

## Paleontological Society

---

Comparative Taphonomy of Bivalves and Foraminifera from Holocene Tidal Flat Sediments, Bahia la Choya, Sonora, Mexico (Northern Gulf of California): Taphonomic Grades and Temporal Resolution

Author(s): Ronald E. Martin, John F. Wehmiller, M. Scott Harris and W. David Liddell

Reviewed work(s):

Source: *Paleobiology*, Vol. 22, No. 1 (Winter, 1996), pp. 80-90

Published by: [Paleontological Society](#)

Stable URL: <http://www.jstor.org/stable/2401043>

Accessed: 15/02/2013 15:48

---

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



<http://www.jstor.org>

*Paleontological Society* is collaborating with JSTOR to digitize, preserve and extend access to *Paleobiology*.

## Comparative taphonomy of bivalves and foraminifera from Holocene tidal flat sediments, Bahia la Choya, Sonora, Mexico (Northern Gulf of California): taphonomic grades and temporal resolution

Ronald E. Martin, John F. Wehmiller, M. Scott Harris, and W. David Liddell

**Abstract.**—We compare the preservation (taphonomic grade) and age of *Chione* (bivalve) and foraminifera from modern siliciclastic tidal flat sediments of Bahia la Choya, Sonora, Mexico (northern Gulf of California). Disarticulated shells of *Chione* collected from the sediment-water interface of Choya Bay exhibit a substantial range in taphonomic grade and age, several hundred years to ~80–125 ka based on Accelerator Mass Spectrometer <sup>14</sup>C dates and D-Alloisoleucine/L-Isoleucine values. There is not, however, a one-to-one correspondence between age and taphonomic alteration of *Chione*: old (or young) valves may be highly altered or they may be relatively pristine. In contrast to *Chione*, most foraminiferal tests at Choya Bay are quite pristine, which suggests a quite young age, but tests are surprisingly old (up to ~2,000 calendar years based on Accelerator Mass Spectrometer <sup>14</sup>C dates).

We suggest that following seasonal pulses in reproduction, some foraminiferal tests are rapidly incorporated into a subsurface shell layer by “Conveyor Belt” deposit feeders and preserved there, while the rest of the reproductive pulse rapidly dissolves. Ultimately, some of these buried tests, along with *Chione*, are transported back to the surface by biological activity and storms. The much greater range of taphonomic grades and ages among *Chione* shells suggests that they, unlike foraminifera, are sufficiently large and preservable (low surface/volume ratio and chemical reactivity) to undergo many cycles of degradation, burial, and exhumation before complete destruction. The age of foraminiferal tests indicates that time-averaging of microfossil assemblages at Choya Bay is much more insidious than would be expected considering the relatively pristine state of the tests alone.

Based on our studies, the lower limit of temporal resolution of shallow shelf microfossil assemblages appears to be ~1000 years. We caution, however, that each depositional setting (taphofacies) should be evaluated on a case-by-case basis before gross generalizations are made. Indeed, the discrepancy between age and taphonomic grade of fossil assemblages at Choya Bay suggests that neither hardpart size or taphonomic grade are infallible indicators of test preservability or likely temporal resolution of the host assemblage, and that the dynamics of hardpart input and loss must also be evaluated.

Ronald E. Martin, John F. Wehmiller, and M. Scott Harris. Department of Geology, University of Delaware, Newark, Delaware 19716

W. David Liddell. Department of Geology, Utah State University, Logan, Utah 84322

Accepted: August 11, 1995

### Introduction

Microfossils—especially foraminifera—and macrofossils (e.g., bivalves) have both been widely used in stratigraphic and paleoecologic investigations. Much less attention has been paid, however, to the formation and temporal resolution of microfossil assemblages. Recent compilations (Martin 1993) suggest that time-averaging of foraminiferal assemblages varies from months or years in shell-poor terrigenous shelf regimes to thousands of years or more in carbonate and shell-rich terrigenous sediments. Although this time range is comparable to that of macroinvertebrate assem-

blages (Kidwell and Behrensmeyer 1993a), macrofossil and foraminiferal assemblages have never, to our knowledge, been compared directly with respect to their taphonomic behavior and temporal resolution, most likely because of the taxonomic specialization of individual workers. Comparison of the time scales of accumulation of hardparts from different taxa bears upon such controversial topics as the effects of relative abundance on fossil occurrence (e.g., Signor and Lipps 1982; Strauss and Sadler 1989; Flessa 1990; Marshall 1990; Meldahl 1990; Holland 1995) and distinguishing reworking from survivorship during and following biotic turnover (e.g., Pospichal

et al. 1990, and references therein; MacLeod and Keller 1994, and references therein; see also Kidwell, 1986, 1989, 1991, 1993a,b).

The concept of "taphonomic grades" (surface condition) of shells (e.g., Flessa and Brown 1983; Cutler 1987; Brandt 1989; Meldahl and Flessa 1990; Feige and Fürsich 1991) has received widespread attention among macro-paleontologists because of its potential utility in reconstructing the "taphofacies"—the physicochemical and biological conditions (e.g., encrusters, borers) under which shells are entombed (e.g., Brett and Baird 1986; Davies et al. 1989; Powell et al. 1989). Although some macroinvertebrates, such as brachiopods, may degrade rapidly (Collins 1985; Daley 1993), the shells of bivalves and most other macrofossils (excluding juveniles) are often assumed to degrade slowly because of their large size (Powell et al. 1984; Staff et al. 1986). This presumably allows sufficient time for taphonomic signatures to be inscribed on the shell surface before final burial. The concept of taphonomic grades has received much less attention among micropaleontologists, however, perhaps because calcareous microfossils are assumed to dissolve too rapidly (because of their small size and large surface/volume ratio) to either experience or register complex taphonomic histories. Although some microfossils may differ in their susceptibility to destruction (e.g., Corliss and Honjo 1981; Bremer and Lohmann 1982; Kotler et al. 1991, 1992; Martin and Liddell 1991), Martin (1993) predicted, primarily on the basis of size, that larger and thus presumably more preservable molluscan debris ought to be significantly older than foraminiferal assemblages of the same horizon; durations of time-averaging of the respective fossil assemblages, and the degree of stratigraphic disorder *between* these taxa (Cutler and Flessa 1990), should therefore be enhanced.

