

**TAPHONOMY OF HOLOCENE CRYPTIC BIOTAS FROM ST.
CROIX, VIRGIN ISLANDS: INFORMATION LOSS AND
PRESERVATIONAL BIASES**

**Kenneth A. Rasmussen
Carlton E. Brett**

Department of Geological Sciences,
University of Rochester,
Rochester, NY 14627

[Converted to electronic format by Damon J. Gomez (NOAA/RSMAS) in 2003. Copy available at the NOAA Miami Regional Library. Minor editorial changes were made.]

Taphonomy of Holocene cryptic biotas from St. Croix, Virgin Islands: Information loss and preservational biases

Kenneth A. Rasmussen,* Carlton E. Brett

Department of Geological Sciences, University of Rochester, Rochester, New York 14627

ABSTRACT

Surveys of submarine caves and overhanging ledges from St. Croix, Virgin Islands, provide new insights into the preservational processes active therein and into the taphonomy of ancient counterparts. Comparisons of preservable, skeletonized versus nonpreservable, unskeletonized components of these modern cryptic communities indicate that there is significant information loss in areal coverage, taxonomic richness, and diversity of fossilized examples. Quantitative estimates of such losses have been made. In addition, skeletal differences between early and late stage successional groups suggest biased representation of the former in the geologic record. Nonpreservable later colonizers may further erase the record of skeletonized forms through destructive life processes. Such forms of taphonomic information loss are probable in ancient counterparts and must be considered in accurate reconstruction of cryptic paleocommunities.

INTRODUCTION

Marine cryptic biotas (coelobionts) include organisms such as algae, sponges, corals, bryozoans, and serpulid worms which encrust sheltered habitats with restricted physical and biological disturbance (Jackson et al., 1971). Modern cryptic biotopes include the undersurfaces of foliose corals, reefal caverns, and overhanging rock ledges (Jackson, 1977). Paleontological studies have documented the existence of evolutionarily conservative cryptic communities in similar sheltered settings as old as the early Paleozoic (Brett and Liddell, 1978; Kobluk and James, 1979; Palmer, 1982). However, despite the paleoecological and evolutionary significance of cryptic hard-substrate biotopes (Kobluk, 1980), relatively little is known of the preservational or taphonomic processes affecting these settings. What percentage of the original community is actually represented in a fossilized cryptic assemblage? Is this assemblage systematically biased in ways that would affect our paleoecological reconstructions? Do the life processes of any coelobionts inhibit the preservation of other community members? In an attempt to answer such questions, we have documented the preservational processes with modern reefal cave-dwelling communities from the Caribbean.

STUDY AREA AND METHODS

Salt River Submarine Canyon, St. Croix, Virgin Islands (Fig. 1), was chosen as the site for the study of taphonomic processes in submarine reef cavities because cave biotas are plentiful and may be studied over considerable depth range (Rasmussen, 1983). Moreover, extended access to deep-water sites was facilitated by the use of National Underwater Laboratory Systems-1 Hydrolab habitat, located at 51 ft (15.5 m) at the mouth of the canyon.

Caves were selected at 50-ft (15.2-m), 75-ft (22.9-m), 105-ft (32.0-m), and 125-ft (38.1-m) depths and were systematically photographed at 10-cm intervals along seven randomly located, 1-3-m roof transects. High-resolution photography along the transects was accomplished by means of underwater cameras equipped with macrolenses, 1:3 framers,

and flash units. Each photographic frame recorded a 5.0×7.5 -cm surficial quadrat (Fig. 2A). An obvious result of our photographic methodology is the exclusion of substrate-penetrating organisms from our data set, assuming they present no surface expression (e.g., oscula, siphons, etc.). Therefore, our data consider only the surficial encrusting community members.

In order to view the potentially preservable surface, original quadrats were manually cleared of unskeletonized and, thus, nonpreservable organic tissue (Fig. 2B). Transect quadrats were then systematically re-photographed to assess taphonomic loss. Later, the pairs of quadrat photos (original and cleared of soft tissue) were projected simultaneously, and the outlines of all encrusting organisms were drawn and digitized to determine the areas occupied by various taxa.

