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Author(s): DAVID L. RODLAND, MARCELLO G. SIMÕES, RICHARD A. KRAUSE, Jr. and MICHAŁ KOWALEWSKI

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STOWING AWAY ON SHIPS THAT PASS IN THE NIGHT: SCLEROBIONT ASSEMBLAGES ON INDIVIDUALLY DATED BIVALVE AND BRACHIOPOD SHELLS FROM A SUBTROPICAL SHELF

DAVID L. RODLAND,¹ MARCELLO G. SIMÕES,² RICHARD A. KRAUSE, JR.,³ AND MICHAŁ KOWALEWSKI⁴

¹Muskingum University, Department of Geology, 163 Stormont Street, New Concord, Ohio 43762, U.S.A.

²Instituto de Biociências, Universidade Estadual Paulista, Campus de Botucatu, Rubião Junior, Botucatu, C.P. 510, CEP 18618-970, São Paulo, Brazil

³Division of Invertebrate Paleontology, Peabody Museum of Natural History, Yale University, P.O. Box 208118, New Haven, Connecticut 06520, U.S.A.

⁴Florida Museum of Natural History, University of Florida, Gainesville, Florida 32611, U.S.A.

e-mail: drodland@muskingum.edu

ABSTRACT: This study evaluates encrustation and bioerosion of brachiopods (*Bouchardia rosea*) and bivalves (*Semele casali*) occurring on the inner shelf of the Southeast Brazilian Bight, accounting for differences in water depth, sediment type, host size, and time averaging. Frequencies of colonization covary across sites, but brachiopods are more frequently encrusted than bivalves at all sites, although this difference may disappear after standardization for shell size, depending on the chosen metric. Size selectivity during sclerobiont colonization appears to change as a function of their population density, rather than substrate differences between hosts. Sediment grain size and composition do not appear to exert environmental controls on encrustation or bioerosion, nor does either vary as a function of water depth alone. Radiocarbon-calibrated aspartic acid racemization dating of individual host valves shows similar age ranges and age structures for both hosts. Both epifaunal brachiopods and infaunal bivalves are colonized rapidly, within years to decades, with no further increase over millennial timescales. Rapid burial and sequestration from sclerobiont larvae is inconsistent with rapid postmortem exhumation and encrustation of infaunal bivalves, and indicates a brief temporal window for colonization. The relative abundance of sclerobionts is volatile over the time interval represented by dated valves, but temporal stability is seen in presence-absence data for epibiont and endobiont taxa. These results support the utility of taphonomic deployment experiments for investigating long-term patterns of hard-substrate colonization, but indicate careful consideration of host size is required for comparison of sclerobiont assemblages within or among taxa.

INTRODUCTION

Shell-encrusting and boring organisms (sclerobionts *sensu* Taylor and Wilson 2002) have an excellent fossil record, and preserve ecological information lacking in many soft-substrate fossil assemblages (e.g., Lescinsky 1997). In many fossil collections, sclerobionts act as stowaways, finding their way into museum drawers even when the collector has no interest in them. Because they live attached to their substrate and are not readily reworked, their spatial resolution is excellent (e.g., Lescinsky 1997). Temporal resolution of sclerobiont assemblages on individual valves can also be excellent, but pooled samples from multiple valves are subject to analytical time averaging and may artificially condense assemblages representing centuries or millennia of colonization, masking variations in productivity and recruitment (Rodland et al. 2006). Bored and encrusted shells of the same age and collected from the same setting serve as naturally occurring replicate samples of sclerobiont assemblages, preserving evidence of colonization from the same larval pool as their contemporaries. When exposed at the surface, these samples are ecosystems in miniature, with clearly defined areas, boundaries, and distinct microenvironments affected by shell structure, topography, and position relative to substrate and currents. Thus, a large amount of quantitative paleoecological data can be collected, analyzed statistically, and even modeled with computer simulations. As a result, sclerobionts provide opportunities to study competition within and among species, preferential settlement trends among larvae, faunal diversity, abundance, and biomass with greater resolution than soft-substrate benthic faunas typically allow (e.g., Jackson 1977).

In the fossil record, the encrustation of Paleozoic brachiopods is well documented (e.g., Richards 1972; Watkins 1981; Alexander and Scharpf 1990; Bordeaux and Brett 1990; Gibson 1992; Lescinsky 1997). In modern oceans, encrustation and bioerosion has been investigated using bivalve shells *in situ* (e.g., Best and Kidwell 2000a, 2000b) and studied in shell deployment experiments (e.g., Parsons-Hubbard et al. 1999, 2011; Lescinsky et al. 2002), but modern brachiopod sclerobionts have received less study (e.g., Rodland et al. 2004, 2006; Tomašových and Rothfus 2005; Tomašových and Zuschin 2009). Assessing the applicability of these modern, bivalve-oriented studies to the fossil record of Paleozoic rhynchonelliform brachiopods requires direct comparative studies using modern representatives. The Southeast Brazilian Bight provides a unique opportunity due to the co-occurrence of abundant bivalve and brachiopod populations on a modern tropical to subtropical shelf.

