

# Comparative Taphonomy of Modern and Pleistocene Corals, San Salvador, Bahamas

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*The taphonomic condition of the corals *Acropora cervicornis* and *A. palmata* obtained from two facies of the late Pleistocene Cockburn Town fossil reef was compared to that of modern subfossil specimens of the same taxa collected from analagous environments. The extent of coverage by potentially preservable and preserved encrusting organisms (coralline algae, worm tubes, bryozoans and corals) and borer organisms (clionid sponges, lithophagid bivalves) was recorded. The degree to which the material had been abraded by a variety of processes was also recorded. Results revealed that the Holocene corals were significantly ( $\alpha = 0.05$ ) more degraded than those preserved in the Pleistocene facies, suggesting that the Pleistocene corals were exposed on the sea floor for less time than the Holocene material currently residing on the sea floor. The recent history of the reefs from which the Holocene corals were collected suggests this interval to be less than ten years; however, sedimentologic evidence indicates that a single storm event buried and killed the Cockburn Town reef during late Pleistocene time. The taphonomic analysis presented here supports this conclusion.*

## INTRODUCTION

The time resolution represented by fossil assemblages has long been a concern to geologists. Kidwell and Behrensmeier (1993) point out that questions of absolute and relative time—how old? how fast? how synchronously?—pervade both paleontology and historical geology. In recent years, much research has indicated that studies of taphonomy can yield valuable data with which to address these questions, (see Kidwell and Behrensmeier, 1993; Kidwell and Bosence, 1991 and Parsons and Brett, 1991, for reviews). Methodologies are highly variable, including: 1) actualistic field and laboratory studies that calibrate rates of taphonomic al-

teration suffered by various taxa [for example, Donovan's (1991) review for many important fossil groups]; 2) stratigraphic case studies that describe patterns of preservation to estimate the time resolution of fossil remains (e.g., Brett and Baird, 1986, 1993; Kidwell and Behrensmeier, 1993); and 3) quantitative simulations that attempt to match known patterns or predict the effects of time-averaging on fossil assemblages (e.g., Miller and Cummins, 1990, 1993; Cutler, 1993).

An implicit rationale for the utility of taphonomic data in addressing time resolution is that in general, one expects that the longer hardparts remain in the taphonomically active zone (TAZ; Davies et al., 1989), the greater the magnitude of taphonomic alteration. However, the correlation between shell age (time since death) and taphonomic condition is generally weak for molluscan material (MacIntyre et al., 1978; Goodfriend, 1987; Powell and Davies, 1990; Flessa, 1993). Driscoll (1970), Powell and Davies (1990) and Flessa (1993) argue that an erratic post-mortem burial history (burial and subsequent exhumation by a variety of physical and

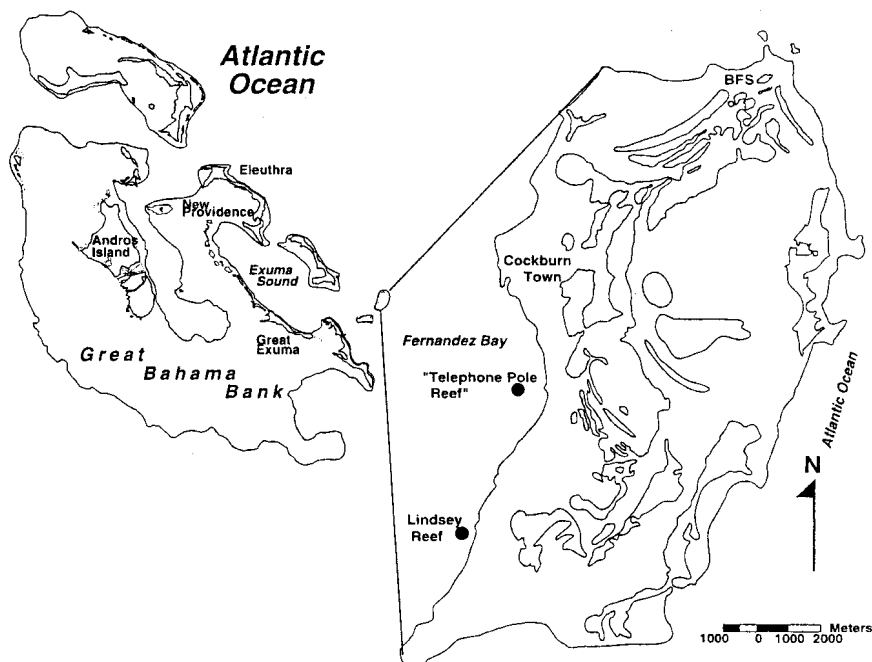


FIGURE 1—Index map for study area. Field work was supported by the Bahamian Field Station (BFS).