We test Martin's (1993) hypothesis using radiocarbon ( $^{14}\text{C}$ ) dates on foraminifera from tidal flat assemblages of Bahía la Choya ("Choya Bay"), Sonora, Mexico (northern Gulf of California; Fig. 1). We compare our results on foraminifera with  $^{14}\text{C}$  dates and D-Alloisoleucine/L-Isoleucine (A/I) values on bivalves (*Chione*) taken from the sediment-water inter-

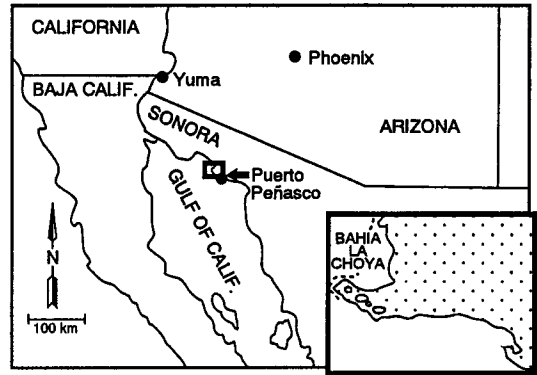


FIGURE 1. Location of Choya Bay (adapted from Fürsich and Flessa 1987).

face (SWI) in the same area in order to assess the relationships between size and taphonomic grade of bivalve shells and foraminiferal tests, and to determine the relative temporal resolution of fossil assemblages formed by these taxa.

#### Geologic and Oceanographic Setting

Choya Bay lies at the northeastern edge of the Gulf of California, adjacent to the Sonoran Desert (Fig. 1). Surficial sediments at Choya Bay are predominantly fine- to coarse-grained sand derived locally from granitic headlands and outcrops of semi-consolidated to well-consolidated sediment (Fürsich and Flessa 1987; Sumpter 1987); there is no indication of input from the Colorado River to subsurface horizons of the tidal flat (K. W. Flessa personal communication 1995). Calculated sediment accumulation rates at Choya Bay for the past few thousand years are quite low,  $\sim 0.038$  cm/yr (Flessa et al. 1993).

Without high sedimentation rates, conveyor belt deposit feeders (CDFs)—primarily callinassid shrimp and polychaetes (Fürsich and Flessa 1987, 1991; Meldahl 1987)—repeatedly remove fine-grained sediment from depth up to the SWI, which tends to concentrate coarse molluscan (mainly bivalve) debris in a relatively distinct subsurface shell layer (Meldahl 1987; see also van Straaten 1952; Rhoads and Stanley 1965). The depth to the shell layer decreases northward from  $>60$  cm on the southern flat to  $\sim 10$  cm in some places (Fig. 2), especially over a Pleistocene coquina ( $\sim 125,000$

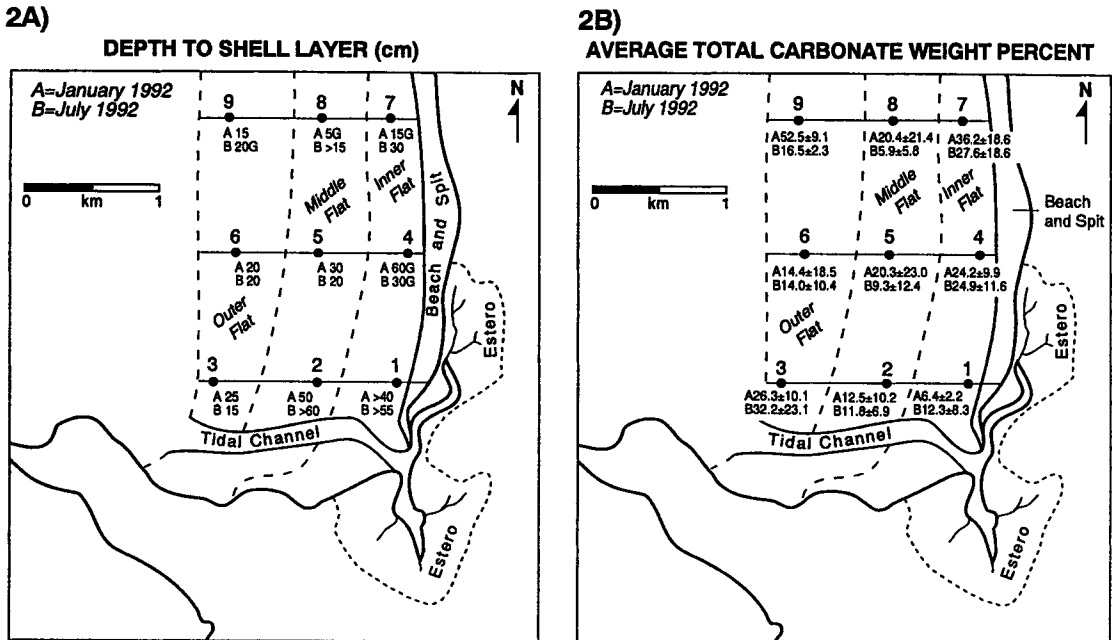


FIGURE 2. A, Location of core sites at Choya Bay and depth (in cm) to shell layer for January and July, 1992; contact between shell layer and overlying shell-poor mixed layer was typically sharp, but sometimes gradational (= G); B, Average downcore total carbonate weight percent (average of total carbonate weight percent for each horizon at each site  $\pm$  1 standard deviation) for January and July 1992 (cf. figs. 3, 4).

years old; oxygen isotope stage 5) (Aberhan and Fürsich 1987) that crops out over the northern margin of the flat. Consequently, total carbonate weight percent (shell content) of sediments near the SWI tends to increase to the north (Fig. 2) (Martin et al. 1996).

The activities of CDFs also influence pore-water chemistry (Martin et al. 1996). Burrowing organisms pump oxygenated water into subsurface sediment, where carbonic and sulfuric acids are produced through the oxidation of organic matter and sulfides ( $\text{HS}^-$ ), respectively (e.g., Walter and Burton 1990; Canfield and Raiswell 1991). Activities of CDFs are most intense on the inner and southern flat and decrease toward the outer flat, where sediment mixing is relatively shallow and is largely accomplished by breaking waves and vagile benthos, such as sand dollars (Fürsich and Flessa 1987; Martin et al. unpublished data).

CDF burrow densities also decline to the north, especially where sediment thickness is  $< \sim 20$ –25 cm (Martin et al. 1996), and sediment tends to become anoxic. Sulfate-reduc-

ing bacteria, which oxidize organic matter to  $\text{HCO}_3^-$  and  $\text{CO}_3^{2-}$  by using dissolved  $\text{SO}_4^{2-}$  as an electron acceptor, appear to thrive at northern flat sites. This is evidenced by pore water alkalinity (mainly  $\text{HCO}_3^-$  and  $\text{CO}_3^{2-}$ ) as high as  $\sim 50$  meq/l (normal seawater alkalinity is  $\sim 2.5$  meq/l [C. Culberson personal communication 1991]) during the summer, when ambient temperatures are highest (Martin et al. 1996; see also discussion of FOAM and NWC sites of Long Island Sound in Canfield and Raiswell 1991).