Our procedures divided all space into three categories: preservable organism coverage, nonpreservable organism coverage, and "open substrate," including coralline algae (Table 1); we included demosponges in the nonpreservable category because their spicules, although possibly preservable, will not remain directly associated with the cave roof substrate. We observed no instances of successful overgrowth of coralline algae over any other organisms, solitary or colonial. Conversely, algae are overgrown by all other groups. Our observations and data of Jackson and Winston (1982) suggest that coralline algal cover should be considered as a part of the open substrate by virtue of its relatively passive overgrowth attributes.

Data derived from photographs were used in the calculation of areal coverage, taxonomic richness, and dominance diversity indices for both preservable and nonpreservable organisms (Table 1). The Shannon-Weaver diversity index ($H = -\sum_{i=1}^n P_i \log P_i$) was computed using proportional areal coverages for "importance" values (P_i).

TAPHONOMY OF CRYPTIC BIOTAS Preservational Information Loss

Typical encrusting cryptobiontic organisms in St. Croix submarine caves include green and coralline algae, foraminifera, demosponges,

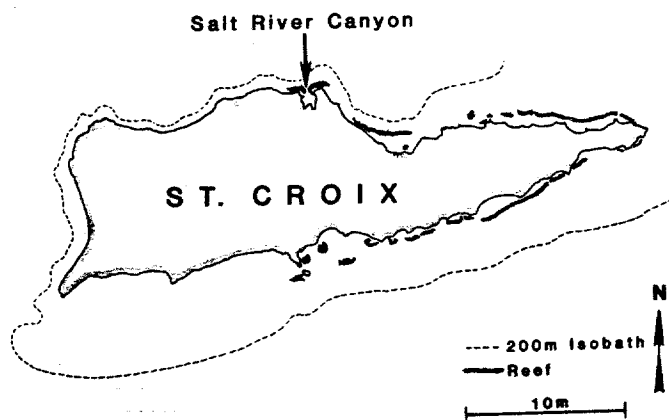


Figure 1. Map showing location of reef-walled Salt River Submarine Canyon, St. Croix, Virgin Islands. All cave sites are between 50 and 125 ft (15.2-38.1 m) on the westward, nearly vertical reef wall. Modified from Hubbard et al. (1981).

*Present address: Curriculum in Marine Sciences, University of North Carolina at Chapel Hill, 12-5 Venable Hall, Chapel Hill, North Carolina 27514.

sclerosponges, corals, bryozoans, ascidians, serpulids, and bivalves. A total of 56 distinct taxa was observed in this study (Table 1). A large proportion of these organisms consists of largely or exclusively soft-bodied taxa.

All three community indices (i.e., richness, diversity, and coverage) show a substantial loss of information due to nonpreservation of unskeletonized organisms (Table 1). On the basis of the assumption that unskeletonized cryptobionts are completely nonpreservable, we find that about 62% of the originally observed taxa in the St. Croix cryptic settings would be removed from the geologic record. Hence, observed values of taxonomic richness would reflect only about 38% of the original community. Similarly, dominance diversity shows a 58% information loss. The taphonomic loss of these organisms results in a reduction in the proportion of substrate coverage from greater than 70% coverage in the original living community to a value of only 15% for the skeletonized assemblage. The mean loss of information for areal coverage is therefore about 85%. This observation suggests that a significant proportion of the "blank space" observed in fossil cryptic assemblages was originally occupied by nonpreservable, soft-bodied organisms. These calculations exclude coralline algal coverage from the skeletonized category; inclusion of

algal cover would result in a considerably lower percentage of coverage loss—about 55%.

We also examined the data for any systematic increase or decrease of information loss with depth (Table 1). Coverage by the skeletonized, preservable organism subset was consistently low and showed only minor increase, between 105 and 125 ft (32 and 38 m), probably due to the appearance of sclerosponges at greater than 75 ft (23 m) (see Table 1, left). The richness and dominance diversity values for the entire community also are relatively constant over the depth range observed. In each case skeletonized organism levels are, again, significantly lower than total values. This factor accounts for information losses that remain generally high and constant with depth.

Successional Bias

Controlled experiments in cryptic substrate colonization have been performed by Jackson and Buss (1975), Jackson (1977), and Russ (1982). Their results show that early settling "pioneer" organisms are predominantly solitary (e.g., solitary scleractinian corals and serpulid worms) but also include certain colonial organisms (e.g., some bryozoans). This contrasts with later stage colonizers that are predominantly composed of encrusting demosponges. Modular demosponges easily overgrow earlier colonizing solitary organisms by virtue of their rapid areal expansion (Buss and Jackson, 1981; Jackson and Winston, 1982). However, we note that later successional groups tend to be poorly skeletonized and therefore leave little, if any, directly preservable evidence in the fossil record. This distinction leads to a critical, and previously unrecognized, successional bias in the preservation of encrusting cryptic communities: preserved coelobionts are strongly biased toward early successional stages.

