight of the specimens. Each point represents the mean weight loss (mg/hr/mg original test weight) as calculated by measuring Ca$^{2+}$ released with Flame Atomic Absorption Spectrophotometry.

**IMPLICATIONS FOR THE PRESERVATION OF BIOGENIC CARBONATE**

Carbonate and shell-poor siliclastic regimes appear to differ fundamentally in the taphonomic constraints they place on our interpretation of the paleoecology, biostratigraphy, and evolution of ancient microorganisms. Preservation in shelfal carbonate sediments appears to mimic that of condensed intervals of siliciclastic environments, or high productivity communities like oyster banks, in which shell-rich layers create an environment favorable to their preservation by buffering pore waters of the surface mixed layer against dissolution (Kidwell, 1989; 'sheltered preservation' of Maeda, 1991). This assertion is undoubt-
edly simplistic, however, because condensed shell beds of siliciclastic regimes can form by a variety of physical and biological mechanisms (Norris, 1986; Meldahl, 1987; Kidwell, 1989).

Conversely, carbonate and shell-poor terrigenous regimes should differ in the intensity of taphonomic processes affecting incipient fossil assemblages. Rates of carbonate destruction, especially through dissolution, are predicted to be much higher in shell-poor terrigenous sediments than in carbonate deposits (Smith, 1971; Alexandersson, 1976; Davies et al., 1989a; Kotler et al., 1989; Kotler, 1990; Walter and Burton, 1990, p. 603). Preliminary studies of foraminiferal preservation in Holocene siliciclastic tidal flat sediments of the northern Gulf of California (Bahia la Choya, Sonora, Mexico), however, indicate that dissolution is not solely dependent upon carbonate availability. Rates of dissolution in terrigenous regimes vary according to sedimentation rate, shell input and organic matter concentration (productivity; Lin and Morse, 1991; Loubere, 1991), and extent of bioturbation and bioirrigation (which accelerates dissolution of shells in near-surface sediment while concentrating them at depth; Aller, 1982; Meldahl, 1987).

Carbonate and terrigenous sedimentary regimes also differ in the continuity and rate of sedimentation. Although sedimentation in carbonate environments may be exceedingly rapid in the short-term (Milliman, 1974), long-term carbonate accumulation tends to be slower (and more discontinuous) than in terrigenous environments (Wilson, 1975; Schindel, 1980). In other words, not all shell beds are created equal (Kidwell, 1989), and they may contain distinctive signatures of geohistorical, biohistorical and paleoceanographic significance (e.g., Worsley et al., 1986). Obviously, these considerations may bear upon phylogenetic reconstructions, sampling strategies, biostratigraphic schemes (e.g., the use of condensed sections in dating and correlation of seismic reflectors; Loutit et al., 1988; Martin, 1991), and paleoenvironmental resolution (e.g., Schindel, 1982; Signor and Lipp, 1982).

Differential preservation in carbonate and siliciclastic regimes in turn affects diagenetic potential; i.e., the degree of diagenetic alteration that a fossil assemblage undergoes upon burial (Schlanger and Douglas, 1974). Conversely, diagenetic potential affects differential preservation. Diagenetic potential and differential preservation are also commonly involved in the formation of seismic reflectors (e.g., Schlanger and Douglas, 1974; Berger and Mayer, 1978). Indeed, we may view (conceptually, at least) the latitudinal transition zone between temperate siliciclastic and tropical carbonate environments as a sort of "latitudinal lysocline" that has moved across the surface of the Earth in response to perturbations of the CO_2-bicarbonate-carbonate equilibrium of the ocean-atmosphere system (Martin, 1991), just as the deep-sea lysocline (depth below which significant carbonate dissolution takes place) adjusts its depth to similar perturbations (Berger, 1970). Thus, the preservation of calcareous fossil biotas may be intimately tied to the generation of systemic geochemical (taphonomic) signals (seismic reflectors) of regional significance (Berger and Mayer, 1978). We must, however, be able to distinguish regional from local taphonomic signals (cf. Staff and Powell, 1990).