In late March–April and again in late fall there is periodic overturn of the nutrient-rich thermocline in the northern Gulf of California, as indicated by depth to the thermocline (Roden 1964; Robinson 1973). Overturn of the water column causes seasonal phytoplankton blooms (Maluf 1983; Pride et al. 1994) to which foraminifera at Choya Bay apparently respond with discrete ( $\sim$ a few weeks) seasonal reproductive pulses of their own (Fig. 3). Tests from Choya Bay are quite small ( $< \sim 250$   $\mu\text{m}$ ), and are characterized by a high surface/volume ratio and presumably high chemical reac-

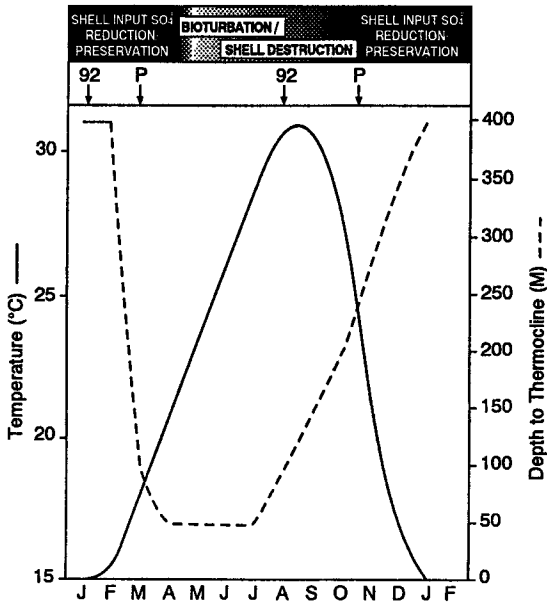


FIGURE 3. Sampling times (arrows, January and July 1992) and seasonal reproduction of foraminifera (= P) in relation to overturn of nutrient-rich thermocline in the Gulf of California (based on depth to thermocline, [Robinson 1973]), associated phytoplankton blooms, and to intensity of bioturbation and  $\text{SO}_4^{2-}$  reduction (after Martin et al. 1996).

tivity. Indeed, reproductive pulses of foraminifera are followed in the late spring and summer months by disappearance of almost the entire reproductive pulse (Fig. 3; cf. Fig. 4), presumably via dissolution (Martin et al. 1996). Nevertheless, foraminiferal number (number of tests/gram sediment) increases northward across the flat (Fig. 4). This is apparently due to two factors that buffer against dissolution: (1) increasing total carbonate weight percent (largely a result of molluscan shell content) of sediments near the surface (Fig. 2), and (2) alkalinity buildup (resulting from decreased rates of bioturbation) (e.g., Berner et al. 1970; Ben-Yaakov 1973; Aller 1982).

### Methods

Accelerator Mass Spectrometer (AMS) radiocarbon ( $^{14}\text{C}$ ) analyses were performed at the NSF-University of Arizona (Tucson) facility. In order to assess age versus taphonomic grade of foraminiferal tests, we analyzed hand-picked samples of predominantly *Buccella mansfieldi*, plus a few specimens of *Elphi-*

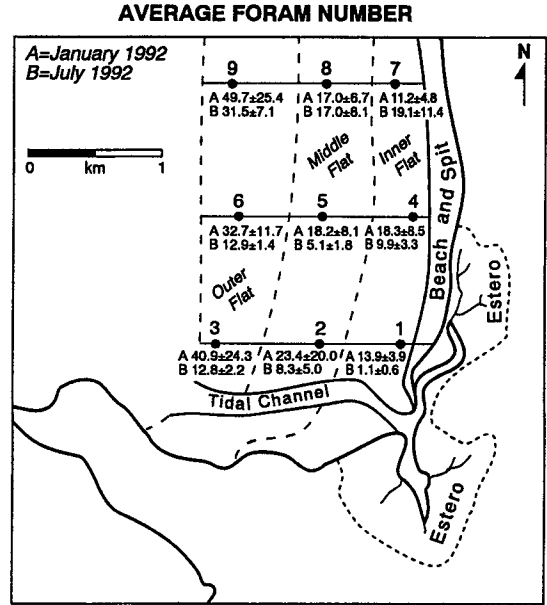


FIGURE 4. Average downcore foraminiferal number (number of tests per gram sediment; average of counts for each horizon sampled at each site  $\pm 1$  standard deviation) for January and July 1992. Decay of the reproductive pulse during July 1992 was also observed in samples collected during the previous summer (July 1991), which were used primarily for reconnaissance (see Martin et al. 1996).

*dium* cf. *E. crispum* ( $\sim 100$  specimens total for both species combined). Both species were most abundant at northern flat sites 8 and 9. Tests came from cores taken at site 8 (0–15 cm depth; above shell layer) and site 9 (20–25 cm depth; within shell layer) during July 1992 (table 1, Fig. 2) (see Martin et al. 1996 for details of site locations and coring methods). Tests from July cores were used in order to maximize the loss of tests from previous reproductive pulses (Fig. 3) and therefore increase the likelihood of possible reworking of older tests from the subsurface shell layer. Sites 8 and 9 were chosen so as to accumulate sufficient tests ( $\geq 1$  mg  $\text{CaCO}_3$ ) for analysis; relative to sites farther south on the flat, these sites have high total shell content near the SWI (Fig. 2), high alkalinity, and high foraminiferal abundance (Fig. 4) (Martin et al. 1996). Only pristine tests were used in AMS analyses so as to test the relation between taphonomic grade and test age (i.e., pristine tests should be young); degraded tests were uncommon at all

sites and were not used because it was more likely that they were indeed old.

Both  $^{14}\text{C}$  and A/I results were obtained for disarticulated valves of the bivalve *Chione* collected from the SWI during July 1992. Dead, disarticulated shells of *Chione* were abundant at this time at northern flat site 8, the strandline of the northern tidal flat, and middle flat site 5 (Fig. 2). We assigned taphonomic grades of *Chione* shells using categories proposed by Flessa et al. (1993; 1 = excellent preservation to 4 = poor preservation). A/I values for *Chione* were calculated from peak areas obtained by conventional HPLC methods (Wehmiller 1984a, b, 1990).

All radiocarbon dates discussed herein were obtained via the protocol described in Flessa et al. (1993) (see also references therein). Radiocarbon dates reported from the NSF-University of Arizona laboratory were "conventional" dates; i.e., by convention, dates were normalized to  $\delta^{13}\text{C} = -25\text{‰}$  (assuming an initial value of  $\delta^{13}\text{C} = 0\text{‰}$ ) and reported with respect to the Libby half-life of 5568 years as years before 1950. We converted conventional dates to calendar years using the calibration software of Stuiver and Reimer (1993).

One source of error in determining conventional dates is isotopic fractionation ("vital effect"), in which the test of some foraminifera (especially symbiont-bearing species; Reiss and Hottinger 1984) exhibits significant positive deviations in  $\delta^{13}\text{C}$ . Positive deviations in  $\delta^{13}\text{C}$  from 0.0‰ add ~16 years for every +1‰ (Bowman 1990). To our knowledge, *Buccella* and *Elphidium* do not harbor algal symbionts, which could cause significant fractionation, and most shell carbonates have values ranging only from 0.0 to +2.0‰ (Bowman 1990). We therefore assume that the  $\delta^{13}\text{C}$  values of these tests lie somewhere in the range of marine carbonates, which would cause a maximum error, for this factor, of only ~32 years.