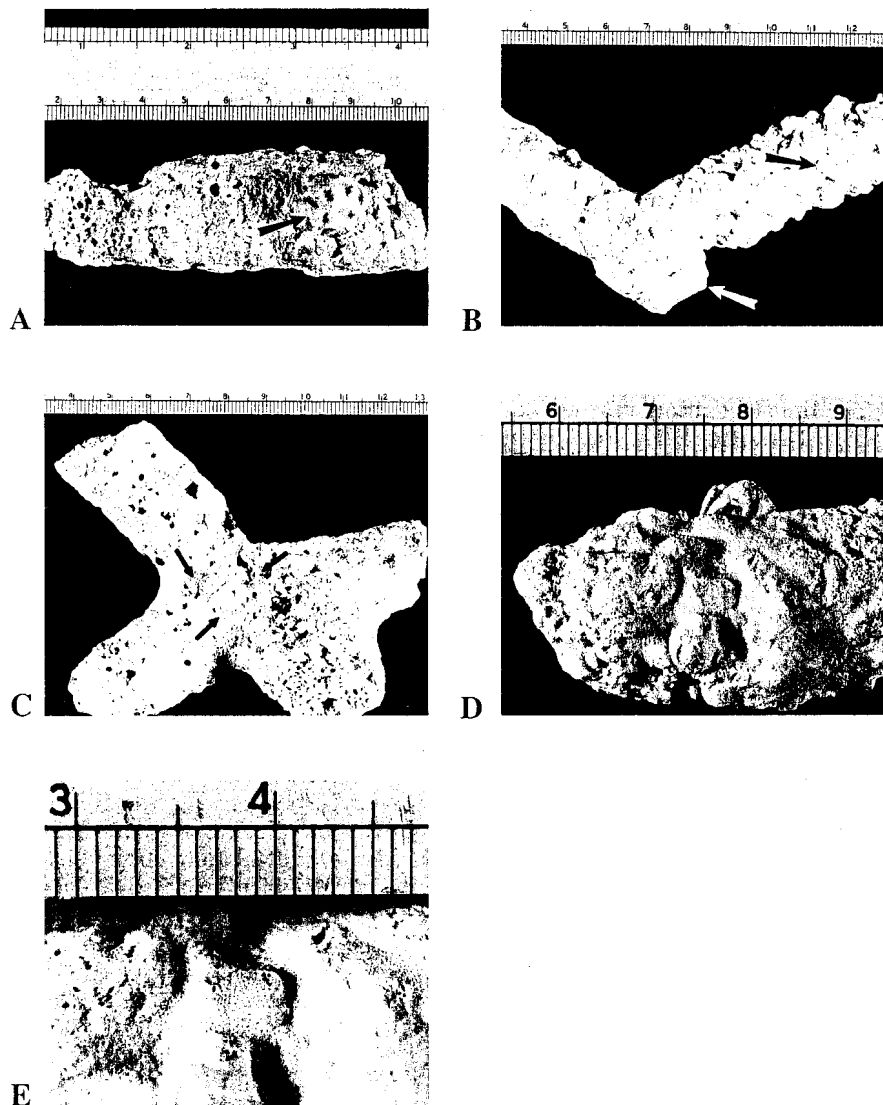


FIGURE 2—Encrusting organisms examined for this study, scale bars in cm: A) The scleractinian coral *Favia fragum* (arrow) attached to *Acropora cervicornis*; B) Bulbous (black arrow) and sheet-like (white arrow) encrusting coralline algae; C) worm tubes (arrows); D) encrusting bryozoan colony; E) close-up of colony. All are modern specimens.

biological processes) obscures the relationship between shell age and taphonomic condition. Thus, the taphonomic condition of hardparts serves as an indicator of residence time on the sea floor rather than the total span of the post-mortem interval (Flessa, 1993). The purpose of this study is to use taphonomic analyses of Holocene and Pleistocene coral material to better understand the rate at which a spectacular exposure of Pleistocene coral reef and near-reef facies was removed from exposure on

the sea floor and consequently preserved.

The late Pleistocene Cockburn Town Reef (San Salvador Island, Bahamas) displays a shallowing upward sequence reflecting a post-Sangamon lowering of sea level (White et al., 1984). The reef has been dated radiometrically to have flourished between 131–119 ky before present (Chen et al., 1991), and there is sedimentologic evidence suggesting that a single storm event may have abruptly buried the major parts of a

once thriving *A. palmata*-dominated coral assemblage (White et al., 1984; Curran and White, 1984; Curran et al., 1989). Additional data concerning the timing of the reef's demise have remained elusive.

Here, we quantify the taphonomic condition of modern (subfossil) coral material having a relatively well-known post-mortem residence time on the sea floor and compare the results to those obtained for Pleistocene specimens of the same taxa. Our results reveal that physical and biological degradation is significantly ( $\alpha = 0.05$ ) higher in the subfossil material, suggesting that the Pleistocene specimens were removed from exposure on the sea floor by a rapid burial event.