Unfortunately, our knowledge of shelfal carbonate budgets and the relative rates of skeletal breakdown in carbonate and terrigenous environments is meager at best (e.g., Chave et al., 1972; Land, 1979; Land and Moore, 1980; Scoffin et al., 1980; Hubbard et al., 1990; Crossland et al., 1991; Kinsey and Hopley, 1991). Most paleoceanographers view modern carbonate shelves as being relatively unimportant in global carbon (and carbonate) budgets (e.g., Broecker et al., 1979; Broecker and Peng, 1987). Interestingly, though, ancient carbonate shelves may have served as major sinks for calcium carbonate (Opdyke and Wilkinson, 1988), thereby drawing down atmospheric CO_2 (Raymo, 1991) and enhancing preservation of calcareous shelf assemblages during Phanerozoic greenhouse episodes (ca. 100–200 million years duration; Fischer, 1984; Walker and Diehl, 1985). By contrast other workers have concluded that carbonate shelves buffer (via dissolution of biogenic carbonate) short-term (including anthropogenic) increases in atmospheric (and therefore oceanic) carbonate concentrations (Alexandersson, 1976; Hay and Southam, 1977; Walter and Burton, 1990; MacKenzie and Sabine, 1990). Walter and Burton (1990, table 7) calculated dissolution rates for calcium carbonate substrates implanted in nearshore back reef carbonate sediments of the Florida Keys of 0.3–51.2 mg/yr [Neogoniolithon (red algae, 18 mol % Mg-calcite): 5.6–51.2 mg/yr; echinoid (12 mol % Mg-calcite): 0.5–1.4 mg/yr; coral (aragonite): 0.3–1.0 mg/yr]. Some redissolved carbonate may precipitate and perhaps deliver calcium carbonate to deep water adjacent to carbonate bank margins (Shinn et al., 1989; cf. Neumann and Land, 1975).

The dissolution rates calculated by Walter and Burton (1990) are of the same order of magnitude as peak dissolution rates for foraminifera in the dissolution reactor experiment (19.7–98.5 mg/yr; non-normalized to test weight; cf. Fig. 19). As noted previously, however, the extremely corroded surface textures produced on tests in the reactor experiment have only rarely been seen by us in natural foraminiferal assemblages of Discovery Bay and the Florida Keys (Martin, 1986; Martin and Wright, 1988). Implantation of Amphistegina gibbosa (1–2 mm diameter) attached to PVC stakes in back reef sediments at depths of 10, 20, and 30 cm at Discovery Bay for up to 15 months supports this contention: surface textures produced in field experiments strongly resembled those of tests after 2000 hours of exposure to natural seawater.

The carbonate substrates utilized by Walter and Burton (1990) would appear to be far more reactive than the foraminiferal substrates utilized by us. The red algal substrates, in particular, that were utilized by Walter and Burton (1990) are far more soluble than foraminifera. Differences in mineralogy between red alga (e.g., Neogoniolithon: 18 mol % Mg-calcite) and foraminifera are no doubt important in conferring differential chemical reactivity to skeletal grains. Foraminifera used in our study vary between 4–5% (Asterigerina and Amphistegina;
Chave, 1954; Blackman and Todd, 1959) and 14–16% (Archaia angulatus; Blackman and Todd, 1959) Mg-calcite. Despite the wide range in magnesium content of foraminiferal species used in this study, however, they were largely resistant to dissolution in seawater table and field (slake) experiments; the aragonitic Halimeda behaved similarly. Thus, differential solubility of carbonate particles must also result from differences in substrate surface area (high in red algae, relatively low in benthic foraminifera), organic matter content (used as templates for CaCO₃ secretion; see also Kidwell and Baumiller, 1990), microstructure, and architecture (Flessa and Brown, 1983; Walter, 1985; Henrich and Wefer, 1986; Lewis et al., 1990). In other words, not all biogenic particles are equivalent in terms of dissolution (nor abrasion) resistance ("Sorby Principle", Folk and Robles, 1964).

Kidwell and Baumiller (1990) concluded that there is a taphonomic "threshold" in echinoid skeletons beyond which skeletal destruction rapidly occurs. By contrast, advanced stages of skeletal breakdown noted on foraminiferal specimens from natural sediment assemblages suggest the long taphonomic history that each foraminiferal test may undergo before final burial. Moreover, the substantial variation in abrasion (Table 2, Column A) and dissolution (Table 4) resistance between specimens of the same species hints at the apparently subtle changes that each particle may undergo before obvious visual evidence of physical and chemical alteration appears (e.g., surface roughening at the ultrastructural level of Asterigerina carinata; Fig. 6; cf. Flessa and Brown, 1983; Popp et al., 1986; Staff and Powell, 1990). For example, Katz and Man (1980) determined that ultrasonication of foraminiferal tests in excess of 30 minutes alters the amino acid content of the organic matrix, which may in turn enhance particle reactivity.