Other sources of error are corrected during the calibration procedure. The "reservoir effect" makes shells appear too old, primarily because of upwelling of "old" carbon stored in the oceans (Stuiver and Polach 1977; Stuiver et al. 1986; Flessa et al. 1993). In order to correct for the reservoir effect, foraminiferal tests

collected at Choya Bay prior to 1950 are required, but are evidently unavailable. Instead, we used the correction of Flessa et al. (1993), which was based on a specimen of *Chione californiensis* collected at Choya Bay in 1949. Use of a bivalve date to correct foraminiferal dates should make no difference in the correction since the amount of "old" carbon stored in the oceans will appear the same to both foraminifera and bivalves (K. W. Flessa personal communication 1994). Based on ocean mixing models, a shell from the 1949 ocean should have an age of  $490 \pm 65$  years; i.e., the shell is too old (by ~490 years) because of the incorporation of "old" carbon into its  $\text{CaCO}_3$  (Stuiver et al. 1986: Fig. 10A).

A regional offset ( $\Delta R$ ) of the reservoir effect also typically occurs i.e., ages differ from those based on ocean mixing models, (Stuiver et al. 1986: Fig. 10B; Stuiver and Braziunas 1993). In the case of the northern Gulf of California, the conventional age of the specimen of *Chione californiensis* was  $850 \pm 65$  years, which is  $\sim 360 \pm 65$  years older than the age based on ocean-mixing models (This is equivalent to  $\sim 490 \pm 65$  years before 1950 [Flessa et al. 1993; see also Stuiver et al. 1986: Fig. 10A]). Therefore, the regional offset of the reservoir effect for Choya Bay is  $\sim 360 \pm 65$  years, and was used to convert conventional ages of foraminifera to calendar years in our study.

For the sake of comparison, we give ages in both conventional and calendar years. The  $1\sigma$  error (68% probability of the true age falling within the range) for conventional dates represents counting error only, with no correction for reservoir effect. The  $2\sigma$  error (95.4% probability of the true age falling within the range) for calendar year dates includes the effects of error both in counting and in modeling fluctuations in the specific activity of carbon in oceanic and atmospheric reservoirs (Flessa et al. 1993).

## Results

Ages and taphonomic grades of disarticulated valves of *Chione* from the SWI of Choya Bay vary substantially (Table 1). Radiocarbon ages of *Chione* range from 291 to 2071 calendar years (median age: 638 calendar years;  $n = 8$ ), (Table 1). The trend of A/I values in *Chione*

TABLE 1. Radiocarbon dates for *Chione* (bivalve) and foraminifera from tidal flat sites of Choya Bay. A/I values and taphonomic grades of *Chione* are also indicated. *Chione* valves with A/I values >0.7 are beyond range of  $^{14}\text{C}$  dating.

| <i>Chione</i>                 |                                    |                                |       |                  |
|-------------------------------|------------------------------------|--------------------------------|-------|------------------|
| Location                      | Conventional age ( $\pm 1\sigma$ ) | Calendar age ( $\pm 2\sigma$ ) | A/I   | Taphonomic grade |
| Site 5<br>(middle flat)       | 2530 $\pm$ 55                      | 1740<br>(1540–1931)            | 0.120 | 3.1              |
|                               | 1030 $\pm$ 55                      | 291<br>(101–475)               | 0.024 | 1.8              |
|                               |                                    |                                | 0.714 | >3.3             |
|                               |                                    |                                | 0.721 | >3.0             |
|                               |                                    |                                | 0.733 | >4               |
|                               |                                    |                                | 0.741 | >4               |
|                               |                                    |                                | 0.749 | >3.1             |
| Site 8<br>(northern flat)     | 2805 $\pm$ 60                      | 2071<br>(1875–2296)            | 0.100 | 3.3              |
|                               | 1970 $\pm$ 65                      | 1161<br>(956–1305)             | 0.084 | 2.8              |
|                               | 1125 $\pm$ 60                      | 416<br>(244–532)               | 0.028 | 2.9              |
|                               | 1045 $\pm$ 55                      | 299<br>(124–481)               | 0.023 | 2.3              |
|                               |                                    |                                | 0.839 | >3.2             |
| Strandline<br>(northern flat) | 1275 $\pm$ 55                      | 511<br>(363–648)               | 0.023 | 2.8              |
|                               | 1605 $\pm$ 55                      | 766<br>(642–934)               | 0.097 | 3.9              |
|                               |                                    |                                | 0.730 | >3.3             |
| <i>Foraminifera</i>           |                                    |                                |       |                  |
| Location                      | Conventional age ( $\pm 1\sigma$ ) | Calendar age ( $\pm 2\sigma$ ) |       |                  |
| Site 8                        | 2775 $\pm$ 60                      | 2026 (1841–2278)               |       |                  |
| Site 9                        | 2150 $\pm$ 55                      | 1309 (1167–1508)               |       |                  |

from Choya Bay is in basic agreement with AMS radiocarbon dates and taphonomic grades of the same shells (Fig. 5). Nevertheless, highly degraded *Chione* are sometimes substantially younger than older, better-preserved shells (Fig. 5). Moreover, nine specimens have A/I values of 0.714–0.839, which are indicative of the last major interglacial (~80–125 Ka or oxygen isotope stage 5) and beyond the range of  $^{14}\text{C}$  dating (assuming a simple parabolic kinetic model of amino acid racemization). Three of these specimens appeared significantly more degraded than other *Chione* valves (taphonomic grade > 4) (Table 1), whereas the remainder were assigned taphonomic grades ranging from 3.0 to 3.6.

In contrast to *Chione*, most foraminifera were relatively pristine at the light microscope level. Surprisingly, however,  $^{14}\text{C}$  ages of for-

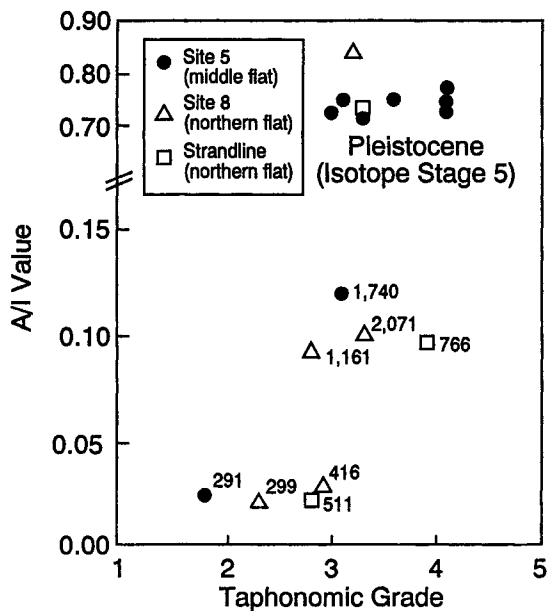


FIGURE 5. D-Alloisoleucine/L-Isoleucine (A/I) values (peak areas) and taphonomic grades (based on Flessa et al. 1993) of *Chione* (bivalve) shells from the sediment-water interface (SWI) of Choya Bay. Numbers next to data points are AMS  $^{14}\text{C}$  ages (calendar years) (see table 1). Shells with A/I values >0.7 are considered to be Pleistocene in age (isotope stage 5) and therefore beyond range of  $^{14}\text{C}$  dating.

miniferal tests from sites 8 and 9 are as old or older than many of the *Chione* shells, and the range in ages of foraminifera falls within the age range for *Chione* valves (Table 1).