#### STUDY SITES AND METHODS

The regressive sequence exposed at Cockburn Town, San Salvador, Bahamas, includes a coral rubblestone facies, composed predominantly of *Acropora cervicornis*, and a coralstone facies which contains abundant in situ *Acropora palmata*. These facies were determined by White et al. (1984) to represent back reef and reef tract environments, respectively. The reef provides an excellent opportunity for a comparative taphonomic study because of its proximity to analogous modern reef environments. Telephone Pole Reef and Lindsey Reef, both located in Fernandez Bay (Fig. 1), were chosen as sample localities because they are modern examples of the coral rubblestone and coralstone facies described by White et al. (1984). Telephone Pole Reef is a mid-shelf patch reef that, in the past, was dominated by *A. cervicornis*. *A. cervicornis* has largely died in recent years and is currently being replaced by *Porites porites* (Curran et al., 1994). Although it is not part of a reef tract, Lindsey Reef is dominated by *A. palmata*, with the percentage of live coral increasing with distance from shore.

#### Field Methods

Fossil coral material was collected from the sandy floor of the quarry in

which the Cockburn Town reef is exposed. Ten specimens of *Acropora* were collected at random from a 9 m<sup>2</sup> grid placed at five distinct sites located along the quarry wall. The chosen sites were located using a map of the fossil reef published by Curran and White (1984). A total of 50 specimens were thus collected and, upon examination, produced *A. cervicornis* and *A. palmata* in a ratio of 4:1. To produce samples of comparative sizes, we reproduced this ratio for the subfossil material by collecting a total of 40 specimens of dead *A. cervicornis* and 10 specimens of dead *A. palmata*. *A. cervicornis* were collected from Telephone Pole Reef by placing a 9 m<sup>2</sup> grid over the reef surface and selecting 10 specimens at random. This process was repeated at four separate sites on the reef. Ten specimens of *A. palmata* were chiseled off a large stand of dead coral on Lindsey reef.

#### Laboratory Methods

Only potentially preservable encrusting and borer organisms were identified and their extent of coverage measured from the subfossil material for comparison with fossil material. Samples were examined using a hand lens and, when necessary, a stereozoom microscope. The presence of encrusting organisms indicates exposure on the sea floor (Parsons and Brett, 1991). Varying amounts of encrustation on coral colonies can thus be used as indicators of relative residence time at the sediment-water interface. Encrusting organisms identified on Pleistocene and modern material included coralline algae, worm tubes, bryozoans and other corals (Fig. 2). The extent of coverage was recorded using a five-point scale where 1 = 0%, 2 = 1–25%, 3 = 26–50%, 4 = 51–75% and 5 = 76–100% coverage. Borer organisms included sponges, molluscs and polychaete worms; coral specimens were cut longitudinally and the amount of boring activity was graded on a scale from 1 (pristine) to 4 (extensive removal of material) (Fig. 3). While the presence of borer organisms may also indicate post-mortem exposure on the

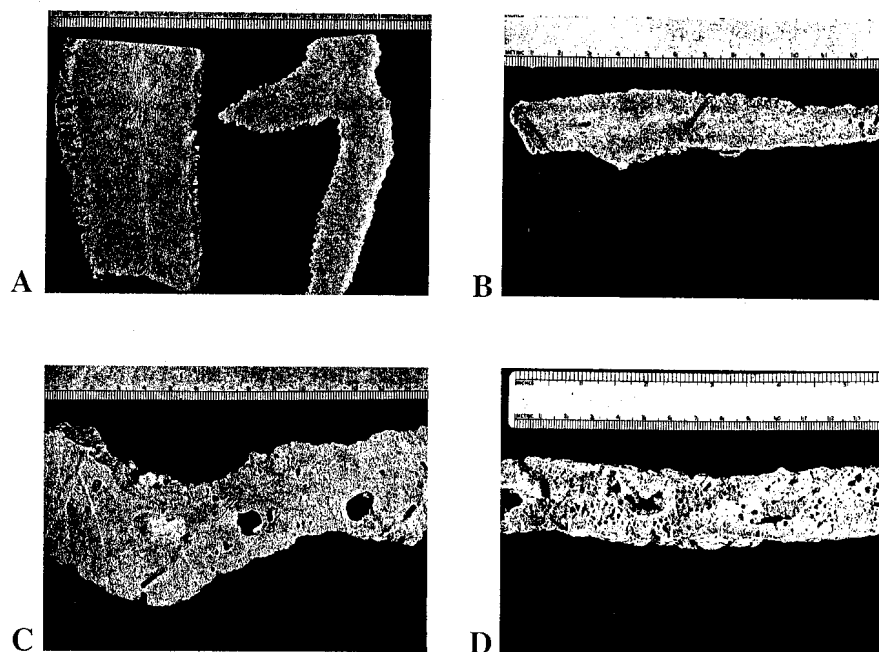


FIGURE 3—Semi-quantitative scale of bioerosion applied for this study. All are modern specimens; the series (A–D) represents grades 1 (pristine) through 4 (extensive removal of material).

sea floor, during the course of our fieldwork we observed a variety of serpulid worms that had excavated bore holes in live coral colonies. Although they prefer dead coral material, lithophagid bivalves are occasionally found in living coral (Soliman, 1969; Jones and Pemberton, 1988). Because we included worm and bivalve borings in our analysis our measurements of degradation by borer organisms do not represent exclusively post-mortem occurrences. Physical degradation in the form of abrasion was measured using a scale similar to that used by Ketcher and Allmon (1993) to quantify smoothing of Pliocene coral colonies. Corals were scored on a scale from 1 (pristine corallites) to 5 (no visible corallites) (Fig. 4).