This taphonomic bias is dramatically illustrated by comparison of original and cleared pairs of quadrat photos (Figs. 2A, 2B). The original, uncleared quadrats are consistently dominated by poorly skeletonized

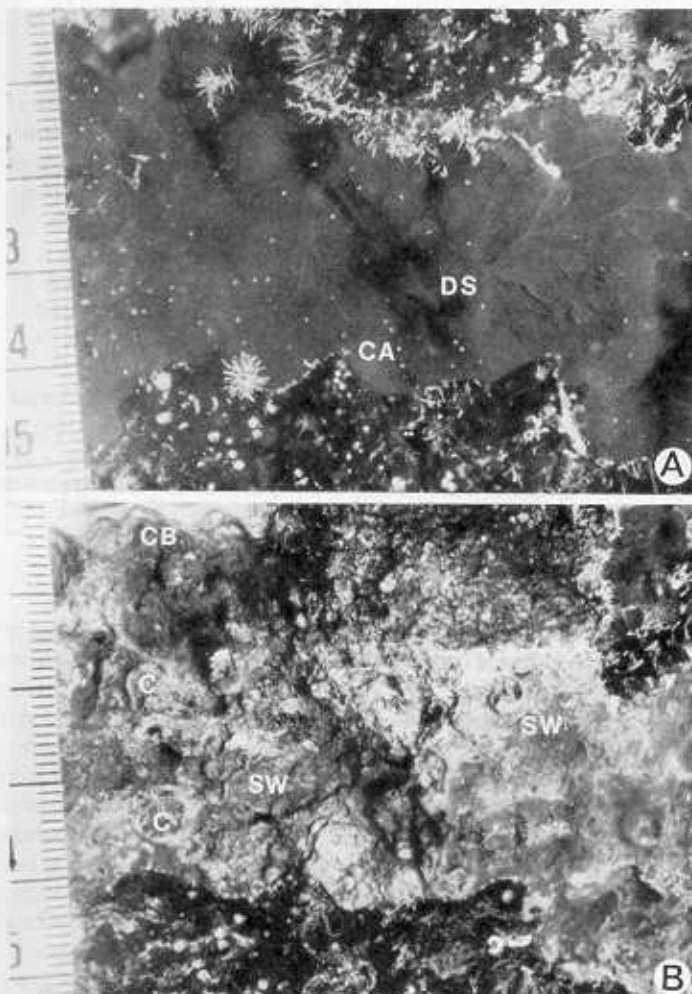


Figure 2. A: Typical original surficial quadrat photograph. Note dominance of encrusting demosponge (DS) over coralline algal substrate (CA). Erect, filamentous green algae are ubiquitous. Scale is in centimetres and corresponds to distance into cave. B: Cleared quadrat photograph of area shown in A. Removal of unskeletonized tissue reveals understorey of earlier colonization, in many cases in corroded state of preservation. Prior colonizers include serpulid worms (SW), cemented bivalve (CB), and solitary corallites (C). Photos by R. Catanach.

TABLE 1. COLONIZATION AND PRESERVATION DATA, SALT RIVER SUBMARINE CAVES

Transect depths (ft):	50	75	105	125
No. quadrats sampled ^a :	25	29	24	8
Organism coverage (%)				
Preservable (skeletonized)				
Foraminiferans	0.06	0.02	0.16	0.00
Sclerosponges	0.00	0.00	10.30	10.90
Hydrozoans	0.03	0.00	0.02	0.00
Corals	5.21	4.11	0.00	0.60
Bryozoans	1.33	3.70	1.74	2.56
Brachiopods	0.00	0.09	0.01	0.00
Serpulid worms	0.64	0.61	0.66	0.31
Bivalves	0.14	0.22	0.11	0.00
Total	7.4	8.8	13.0	14.4
Nonpreservable				
Green Algae	2.34	8.60	9.83	6.57
Demosponges	30.10	54.10	43.00	50.00
Sabellid worms	0.40	0.45	0.00	0.09
Ascidians	2.74	6.41	14.50	11.70
Total	35.6	69.6	67.3	68.4
Area covered by organisms (%)	43.0	78.4	80.3	82.8
Area not covered (%)	57.0	21.6	19.7	17.2
Richness (no. of taxa)				
Preservable	3.2	3.8	3.4	3.1
Nonpreservable	4.6	6.5	5.5	6.3
Total	7.8	10.3	8.9	9.4
Diversity (H)				
Preservable	0.24	0.29	0.22	0.22
Nonpreservable	0.44	0.55	0.44	0.56
Total	0.55	0.65	0.56	0.58