## Discussion

Our findings for Choya Bay bivalves agree with the basic conclusions of Flessa (1993) and Flessa et al. (1993) (see also Flessa and Kowalewski 1994) for *Chione* at the same locality. They found that disarticulated *Chione* that had been collected from the SWI of the inner flat of Choya Bay exhibited a broad range of taphonomic grades, and that taphonomic grade was not an infallible indicator of shell age (time since death); moderately old specimens (~1800 years) were sometimes quite well preserved, whereas younger shells (~several hundred years) were sometimes more highly degraded (Flessa et al. 1993: Table 1) (cf. Fig. 5). Flessa (1993) and Flessa et al. (1993) suggested that a shell's surface condition is primarily indicative of the shell's residence time at the SWI and not its age (see also Driscoll

1975; Kidwell 1991, 1993a,b). Even if a shell is rapidly buried by downward advection by burrowing organisms, such as occurs at Choya Bay, rather than by rapid sediment influx, it may still remain somewhat pristine because it has been removed from the Taphonomically Active Zone (Davies et al. 1989) near the SWI.

Nevertheless, our A/I results indicate that the scale of time-averaging of bivalve assemblages at Choya Bay may be one to two orders of magnitude greater (up to ~125,000 years) than that reported by Flessa (1993) and Flessa et al. (1993). The range and median age of most *Chione* collected by us (Table 1) fall within the age range reported by Flessa et al. (1993): post-bomb to 3569 calendar years (median age: 483 calendar years;  $n = 17$ ). Nine of our specimens had A/I values of 0.714–0.839, however, a range that is indicative of the last major interglacial ~80–125 Ka or oxygen isotope stage 5, assuming a simple parabolic kinetic model. Significantly, six of the nine valves were assigned taphonomic grades of 3 to 3.6 and were therefore indistinguishable from much younger *Chione* valves (Fig. 5). This scale of time-averaging is not unique to Choya Bay. Wehmler et al. (1995) found extensive age-mixing of Pleistocene and modern bivalves, mainly *Mercenaria*, at 21 beach sites between New Jersey and Florida.

Unlike *Chione*, most foraminifera at Choya Bay disappear quite rapidly following reproduction (Figs. 3, 4) (see also Martin et al. 1996). We attribute the rapid disappearance of foraminifera at Choya Bay to the small size, and thus likely chemical reactivity, of the tests rather than to other mechanisms such as transport of tests offshore (Martin 1993; see also further discussion in Martin et al. 1996). Therefore, it is unlikely that test microstructure or mineralogy significantly affect test preservation at Choya Bay (cf. Corliss and Honjo 1981; Bremer and Lohmann 1982; Kotler et al. 1991, 1992; Martin and Liddell 1991). Both species of foraminifera used for  $^{14}\text{C}$  dating in the present study, *Buccella mansfieldi* and *Elphidium* cf. *E. crispum*, apparently occurred in higher abundances at northern flat stations because of increased shell content and alkalinity of the sediment at northern flat sites. The

rocky outcrops around the northern flat may also provide a more suitable habitat for these species than the mobile, sandy substrates found farther south at Choya Bay (cf. Myers 1942, 1943; Atkinson 1969).

Despite the rapid disappearance of much of the seasonal reproductive pulse, foraminifera from above and within the shell layer of northern flat stations (sites 8 and 9, respectively) are as old as some of the much larger *Chione*, which presumably disappear much more slowly. There are several possible explanations for this paradox: (1) tests at northern flat sites are better preserved, and therefore older, because of higher total shell content near the surface (Martin and Liddell 1991; Kotler et al. 1992; Martin, 1993; see also Aller 1982; Kidwell 1989) and because lower rates of bioturbation result in alkalinity buildup; (2) significantly older tests are moved upward by bioturbation or by erosive reworking of storms (sensu Kidwell 1993a: Table 1) from the underlying Pleistocene limestone that rims the northern margin of Choya Bay; and (3) despite apparent extensive dissolution of foraminifera following reproduction at Choya Bay, some tests are rapidly incorporated into the subsurface shell layer by CDFs and preserved there until they are exhumed, much later, by biological activity (e.g., McCave 1988) and storms (K. H. Meldahl and A. Olivera personal communication 1994). The third mechanism is essentially a compromise between mechanisms 1 and 2, as time-averaging is certainly plausible on shorter time scales than those of mechanism 2.

None of these mechanisms is mutually exclusive, although mechanism 3 seems the most reasonable. With respect to mechanism 1, higher shell content and alkalinity near the surface at northern flat sites may indeed slow rates of shell dissolution following reproductive pulses, but it seems unlikely that this mechanism alone can account for the surprisingly old Choya Bay test ages considering the extent of presumed test dissolution in these sediments (Fig. 4) (Martin et al. 1996). Moreover, tests from site 9 came from within the subsurface shell layer (20–25 cm core depth) whereas those from site 8, located landward



on the tidal flat, (Fig. 2) came from above it, yet ages of both samples were quite old.

With respect to mechanism 2, the potential for mixing or reworking of substantially older (Pleistocene) foraminifera into Holocene sediments at Choya Bay is indicated by the high A/I values of certain *Chione* valves (Fig. 5). Mixing or reworking of significantly older calcareous microfossils into much younger sediments is, however, considered to be a rare phenomenon (Berger and Heath 1968; Cutler and Flessa 1990). It is generally assumed substantially older, stratigraphically displaced microfossils can be recognized by their anomalous stratigraphic occurrence and state of preservation, such as surface roughening, breakage, and infilling with foreign sediment (Martin 1993). Such specimens, indicative of reworking from the underlying Pleistocene, were noted only rarely in our samples, especially at site 7 (inner northern flat), and they were not used in  $^{14}\text{C}$  analyses. Nevertheless, extensive mixing or reworking of quite old foraminiferal tests showing little or no surface alteration into much younger sediments may be more widespread than previously thought. Based on amino acid racemization techniques, for example, Murray-Wallace and Belperio (1994) found that uncemented and apparently fresh specimens of the large, symbiont-bearing foraminifer *Marginopora vertebralis* were reworked from late Pleistocene ( $\sim 125$  years Ka) carbonate sediments into the overlying modern carbonate skeletal sands, much as mollusc shells can be reworked (cf. Wehmiller et al. 1995).