## RESULTS AND DISCUSSION

### Encrustation

Modern and Pleistocene specimens of *Acropora palmata* and *Acropora cervicornis* exhibited a variety of potentially preservable (and preserved) encrusting organisms. With the exception of bryozoan col-

onies, all categories of encrusting organisms we recorded covered the Holocene corals to a significantly greater extent (student's t-distribution,  $\alpha = 0.05$ ) than their Pleistocene counterparts (Fig. 5). Much of the Pleistocene material was in pristine condition (Fig. 6). The relative amounts of coverage by the various taxa are approximately the same for both modern and ancient corals: coralline algae predominates on the coral surface followed by worm tubes and bryozoans. Encrusting corals were not observed on the Pleistocene material. Grazing traces were commonly observed on the Holocene material (Fig. 7), but absent from the Pleistocene corals.

### Bioerosion

Examination of the degree to which the coral material had been bored revealed similar results: Pleistocene material exhibited significantly fewer traces of borer organisms than subfossil material (Fig. 8). Two-thirds of the modern specimens (33 out of 50) were categorized as having extensive material removed (Grade 4, see Figure 3D) whereas the same pro-

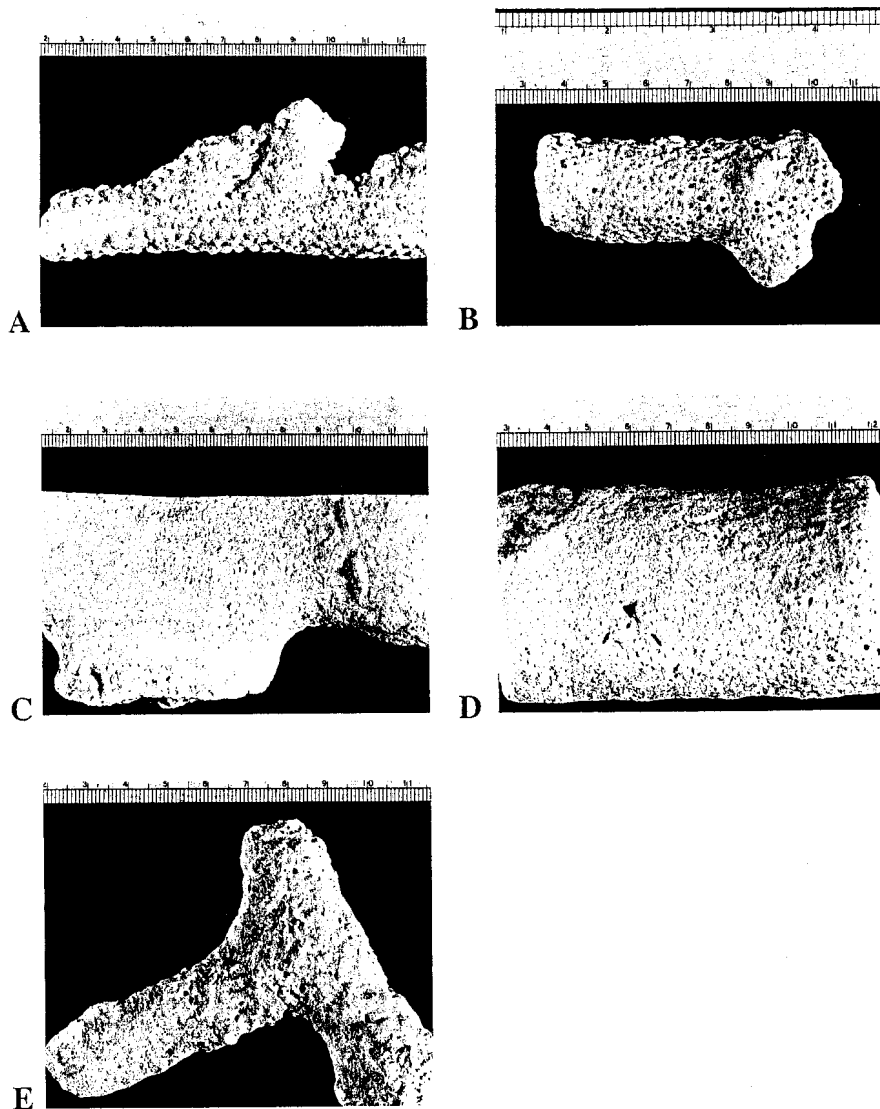


FIGURE 4—Semi-quantitative scale of abrasion applied for this study; all specimens are of late Pleistocene age. The series (A–E) represents grades 1 (pristine) to 5 (no corallites visible on surface) A) pristine, corallite rims raised above corallum; B) corallites visible, rims have been smoothed off; C) corallites visible, further smoothing; D) further abrasion begins to obscure corallites; E) no corallites visible; form suggests coral.