^aValues are means for quadrats in several transects; detailed data on individual transects are given in Rasmussen (1983).

demosponges (DS). When this layer of sponges was stripped away, simulating natural preservation processes, an understory dominated by solitary corals (C), cemented bivalves (CB), serpulid worms (SW), and bryozoans was revealed. This drastically different and pioneer-dominated assemblage represents the type of sample that might be preserved in the geologic record.

Biotic Erasure

Demosponges, the predominant group of nonpreservable cryptobionts, may be divided into nonboring and boring types. Boring siphonodictyid and related clionid sponges contribute to major substrate destruction through bioerosion here, as in many carbonate environments (Neumann, 1966; Warme, 1975, 1977). Our detailed observations of cave roofs also suggest another type of destructive activity by nonboring demosponges.

Skeletons overgrown by sponges exhibit variably corroded surfaces not observed on nonovergrown skeletons. This corrosion phenomenon is distinct from normal bioerosion in that it is not preferential to dead substrates, is not associated with known boring sponges, and is only superficial in extent. The most prominent example of corrosion is a loss of fine septal detail on solitary corallites overgrown by demosponges (Figs. 2B, 2C). The possibility of prior degradation of these skeletons by microendoliths or boring sponges cannot be ruled out. However, it is apparent that areas currently covered by nonboring demosponges are corroded preferentially relative to the uncovered areas. The mechanism of this substrate degradation is unknown but may include biochemical dissolution of skeletons at the demosponge-substrate interface. Hence, life processes of the dominant encrusting sponges may also be responsible for destruction of otherwise preservable skeletons. Over long time spans, exposed skeletons may be degraded to unrecognizable remnants or may be biotically "erased."

DISCUSSION AND SUMMARY

The present investigation of modern cryptic communities in St. Croix caverns has important implications for paleoecology and evolutionary biology. A consistently high level of soft-organism encrustation in modern caves indicates that severe taphonomic information losses in areal coverage are present in similar ancient settings. Data presented here suggest that only a small proportion of the original richness and diversity is preservable, given the normal processes of soft-part destruction. Such alteration of these widely used ecological parameters may strongly bias the interpretation of original paleocommunity structure.

Assuming that the processes observed in modern caves are representative of those occurring in ancient cryptic communities, we suggest the following conclusions: (1) General taphonomic information loss through nonpreservation is characteristically high in cave habitats. Losses approximate 85% of original areal coverage, 62% of original richness, and 58% of original dominance diversity. These values are comparable to those obtained in other studies of preservability of encrusting faunas (e.g., Schopf, 1978, p. 263). (2) Most cryptic pioneers are solitary skeletonized organisms, which are subsequently overgrown by unskeletonized demosponges and colonial organisms. Fossilized cryptic communities are therefore biased toward preservation of earlier successional stages of encrustation. However, the consistent nature of this bias probably permits valid comparisons to be made between ancient cryptic communities. (3) A measurable loss of detail in older skeletal remains beneath unskeletonized or poorly skeletonized demosponges suggests that activities of later stage encrusters may act to erase the potential record of skeletonized forms, especially in stable cryptic environments.

These observations suggest that the biotas of large, stable cavities may be among the least well preserved of hard-substrate fossil assemblages. In contrast, we predict that smaller, less stable cryptic substrates, such as corals and shells, will experience lesser amounts of information loss and will be more readily buried. Our preliminary taphonomic survey of encrusting communities on the undersurfaces of platey *Agaricea* corals

associated with the caves in Salt River Canyon appears to bear out this prediction; assemblages are less dominated by late-stage encrusters and display higher percentage preservation, and skeletons show little effect of biocorrosion.