Our preliminary studies of test ages in pure-carbonate environments (Discovery Bay, Jamaica, and Lee Stocking Island, Bahamas) indicate that time-averaging over just a few thousand years is also quite extensive in assemblages dominated by the large, symbiont-bearing, reef-dwelling foraminifera *Amphistegina gibbosa* and *Archaias angulatus* (data and site locations available from senior author upon request). Pristine and highly degraded tests of both species are commonly found together in our samples of both surface and shallow subsurface (up to  $\sim 60$  cm) assemblages. Mildly to highly degraded tests of both species are  $\geq 500$  calendar years (range,

mildly degraded: 474–2026 calendar years; range, highly degraded: 936–1,839 calendar years); pristine tests, on the other hand, may be modern (as indicated by “post-bomb” ages) or quite old ( $\geq 2000$  years), thereby exceeding the ages of mildly or highly corroded tests and falling within the age range of bulk  $\text{CaCO}_3$  (range: 984–3612 calendar years) (vital effects corrected on the basis of  $\delta^{13}\text{C}$  values of  $\sim +0.7$  to  $+1.5\%$  for *Amphistegina* from 0–10 m in the Gulf of Aqaba, Israel [Buchardt and Hansen 1977], and  $\sim 4.0\%$  for *Archaias angulatus* [Brasier and Green 1993] from back reef environments of the Florida Keys). As in the subsurface shell layer at Choya Bay, high levels of  $\text{CaCO}_3$  in pure-carbonate environments appear to buffer against dissolution, and thus promote extensive mixing of old tests and much younger shells, while inhibiting taphonomic damage to the tests themselves.

### Conclusion

The great range of taphonomic grades and ages among *Chione* in Holocene sediments of Choya Bay suggests that shells of this bivalve are sufficiently large and preservable (low surface/volume ratio and chemical reactivity) to survive many cycles of degradation, burial, and exhumation before complete destruction, thereby accumulating a detectable record of taphonomic damage. Our A/I results suggest that the scale of time-averaging of bivalve assemblages may be up to  $\sim 125,000$  years on high-energy shallow shelves (see also Wehmiller et al. 1995). Similar durations of time-averaging for microfossil assemblages may be more common than previously thought (e.g., Murray-Wallace and Belperio 1994).

Time-averaging of foraminiferal assemblages on shorter time scales of one to a few thousand years at Choya Bay is much more insidious than would be expected given the relatively pristine state of the tests and their presumed inability to withstand numerous cycles of degradation, burial, and exhumation (because of small size, thus high surface/volume ratio and chemical reactivity). These durations of time-averaging also hold for foraminiferal assemblages in carbonate environments of Discovery Bay (Jamaica) and Lee Stocking Island (Bahamas), and would appear to place

severe lower limits on the temporal resolution of paleoecological, biodiversity, and evolutionary studies of this group in nearshore settings in general (Martin 1993; see also Kidwell 1986; Flessa et al. 1993; Kidwell 1991, 1993a,b; Kidwell and Behrensmeier 1993; Flessa and Kowalewski 1994).

We caution, however, that we have dealt with only two taphofacies—carbonate-rich (Discovery Bay, Lee Stocking Island) and carbonate-poor (Choya Bay)—and that the intensity of taphonomic processes and the scale of time-averaging no doubt varies from one taphofacies to another (e.g., Brett and Baird 1986; Kidwell 1986, 1989, 1993a,b; Flessa 1993; Martin 1993). Flessa (1993) estimated time-averaging of bivalve assemblages of up to 10,000 years for deeper shelf settings. Whether shelfal microfossil assemblages from offshore exhibit similar degrees of time-averaging remains to be determined. Study of microfossil assemblages will require study of both the species-specific differences in shell mineralogy and structure (i.e., relative preservability), (e.g., Kotler et al. 1991, 1992), and the sedimentary dynamics of, and fossil input to, each taphofacies (cf. Loubere 1989; Loubere and Gary 1990; Loubere et al. 1993). Indeed, DuBois and Prell (1988) concluded that although sediment may have the same radiocarbon age, the proportions of the components producing that age may not be the same if the particles have different preservational histories, and that in order to use  $^{14}\text{C}$  dates of bulk sediment samples in stratigraphy, the processes controlling hardpart input and loss must be evaluated.

### Acknowledgments

Our studies at Discovery and Choya Bays have been funded by National Science Foundation Grant Numbers EAR-8815997 and EAR-9017864, respectively. We gratefully acknowledge the support of the National Science Foundation–University of Arizona Accelerator Mass Spectrometer Facility. Thanks to K. W. Flessa and J. Pizzuto for their advice on radiocarbon date corrections, and to K. W. Flessa and S. M. Kidwell for constructive criticism of the manuscript, which substantially improved it. Cores from Lee Stocking Island

were collected by S. L. Ohlhorst. Many thanks also to geology undergraduates M. Johnson, D. Lawrence, and D. Rasmussen of Utah State University for their dedicated assistance in the field, without which our studies could not have been completed. B. Broge skillfully drafted the figures.

### Literature Cited

- Aberhan, M., and F. T. Fürsich. 1987. Paleocology and paleoenvironments of the Pleistocene deposits of Bahia la Choya (Gulf of California, Sonora, Mexico). *In* F. T. Fürsich, and K. W. Flessa, eds. Ecology, taphonomy, and paleoecology of Recent and Pleistocene molluscan faunas of Bahia la Choya, northern Gulf of California. *Zitteliana* 18:135–163.
- Aller, R. C. 1982. Carbonate dissolution in nearshore terrigenous muds: the role of physical and biological reworking. *Journal of Geology* 90:79–95.
- Atkinson, K. 1969. The association of living foraminifera with algae from the littoral zone, South Cardigan Bay, Wales. *Journal of Natural History* 3:517–542.
- Ben-Yaakov, S. 1973. pH buffering of pore water of recent anoxic marine sediments. *Limnology and Oceanography* 18:86–94.
- Berner, R. A., M. R. Scott, and C. Thomlinson. 1970. Carbonate alkalinity in the pore waters of anoxic marine sediments. *Limnology and Oceanography* 15:544–549.
- Berger, W. H., and G. R. Heath. 1968. Vertical mixing in pelagic sediments. *Journal of Marine Research* 26:134–143.
- Bowman, S. 1990. Radiocarbon dating. University of California Press, Berkeley.
- Brandt, D. S. 1989. Taphonomic grades as a classification for fossiliferous assemblages and implications for paleoecology. *Palaios* 4:303–309.
- Brasier, M. D., and O. R. Green. 1993. Winners and losers: stable isotopes and microhabitats of living Archaiadae and Eocene *Nummulites* (larger foraminifera). *Marine Micropaleontology* 20:267–276.
- Bremer, M. L., and G. P. Lohmann. 1982. Evidence for primary control of the distribution of certain Atlantic Ocean benthic foraminifera by degree of carbonate saturation. *Deep-Sea Research* 29:987–998.
- Brett, C. E., and G. C. Baird. 1986. Comparative taphonomy: a key to paleoenvironmental interpretation based on fossil preservation. *Palaios* 3:207–227.
- Buchardt, B., and H. J. Hansen. 1977. Oxygen isotope fractionation and algal symbiosis in benthic foraminifera from the Gulf of Elat, Israel. *Bulletin of the Geological Society of Denmark* 26:185–194.
- Canfield, D. E., and D. R. Raiswell. 1991. Carbonate precipitation and dissolution: its relevance to fossil preservation. Pp. 411–453 *in* P. A. Allison and D. E. G. Briggs, eds. *Taphonomy: releasing the data locked in the fossil record*. Plenum, New York.
- Collins, M. J. 1985. Post mortality strength loss in shells of the Recent articulate brachiopod *Terebratulina retusa* (L.) from the west coast of Scotland. *Biostratigraphie du Paleozoique* 4: 209–218.
- Corliss, B. H., and S. Honjo. 1981. Dissolution of deep-sea benthic foraminifera. *Micropaleontology* 27:356–378.
- Cutler, A. H. 1987. Surface textures of shells as taphonomic indicators. *In* K. W. Flessa, ed. *Paleoecology and taphonomy of Recent to Pleistocene intertidal deposits, Gulf of California*. Paleontological Society Special Publication No. 2:164–176.
- Cutler, A. H., and K. W. Flessa. 1990. Fossils out of sequence:

- computer simulations and strategies for dealing with stratigraphic disorder. *Palaios* 5:227–235.
- Daley, G. M. 1993. Passive deterioration of shelly material: a study of the Recent eastern Pacific articulate brachiopod *Terebratalia transversa* Sowerby. *Palaios* 8:226–232.
- Davies, D. J., E. N. Powell, and R. J. Stanton. 1989. Taphonomic signature as a function of environmental process: shells and shell beds in a hurricane-influenced inlet on the Texas coast. *Palaeogeography, Palaeoclimatology, Palaeoecology* 72:317–356.
- Driscoll, E. G. 1975. Sediment-animal-water interaction, Buzzards Bay, Massachusetts. *Journal of Marine Research* 33:275–302.
- Dubois, L. G., and W. L. Prell. 1988. Effects of carbonate dissolution on the radiocarbon age structure of sediment mixed layers. *Deep-Sea Research* 35:1875–1885.
- Feige, A., and F. T. Fürsich. 1991. Taphonomy of the Recent molluscs of Bahia la Choya (Gulf of California, Sonora, Mexico). In F. T. Fürsich and K. W. Flessa, eds. *Ecology, taphonomy, and paleoecology of Recent and Pleistocene molluscan faunas of Bahia la Choya, northern Gulf of California*. *Zitteliana* 18:89–133.
- Flessa, K. W. 1990. The “facts” of mass extinctions. In V. L. Sharpton and P. D. Ward, eds. *Global catastrophes in earth history: an interdisciplinary conference on impacts, volcanism, and mass mortality*. Geological Society of America Special Paper 247:1–7. Boulder, Colo.
- . 1993. Time-averaging and temporal resolution in Recent marine shelly faunas. Pp. 9–33 in Kidwell and Behrensmeyer 1993b.
- Flessa, K. W., and T. J. Brown. 1983. Selective solution of macroinvertebrate calcareous hard parts: a laboratory study. *Lethaia* 16:193–205.
- Flessa, K. W., and M. Kowalewski. 1994. Shell survival and time-averaging in nearshore and shelf environments: estimates from the radiocarbon literature. *Lethaia* 27:153–165.
- Flessa, K. W., A. H. Cutler, and K. H. Meldahl. 1993. Time and taphonomy: quantitative estimates of time-averaging and stratigraphic disorder in a shallow marine habitat. *Paleobiology* 19:266–286.
- Fürsich, F. T., and K. W. Flessa. 1987. Taphonomy of tidal flat molluscs in the northern Gulf of California: paleoenvironmental analysis despite the perils of preservation. *Palaios* 2:543–559.
- , eds. 1991. *Ecology, taphonomy, and paleoecology of Recent and Pleistocene molluscan faunas of Bahia la Choya, northern Gulf of California*. *Zitteliana* 18:1–180.
- Holland, S. M. 1995. The stratigraphic distribution of fossils. *Paleobiology* 21:92–109.
- Kidwell, S. M. 1986. Models for fossil concentrations: paleobiologic implications. *Paleobiology* 12:6–24.
- . 1989. Stratigraphic condensation of marine transgressive records: origin of major shell deposits in the Miocene of Maryland. *Journal of Geology* 97:1–24.
- . 1991. The stratigraphy of shell concentrations. Pp. 211–290 in P. A. Allison and D. E. G. Briggs, eds. *Taphonomy: releasing the data locked in the fossil record*. Plenum, New York.
- . 1993a. Patterns of time-averaging in the shallow marine fossil record. Pp. 275–300 in Kidwell and Behrensmeyer 1993b.
- . 1993b. Taphonomic expressions of sedimentary hiatuses: field observations on bioclastic concentrations and sequence anatomy in low, moderate, and high subsidence settings. *Geologische Rundschau* 82:189–202.
- Kidwell, S. M., and A. K. Behrensmeyer. 1993a. Summary: estimates of time-averaging. Pp. 301–302 in Kidwell and Behrensmeyer 1993b.
- , eds. 1993b. Taphonomic approaches to time resolution in fossil assemblages: Paleontological Society Short Courses in Paleontology No. 6. University of Tennessee, Knoxville.
- Kotler, E., R. E. Martin, and W. D. Liddell. 1991. Abrasion-resistance of modern reef-dwelling foraminifera from Discovery Bay, Jamaica—implications for test preservation. Pp. 125–138 in R. Bain, ed. *Proceedings of the Fifth Symposium on the Geology of the Bahamas*.
- . 1992. Experimental analysis of abrasion and dissolution resistance of modern reef-dwelling foraminifera: implications for the preservation of biogenic carbonate. *Palaios* 7:244–276.
- Loubere, P. 1989. Bioturbation and sedimentation rate control of benthic microfossil taxon abundances in surface sediments: a theoretical approach to the analysis of species microhabitats. *Marine Micropaleontology* 14:317–325.
- Loubere, P., and A. Gary. 1990. Taphonomic process and species microhabitats in the living to fossil assemblage transition of deeper water benthic foraminifera. *Palaios* 5:375–381.
- Loubere, P., A. Gary, and M. Lagoe. 1993. Generation of the benthic foraminiferal assemblage: theory and preliminary data. *Marine Micropaleontology* 20:165–181.
- MacLeod, N., and G. Keller. 1994. Comparative biogeographic analysis of planktic foraminiferal survivorship across the Cretaceous/Tertiary (K/T) boundary. *Paleobiology* 20:143–177.
- Maluf, L. Y. 1983. Physical Oceanography. Pp. 26–45 in T. J. Case and M. L. Cody, eds. *Island biogeography in the Sea of Cortez*. University of California Press, Berkeley.
- Marshall, C. R. 1990. Confidence intervals on stratigraphic ranges. *Paleobiology* 16:1–10.
- Martin, R. E. 1993. Time and taphonomy: actualistic evidence for time-averaging of benthic foraminiferal assemblages. Pp. 34–56 in Kidwell and Behrensmeyer 1993b.
- Martin, R. E. and W. D. Liddell. 1991. Taphonomy of foraminifera in modern carbonate environments: implications for the formation of foraminiferal assemblages. Pp. 170–194 in S. K. Donovan, ed. *Fossilization: the processes of taphonomy*. Belhaven, London.
- Martin, R. E., M. S. Harris, and W. D. Liddell. 1996. Taphonomy and time-averaging of foraminiferal assemblages in Holocene tidal flat sediments, Bahia la Choya, Sonora, Mexico (northern Gulf of California). *Marine Micropaleontology* (in press).
- McCave, I. N. 1988. Biological pumping upwards of the coarse fraction of deep-sea sediments. *Journal of Sedimentary Petrology* 58:148–158.
- Meldahl, K. H. 1987. Sedimentologic and taphonomic implications of biogenic stratification. *Palaios* 2:350–358.
- . 1990. Sampling, species abundance, and the stratigraphic signature of mass extinction: a test using Holocene tidal flat molluscs. *Geology* 18:890–893.
- Meldahl, K. H. and K. W. Flessa. 1990. Taphonomic pathways and comparative biofacies and taphofacies in a Recent intertidal/shallow shelf environment. *Lethaia* 23:43–60.
- Murray-Wallace, C. V., and A. P. Belperio. 1994. Identification of remanent fossils using amino acid racemisation. *Alcheringa* 18:219–227.
- Myers, E. H. 1942. A quantitative study of the productivity of the foraminifera in the sea. *Proceedings of the American Philosophical Society* 85:325–342.
- . 1943. Life activities of foraminifera in relation to marine ecology. *Proceedings of the American Philosophical Society* 86:439–458.
- Pospichal, J. J., S. W. Wise, F. Asaro, and N. Hamilton. 1990. The effects of bioturbation across a biostratigraphically complete high southern latitude Cretaceous/Tertiary boundary. In V. L. Sharpton and P. D. Ward, eds. *Global catastrophes in earth history: an interdisciplinary conference on impacts, volcanism, and mass mortality*. Geological Society of America Special Paper 247:497–507. Boulder, Colo.