In contrast to calcareous algae, foraminifera typically comprise only a few percent of modern and ancient shallow-water carbonate sediments (Bass and Liddell, 1987). They may still, however, produce upwards of several hundred g/m²/yr (or more) in carbonate environments in the case of larger genera like Amphiostegina and Archaia (Hallock et al., 1986a, b). In the terrigenous sediments of the continental borderland of southern California, however, benthic foraminiferal productivity decreases by an order of magnitude (to ~17 g/m²/yr), although it still exceeds productivity of most calcareous macrobenthos (Smith, 1971). Hence, foraminifera are often sufficiently abundant—and persistent—in modern and ancient sediments (both carbonate and terrigenous) that the taphonomic "grades" (Brett and Baird, 1986; Speyer and Brett, 1988) and "signatures" (Brandt, 1989) recorded by foraminiferal assemblages and test surface features (Peebles and Lewis, 1989) may eventually allow us to distinguish the differing sedimentological and geochemical conditions (and time scales) of shell accumulation in carbonate, terrigenous, and mixed carbonate-siliciclastic taphofacies. We caution, however, that although the concepts developed by macroinvertebrate taphonomists are undoubtedly transferable to the microfossil realm, the actual behavior of microfossils as sedimentary particles may differ from the behavior of macroinvertebrate hardparts. Consequently, taphonomic information recorded by microfossil assemblages may differ from that of macrofossil taphocoenoses. Conversely, micropaleontological taphonomy may generate testable hypotheses that are applicable to microfossil accumulations at scales not normally considered by paleontologists.

CONCLUSION

The majority of previous studies on microfossil taphonomy have been restricted to either certain aspects of microfossil taphonomy or to single species. In contrast, our investigations represent an integrated approach, which utilizes both abrasion and dissolution resistance to formulate and test model-based predictions about information loss in the transition from living foraminiferal populations to incipient fossil assemblages (i.e., the formation of taphofacies). We have used a variety of species from different habitats (and taphonomic regimes) that reflect a diversity of shapes, sizes, wall thicknesses, compositions and microstructures. Eventually, we may be able to infer taphonomic characteristics of species for which there are no modern analogs, and to interpret ancient taphofacies based upon morphotype, wall structure and composition, and taphonomic behavior. By doing so, we will be able to determine the extent to which observed test traits are a reflection of adaptation and evolution by the living animal to its habitat and the extent to which test traits reflect taphonomic regime (Martin and Liddell, 1991). In other words, to what extent is homeomorphy within the foraminifera (e.g., Bandy, 1964) a reflection of convergent (or parallel) evolution, and to what extent is it a reflection of taphonomic "selection"? The answer(s) to this question are no doubt complex, but of fundamental importance in phylogenetic reconstructions, sampling strategies, and biostratigraphic and paleoenvironmental analyses.

ACKNOWLEDGMENTS

Our investigations of foraminiferal taphonomy at Discovery Bay have been supported by National Science Foundation Grant Number EAR-8815997 (Stratigraphy and Paleontology) and at Bahia la Choya by Grant Number EAR-9017864 (Geology and Paleontology) to REM. Thanks to W.J. Ullman and S. Welch of the College of Marine Studies, University of Delaware, for running the dissolution reactor experiment, and for their counsel on calcium-carbonate dissolution. Sue Goldstein and Steve Culver provided constructive, thoughtful reviews of the manuscript. Our deep appreciation to Karl Flessa, Sue Kidwell, and Carl Brett for moral support. Barbara Broge drafted figures and Pat Musa carefully, and cheerfully, typed numerous versions of the manuscript.

REFERENCES


NEUHANN, A.C., and LAND, L.S., 1975. Lime mud deposition and


Wilson, J.L., 1975, Carbonate Facies in Geologic History: Springer-Verlag, New York, 472 p.


ACCEPTED DECEMBER 5, 1991