Ancient cryptic substrates display percentages of coverage and species richness of skeletonized encrusters comparable with those observed in modern communities (see Liddell and Brett, 1981, 1982, for Silurian and Devonian examples). Certain encrusting fossils, at least as old as the Middle Ordovician, also exhibit corrosion similar to that seen on modern skeletons (Brett and Liddell, 1978). Thus, taphonomic processes observed in Holocene communities may well have been operational during much of the Phanerozoic. Paleontologists can and should apply "taphonomic uniformitarianism" in reconstructing ancient hard-substrate communities.

REFERENCES CITED

- Brett, C.E., and Liddell, W.D., 1978, Preservation and paleoecology of a Middle Ordovician hardground community: *Paleobiology*, v. 4, p. 329-348.
- Buss, L.W., and Jackson, J.B.C., 1981, Planktonic food availability and suspension feeder abundance: Evidence of in situ depletion: *Journal of Experimental Marine Biology and Ecology*, v. 49, p. 151-161.
- Hubbard, D.K., Sadd, J.L., Miller, A.I., Gill, I.P., and Dill, R.F., 1981, The production, transportation, and deposition of carbonate sediments on the insular shelf of St. Croix, U.S. Virgin Islands: West Indies Laboratory Technical Report No. MG-1, 145 p.
- Jackson, J.B.C., 1977, Competition on marine hard substrata: The adaptive significance of solitary and colonial strategies: *American Naturalist*, v. 111, p. 743-769.
- Jackson, J.B.C., and Buss, L., 1975, Allelopathy and spatial competition among coral reef invertebrates: *National Academy of Sciences Proceedings*, v. 72, p. 5160-5163.
- Jackson, J.B.C., and Winston, J., 1982, Ecology of cryptic coral reef communities. I. Distribution and abundance of major groups of encrusting organisms: *Journal of Experimental Marine Biology and Ecology*, v. 57, p. 135-147.
- Jackson, J.B.C., Goreau, T.F., and Hartman, W.D., 1971, Recent brachiopod-coraline sponge communities and their paleoecological significance: *Science*, v. 173, p. 623-625.
- Kobluk, D.R., 1980, The record of cavity-dwelling (coelobiontic) organisms in the Paleozoic: *Canadian Journal of Earth Sciences*, v. 18, p. 181-190.
- Kobluk, D.R., and James, N.P., 1979, Cavity dwelling organisms in Lower Cambrian patch reefs from southern Labrador: *Lethaia*, v. 12, p. 193-218.
- Liddell, D.W., and Brett, C.E., 1981, A Devonian cryptofauna from Michigan: *Geological Society of America Abstracts with Programs*, v. 13, p. 497.
- 1982, Skeletal overgrowths among epizoans from the Silurian (Wenlockian) Waldron Shale: *Paleobiology*, v. 8, p. 67-78.
- Neumann, A.C., 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.
- Palmer, T.J., 1982, Cambrian to Cretaceous changes in hardground communities: *Lethaia*, v. 15, p. 309-323.
- Rasmussen, K.A., 1983, An ecologic and taphonomic analysis of submarine cave communities: Salt River Canyon, St. Croix, USVI [M.Sc. thesis]: Rochester, New York, University of Rochester, 148 p.
- Russ, G.R., 1982, Overgrowth in a marine epifaunal community: Competitive hierarchies and competitive networks: *Oecologia*, v. 53, p. 12-19.
- Schopf, T.J.M., 1978, Fossilization potential of an intertidal fauna: Friday Harbor, Washington: *Paleobiology*, v. 4, p. 261-270.
- Warme, J., 1975, Borings as trace fossils, and the processes of marine bioerosion, in Frey, R.W., ed., *The study of trace fossils*: New York, Springer-Verlag, p. 181-227.
- 1977, Carbonate borers—Their role in reef ecology and preservation: *American Association of Petroleum Geologists Studies in Geology*, v. 4, p. 261-279.

ACKNOWLEDGMENTS

Field work supported by National Oceanographic and Atmospheric Administration Grant NA 82AAA-01462 and a Sigma Xi Grant-In-Aid of Research. We thank the National Underwater Laboratory Systems-1 Hydrolab support group, especially Ivan Gill, Rod Catanach, W. David Liddell, and Stephen Palumbi, for their skills and discussion during mission No. 82-11. Ivan Gill was instrumental in the initiation of this research. Earlier drafts of this paper benefited from the comments of Curt Teichert and Joseph Carter. We also thank Margrit Gardner for her assistance.

Manuscript received October 25, 1984

Revised manuscript received April 19, 1985

Manuscript accepted April 26, 1985