portion of Pleistocene specimens were categorized as having suffered less degradation by borer organisms (Grade 2, see Figure 3B). Galleries produced by clionid sponges comprised the vast majority of bioerosion observed, and boreholes constructed by lithophagid bivalves were also abundant. These observations corroborate reports by numerous workers (e.g., Cobb, 1969; MacGeachy and Stearn, 1976; Neumann, 1966; Jones

and Pemberton, 1988) concerning the importance of these organisms for destroying calcareous substrates.

#### Abrasion

Modern (subfossil) coral material produced significantly higher abrasion indices ( $\alpha = 0.05$ ) than the Pleistocene coral material (Fig. 5) although differences in the sources of abrasion were observed. Abrasion of

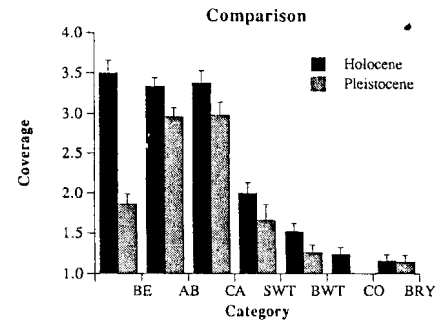


FIGURE 5—Comparison of the extent of coverage of biological and physical factors on modern and Pleistocene specimens of *Acropora palmata* and *A. cervicornis*. BE = borer organisms (primarily clionid sponges and lithophagid bivalves); AB = abrasion; CA = coralline algae; SWT = worm tubes < 1 mm in diameter; BWT = worm tubes > 1 mm in diameter; CO = corals; BRY = bryozoans. N = 50 for modern and Pleistocene specimens. Bars represent 95% confidence intervals about the average value obtained.

corallites may be the result of biological or physical processes (Ketcher and Allmon, 1993). Biologic processes might include grazing by a variety of organisms, whereas physical abrasion may be the result of movement of sand relative to the coral surface or dissolution of surface sculpture by groundwater. A physical process, sand blasting, was invoked by Ketcher and Allmon (1993) as an agent through which corallites preserved in a Pliocene coral thicket were differentially abraded: recesses and protected areas of the coralla were left unabraded while exposed surfaces were smooth. Although we did not observe differential abrasion on our material, the lack of recessed areas in specimens of *Acropora palmata* and *A. cervicornis* may have influenced this pattern. The material was collected well within storm wave base, thus sand blasting cannot be ruled out as a source of the abrasion observed on modern specimens. Graze marks were also abundant on the modern material. No evidence of biologically induced abrasion was observed on the Pleistocene corals, suggesting that sand blasting and dissolution by ground water may have been the most prevalent sources.



FIGURE 6—Pleistocene (top) and modern (bottom) specimens of *Acropora cervicornis*. The Holocene specimen was freshly killed prior to this photograph. Note the similarity in taphonomic condition.

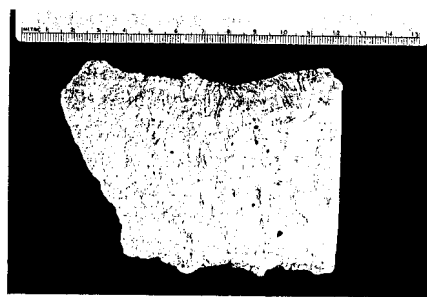


FIGURE 7—Grazing traces, possibly from an echinoid, on a modern specimen of *Acropora palmata*. These traces were subsequently covered by coralline algae: specific determination of the trace maker was therefore impossible.

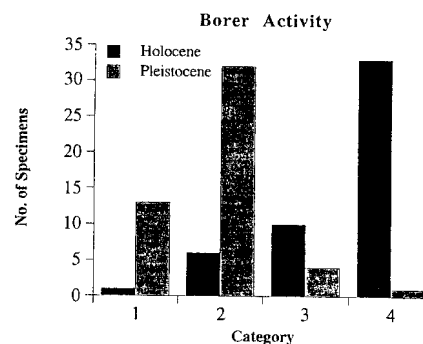


FIGURE 8—Frequency distribution of the scales of borer activity assigned to modern and Pleistocene coral specimens. Extent of material removed increases to the right of the histogram.  $N = 50$  for modern and Pleistocene specimens.