- Powell, E. N., H. Cummins, R. J. Stanton, and G. Staff. 1984. Estimation of the size of molluscan larval settlement using the death assemblage. *Estuarine and Coastal Shelf Science* 18: 367–384.
- Powell, E. N., G. M. Staff, D. J. Davies, and W. Russell Callender. 1989. Macrobenthic death assemblages in modern marine environments: formation, interpretation, and application. *CRC Critical Reviews in Aquatic Sciences* 1:555–589.
- Pride, C. J., W. E. Dean, and R. C. Thunell. 1994. Sedimentation in the Gulf of California: fluxes and accumulation rates of biogenic sediments and trace elements. *Geological Society of America Abstracts with Programs* 26:A23.
- Reiss, Z., and L. Hottinger. 1984. *The Gulf of Aqaba: ecological micropaleontology*. Springer, Berlin.
- Rhoads, D. C., and D. J. Stanley. 1965. Biogenic graded bedding. *Journal of Sedimentary Petrology* 35:956–963.
- Robinson, M. K. 1973. *Atlas of monthly mean sea surface and subsurface temperatures in the Gulf of California*. San Diego Society of Natural History Memoir 5.
- Roden, G. I., 1964. Oceanographic aspects of Gulf of California. In van Andel, Tj., and G. G. Sjøer, eds. *Marine geology of the Gulf of California*. American Association of Petroleum Geologists Memoir 3:30–58. Tulsa, Okla.
- Signor, P. W., and J. H. Lipps. 1982. Sampling bias, gradual extinction patterns and catastrophes in the fossil record. In L. T. Silver and P. H. Schulz, eds. *Geological implications of impacts of large asteroids and comets on the Earth*. Geological Society of America Special Paper 190:291–296. Boulder, Co.
- Staff, G. M., R. J. Stanton, E. N. Powell, and H. Cummins. 1986. Time-averaging, taphonomy, and their impact on paleocommunity reconstruction: death assemblages in Texas bays. *Geological Society of America Bulletin* 97:428–443.
- Strauss, D., and P. M. Sadler. 1989. Classical confidence intervals and Bayesian probability estimates for ends of local taxon ranges. *Mathematical Geology* 21:411–427.
- Stuiver, M., and T. F. Braziunas. 1993. Modeling atmospheric  $^{14}\text{C}$  influences and  $^{14}\text{C}$  ages of marine samples to 10,000 B.C. *Radiocarbon* 35:137–189.
- Stuiver, M., and H. A. Polach. 1977. Discussion: reporting of  $^{14}\text{C}$  data. *Radiocarbon* 19:355–363.
- Stuiver, M., and P. J. Reimer. 1993. Extended  $^{14}\text{C}$  data base and revised CALIB 3.0  $^{14}\text{C}$  age calibration program. *Radiocarbon* 35:215–230.
- Stuiver, M., G. W. Pearson, and T. F. Braziunas. 1986. Radiocarbon age calibration of marine samples back to 9,000 Cal Yr B.C. *Radiocarbon* 28:980–1021.
- Sumpter, L. T. 1987. Grain size and provenance of Bahia la Choya sediments. In K. W. Flessa, ed. *Paleoecology and taphonomy of Recent to Pleistocene intertidal deposits, Gulf of California*. Paleontological Society Special Publication No. 2: 44–51.
- van Straaten, L. M. J. U. 1952. Biogenic textures and the formation of shell beds in the Dutch Wadden Sea. *Koninklijke Nederlandse Akademie van Wetenschappen, Proceedings. Series B, Physical Sciences* 55:500–516.
- Walter, L. M., and E. A. Burton. 1990. Dissolution of recent platform carbonate sediments in marine pore fluids. *American Journal of Science* 290:601–643.
- Wehmiller, J. F. 1984a. Interlaboratory comparison of amino acid enantiomeric ratios in fossil Pleistocene mollusks. *Quaternary Research* 22:109–120.
- . 1984b. Relative and absolute dating of Quaternary mollusks with amino acid racemization: evaluation, applications, questions. Pp. 171–193 in W. C. Mahaney, ed. *Quaternary dating methods*. Elsevier, Amsterdam.
- . 1990. Amino acid racemization: applications in chemical taxonomy and chronostratigraphy of Quaternary fossils. Pp. 583–608 in J. G. Carter, ed. *Skeletal biomineralization: Patterns, processes, and evolutionary trends*, Vol. 1. Van Nostrand Reinhold, New York.
- Wehmiller, J. F., L. L. York, and M. L. Bart. 1995. Amino acid racemization geochronology of reworked Quaternary mollusks on U.S. Atlantic coast beaches: implications for chronostratigraphy, taphonomy, and coastal sediment transport. *Marine Geology* 124:303–337.