#### Timing of Burial of the Cockburn Town Reef

Results of our comparative taphonomic study suggest that the Pleistocene material was exposed on the sea floor over a shorter time interval than the modern material. The *Acropora cervicornis* death assemblage from which our samples were taken at Telephone Pole Reef was alive as recently as 1983 (Curran et al., 1994), while the *A. palmata* assemblage present at Lindsey Reef has died even more recently (Curran, personal communication). The epifaunal and endobiotic communities observed on and in the coral substrates could have developed over this interval (e.g., Neumann, 1966; Driscoll, 1970; Driscoll and Swanson, 1973; Adey and Vassar, 1975; Jones and Pemberton, 1988). Two alternative hypotheses may be proposed: 1) An unknown source of mortality resulted in the demise of the corals comprising the Cockburn Town reef. The death assemblage was exposed for a period of less than 10 years before it was removed from the taphonomically active zone by sudden burial during a storm event during the post-Sangamon regression. 2) A living coral assemblage was buried by a storm event or events during the post-Sangamon regression and consequently removed from the taphonomically active zone. We favor the second hypothesis for the following reasons:

#### Taphonomic Condition

The pristine condition of much of the Pleistocene material when compared to the modern material suggests that many of the *Acropora palmata* and *A. cervicornis* colonies were not exposed on the sea floor post-mortem. Results of field experiments by Adey and Vasser (1975) revealed that colonization of hard substrates ("PVC Palmata") by crustose corallines follows a complex succession, but begins as early as 20 days after material is exposed. Algal crusts completely covered bare material within 100 days, although variation due to differing light intensities and grazing pressure existed. Published rates of boring by clionid sponges (e.g., Neumann, 1966) and lithophagid bivalves (e.g., Jones and Pemberton, 1988) also support burial as a source of mortality and subsequent protection of freshly-killed corals from epifaunal and endobionts. We have observed thriving *Acropora*-dominated assemblages today that contain stands of dead coral interspersed with living coral, and these substrates serve as sites for encrusting and borer organisms. We submit that the limited degradation of the Pleistocene material by encrusting and borer organisms reflects the combination of live and dead coral components of a living reef that was killed by a burial event during the post-Sangamon regression. This conclusion may be tested

by performing a similar taphonomic analysis of live and dead coral material collected at random from an *Acropora*-dominated life assemblage. Moreover, our results can be used as a standard to assess the taphonomic history of additional well-preserved Pleistocene, Holocene, and modern reef material (e.g., Curran et al., 1989; Jackson, 1992; Taggart et al., 1993).

#### Lack of Grazers

The coral death assemblages present at Telephone Pole and Lindsey reefs provide a large area of occupation for a variety of organisms known to graze on coral substrates including echinoids (Sammarco, 1982), parrotfish (Ogden, 1977) and gastropods (Adey and Vassar, 1975). The presence of grazing traces on the modern material and their absence on the Pleistocene material is consistent with the hypothesis that the Pleistocene specimens represent a sample taken from a mixed life and death assemblage; grazing traces would only occur on coral substrates that were dead at the time the reef was buried. Thus it is less likely that grazing traces would be observed in the sample containing fewer suitable substrates on which grazing organisms could act. We do not propose that grazing traces are wholly absent from either species of *Acropora* pre-

served in the Cockburn Town reef, but that fossil corals hosting recognizable traces of grazing are less common than in the modern death assemblages we sampled.

#### Sedimentologic Evidence

The sedimentary sequence of the Cockburn Town reef and its overlying beds indicates that the reef began to decline as trough cross bedded, subtidal sands approached (White et al., 1984). Curran et al. (1989) determined this to have occurred between 119–120 kybp. At about this time, a set of tabular cross beds, at least 1 m thick, was deposited over much of the reef. These have been interpreted by White et al. (1984) to be the result of a large scale storm event, perhaps a hurricane, that transported sediment over sections of the reef assemblage. While we do not suggest that this set of cross beds represents the event that buried the corals we examined, the sedimentologic regime was clearly one in which event-driven burial could occur. The results of this study are consistent with such a scenario.

Given the syndepositional processes that destroy modern reefs, the preservation of reef framework requires extraordinary taphonomic circumstances (Hubbard et al., 1990). These include syndepositional binding of reef framework by soft-bodied or coralline algae (Davies and Hopley, 1983; Hubbard et al., 1990), decreased nutrient availability and consequent decrease of bioeroding organisms (Hallock, 1988) and rapid burial (Zankl et al., 1987). The results of this study document the role of rapid burial in preserving reef framework material. Ironically, the unique combination of circumstances that entombed the coral assemblage preserved at Cockburn Town may not allow the reef to escape subsequent geologic processes—the outcrop is currently being eroded during the present transgression.

#### CONCLUSIONS

By using a variety of taphonomic features as proxy for residence time

on the sea floor, our comparative study of Pleistocene and modern specimens of *Acropora cervicornis* and *A. palmata* suggest significant differences in the post-mortem history of the material examined. We suggest that rapid burial events occurring during regression killed an *Acropora* dominated life assemblage during Pleistocene time. The rapid burial of the life assemblage resulted in the relatively pristine condition of fossil coral material when compared to modern subfossil specimens that had been exposed on the sea floor for less than ten years. Specifically:

1. Encrusting coralline algae, worm tubes >1 mm in size, worm tubes <1 mm in size and corals covered modern specimens of *Acropora cervicornis* and *A. palmata* to a significantly greater extent ( $\alpha = 0.05$ ) than Pleistocene specimens of the same taxa; the relative amounts of coverage by these taxa are approximately the same for both modern and ancient corals.
2. Pleistocene corals were less degraded by boring sponges and bivalves than modern corals.
3. Grazing traces were common on modern coral material and absent from the Pleistocene material.
4. Pleistocene corals were less abraded than modern corals, although the sources of abrasion were different: primarily biological for the modern material vs. primarily physical and chemical for the Pleistocene material.

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#### LITERATURE CITED

- ADEY, W.H., and VASSAR, J.M., 1975, Colonization, succession and growth rates of tropical crustose coralline algae (Rhodophyta, Cryptonemiales): *Phycologia*, v. 14, p. 55–69.
- BRETT, C.E., and BAIRD G.C., 1986, Comparative taphonomy: A key to paleoenvironmental interpretation based on fossil preservation: *PALAIOS*, v. 1, p. 207–227.
- BRETT, C.E., and BAIRD, G.C., 1993, Taphonomic approaches to time resolution in stratigraphy: Examples from Paleozoic marine mudrocks: in KIDWELL, S.M., and BEHRENSMEYER, A.K., eds., *Taphonomic Approaches to Time Resolution in Fossil Assemblages: Short Courses in Paleontology*, no. 6, University of Tennessee, Knoxville, p. 250–274.
- CHEN, J.H., CURRAN, H.A., WHITE, B., and WASSERBURG, G.J., 1991, Precise chronology of the interglacial period:  $Th^{230}/U^{234}$  data from fossil coral reefs in the Bahamas: *Geological Society of America Bulletin*, v. 103, p. 82–97.
- COBB, W.R., 1969, Penetration of calcium carbonate substrate by the boring sponge, *Cliona*: *American Zoologist*, v. 9, p. 783–790.
- CURRAN, H.A., and WHITE, B., 1984, Field guide to the Cockburn Town fossil coral reef: in TEETER, J.W., ed., *Proceedings of the Second Symposium on the Geology of the Bahamas: CCFL Bahamian Field Station, Ft. Lauderdale, Florida*, p. 71–96.
- CURRAN, H.A., SMITH, D.P., MEIGS, L.C., PUFALL, A.E., and GREER, M.L., 1994, The health and short-term change of two coral patch reefs, Fernandez Bay, San Salvador Island, Bahamas: in GINSBURG, R.N., ed., *Proceedings of the Colloquium on Global Aspects of Coral Reefs: Health, Hazards, and History, 1993: Rosenstiel School of Marine and Atmospheric Science, University of Miami, Florida*, p. 147–153.
- CURRAN, H.A., WHITE, B., CHEN, J.H., and WASSERBURG, G.J., 1989, Comparative morphologic analysis and geochronology for the development and decline of two Pleistocene coral reefs, San Salvador and Great Inagua Islands, Bahamas: in MYLROIE, J., ed., *Proceedings of the Fourth Symposium on the Geology of the Bahamas, San Salvador, Bahamian Field Station*, p. 107–117.
- CUTLER, A.H., 1993, Mathematical models of temporal mixing in the fossil record: in KIDWELL, S.M., and BEHRENSMEYER, A.K., eds., *Taphonomic Approaches to Time Resolution in Fossil Assemblages: Short Courses in Paleontology*, no. 6, University of Tennessee, Knoxville, p. 169–187.

- DAVIES, D.J., POWELL, E.N., and STANTON, R.J., JR., 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*, v. 7, p. 317-356.
- DAVIES, P.J., and HOPLEY, D., 1983, Growth facies and growth rates of Holocene reefs in the Great Barrier Reef: *BMR Journal of Australian Geology and Geophysics*, v. 8, p. 237-252.
- DONOVAN, S.K., ed., 1991, *The Processes of Fossilization*: Columbia University Press, New York, 303 p.
- DRISCOLL, E.G., 1970, Selective bivalve destruction in marine environments: A field study: *Journal of Sedimentary Petrology*, v. 40, p. 898-905.
- DRISCOLL, E.G., and SWANSON, R.A., 1973, Diversity and structure of epifaunal communities on mollusc valves, Buzzards Bay, Massachusetts: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 14, p. 229-247.
- FLESSA, K.W., 1993, Time-averaging and temporal resolution in Recent marine shelly faunas: in KIDWELL, S.M., and BEHRENSMEYER, A.K., eds., *Taphonomic Approaches to Time Resolution in Fossil Assemblages: Short Courses in Paleontology*, no. 6, University of Tennessee, Knoxville, p. 9-33.
- GOODFRIEND, G.A., 1987, Chronostratigraphic studies of sediments in the Negev Desert, using amino acid epimerization analysis of land snail shells: *Quaternary Research*, v. 28, p. 374-392.
- HALLOCK, P., 1988, The role of nutrient availability in bioerosion: Consequences to carbonate buildups: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 63, p. 275-291.
- HUBBARD, D.K., MILLER, A.I., and SCATURO, D., 1990, Production and cycling of calcium carbonate in a shelf-edge reef system (St. Croix, U.S. Virgin Islands): Applications to the nature of reef systems in the fossil record: *Journal of Sedimentary Petrology*, v. 60, p. 335-360.
- JACKSON, J.B.C., 1992, Pleistocene perspectives on coral reef community structure: *American Zoologist*, v. 32, p. 719-731.
- JONES, B., and PEMBERTON, S.G., 1988, *Lithophaga* borings and their influence on the diagenesis of corals in the Pleistocene Ironshore Formation of Grand Cayman Islands British West Indies: *Palaaios*, v. 3, p. 3-21.
- KETCHER, K., and ALLMON, W.D., 1993, Environment and mode of deposition of a Pliocene coral bed: Coral thickets and storms in the fossil record: *PALAIOS*, v. 8, p. 3-17.
- KIDWELL, S.M., and BEHRENSMEYER, A.K., 1993, Introduction: in KIDWELL, S.M., and BEHRENSMEYER, A.K., eds., *Taphonomic Approaches to Time Resolution in Fossil Assemblages: Short Courses in Paleontology*, no. 6, University of Tennessee, Knoxville, p. 1-8.
- KIDWELL, S.M., and BOSENCE, D.W.J., 1991, Taphonomy and time-averaging of marine shelly faunas: in ALLISON, P.A., and BRIGGS, D.E.G., eds., *Taphonomy: Releasing the Data Locked in the Fossil Record*, Plenum Press, New York, 560 p.
- MACINTYRE, I.G., PILKEY, O.H., and STUCKENRATH, R., 1978, Relict oysters on the United States Atlantic coastal shelf: A reconsideration of their usefulness in understanding late Quaternary sea-level history: *Geological Society of America Bulletin*, v. 89, p. 277-282.
- MACGEACHY, J.K., and STEARN, C.W., 1976, Boring by micro-organisms in the coral *Montastrea annularis* on Barbados reefs: *Internationale Revue der Gesamten Hydrobiologie*, v. 61, p. 715-745.
- MILLER, A.I., and CUMMINS, H., 1993, Using numerical models to evaluate the consequences of time-averaging in marine fossil assemblages: in KIDWELL, S.M., and BEHRENSMEYER, A.K., eds., *Taphonomic Approaches to Time Resolution in Fossil Assemblages: Short Courses in Paleontology*, no. 6, University of Tennessee, Knoxville, p. 150-168.
- MILLER, A.I., and CUMMINS, H., 1990, A numerical model for the formation of fossil assemblages: Estimating the amount of post-mortem transport along environmental gradients, *PALAIOS*, v. 5, p. 303-316.
- NEUMANN, C.A., 1966, Observations on coastal erosion in Bermuda and measurements of the boring rate of the sponge *Cliona lampa*: *Limnology and Oceanography*, v. 11, p. 92-108.
- OGDEN, J.C., 1977, Carbonate sediment production by parrotfish and sea urchins on Caribbean reefs: in FROST, S.H., WEISS, M.P., and SAUNDERS, J.B., eds., *Reefs and Related Carbonates—Ecology and Sedimentology*: American Association of Petroleum Geologists, *Studies in Geology* No. 4, p. 281-288.
- PARSONS, K.M., and BRETT, C.E., 1991, Taphonomic processes and biases in modern marine environments: An actualistic perspective on fossil preservation: in DONOVAN, S., ed., *The Processes of Fossilization*: Columbia University Press, New York, p. 22-64.
- POWELL, E.N., and DAVIES, D.J., 1990, When is an "old" shell really old?: *Journal of Geology*, v. 98, p. 823-844.
- SAMMARCO, P.W., 1982, Echinoid grazing as a structuring force in coral communities: Whole reef manipulations: *Journal of Experimental Marine Biology and Ecology*, v. 61, p. 245-272.
- SOLIMAN, G.M., 1969, Ecological aspects of some coral-boring gastropods and bivalves of the northwestern Red Sea: *American Zoologist*, v. 9, p. 887-894.
- TAGGART, B.E., LUNDBERG, J., CAREW, J.L., and MYLROIE, J.E., 1993, Holocene reef-rock boulders on Isla de Mona, Puerto Rico transported by a hurricane or seismic sea wave: *Geological Society of America Abstracts with Programs*, v. 25, p. A61.
- WHITE, B., KURKJY, K.A., and CURRAN, H.A., 1984, A shallowing-upward sequence in Pleistocene coral reef and associated facies, San Salvador, Bahamas: in TEETER, J.W., ed., *Proceedings of the Second Symposium on the Geology of the Bahamas*: CCFL Bahamian Field Station, Ft. Lauderdale, Florida, p. 53-70.
- ZANKL, H., WILSON, J.L., and BOSELLINI, A., 1987, Outcrop models for seismic stratigraphy: Field guide for ERICO field trip through the Triassic Alps of Southern Europe, August 1987, 79 p.

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