The superficial similarities of bivalve mollusks and rhynchonelliform (“articulate”) brachiopods are remarkable: both groups are typified by benthic filter-feeding organisms with two valves biomimicized with phases of calcium carbonate. In large part because of these similarities, the fossil records of bivalves and brachiopods have been the subjects of decades of comparative study. These comparisons cover many topics, including their distribution among different paleoenvironments (e.g., Olszewski and Patzkowsky 2001), functional morphology and biomechanics (e.g., Alexander 2001), diversification histories (e.g., Gould and Calloway 1980), susceptibility to potential causes of mass extinction (e.g., Knoll et al. 1996), drilling predation histories (e.g., Kowalewski et al. 2005; Simões et al. 2007), comparative taphonomy (e.g., Rodrigues 2006;

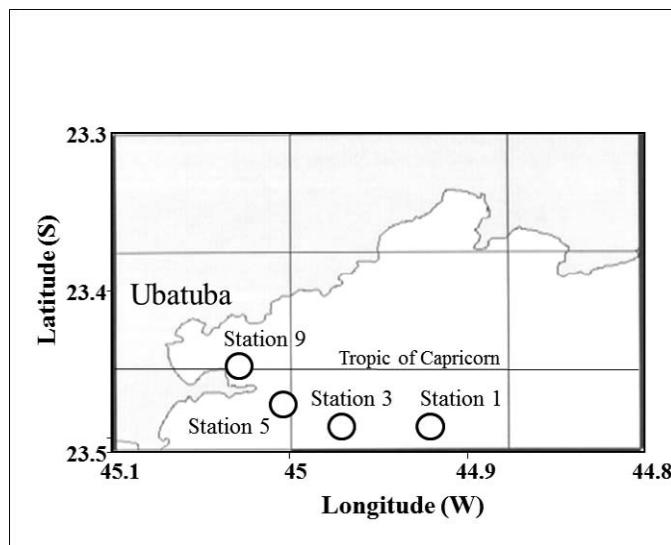


FIG. 1.—Map of the study area showing position of inner shelf sites and the abundance of brachiopods at each site. Adapted from figures generated using Generic Mapping Tools (Wessel and Smith 1998).

Simões et al. 2009; Rodrigues and Simões 2010), shell durability (e.g., Emig 1990; Daley 1993; Torello et al. 2002), and time averaging (e.g., Carroll et al. 2003; Krause et al. 2010; Kosnik et al. 2011).

Even controlling for host identity and paleoenvironment, encrustation and bioerosion patterns are likely to have changed through geologic time. There are many factors that might have influenced the geologic record of hard-substrate colonization, such as shifts in the relative abundance of brachiopod and bivalve hosts through time (e.g., Gould and Calloway 1980) and between environments (e.g., Olszewski and Patzkowski 2001), differences in host preservation potential (Cherns and Wright 2000; Wright et al. 2003), changes in encrusting faunas (e.g., Lescinsky 1997), or increasing nutrient availability through the Phanerozoic (Bambach 1993; Vermeij 1995). Consideration of encrustation patterns within paleoenvironmental and stratigraphic contexts should clarify the relative roles of such factors in the macroevolutionary history of epibionts.

The benthic fauna of the Southeast Brazilian Bight includes large numbers of rhynchonelliform brachiopods and bivalve mollusks, and represents a modern analog for tropical Paleozoic open marine fossil assemblages (Kowalewski et al. 2002). We present the results of a comparative study of the encrustation and bioerosion of the bivalve *Semele casali* and the brachiopod *Bouchardia rosea* collected from the same sites on the inner shelf. Patterns of spatial variability in brachiopod encrustation across these sites have been presented previously (Rodland et al. 2004) and provide spatial context for these analyses. Temporal context is provided by individual shell dating via radiocarbon and amino acid racemization (Krause et al. 2010). Unlike experimental taphonomic deployment studies, individually dated valves provide a temporal framework extending over centuries to millennia (e.g., Carroll et al. 2003; Rodland et al. 2006).

By utilizing naturally occurring shells collected from the same location, differences in encrustation patterns can be examined with respect to host-specific parameters such as shell size, mineralogy, life position, and taphonomic history. Life position and taphonomic history may impact colonization as infaunal bivalves must be exhumed (via storm currents, bioturbation, etc.) prior to settlement by sclerobionts, whereas epifaunal brachiopods are exposed to colonization continuously through life until burial. In addition, some effort must be made to evaluate and standardize for potential differences in shell size, both within and among host taxa.

This direct comparison provides a critical test to evaluate whether colonization frequency, sclerobiont abundance, and diversity differ substantially between naturally co-occurring subtropical brachiopods and bivalves. Such differences carry implications for the direct applicability of modern studies to ancient assemblages.

STUDY AREA

The specimens for this study were collected from four sites in near-coastal areas of the inner shelf of the Southeast Brazilian Bight, immediately to the south of the Tropic of Capricorn (Fig. 1). The study sites fall along a transect running from northwest to southeast, deepening from 10 to 30 m water depth toward the southeast, and include Ubatuba Stations 9, 5, 3, and 1. The study area and sampling protocol are discussed in detail elsewhere (Kowalewski et al. 2002; Simões et al. 2004).

Ubatuba Station 9 was the most extensively sampled site. Water depth at Station 9 is approximately 10 meters, and the sediment is primarily coarse quartz sand. Carbonate comprises 25% of the sediment by weight, while an additional 7% of the sediment is organic matter, probably derived from abundant leaves found in grab and dredge samples.

The next station offshore is Station 5, collected from a water depth of 20 meters. Coarse sand still predominates but carbonate composes only 17% of the sediment. Organic material is much less abundant; approximately 1% by weight. Station 3 was located at 25 meters depth, and unlike the others, the bottom sediments are primarily very fine sand. Carbonate composes only 1% of the sediment and organic matter accounts for an additional 2%. Station 1 occurs at a water depth of 30 meters, and like Stations 9 and 5, the sediment is primarily coarse sand; 25% of the sediment is carbonate and 3% organic matter by weight.

MATERIALS AND METHODS

Specimens of the terebratulid brachiopod *Bouchardia rosea* and the tellinid bivalve *Semele casali* were collected by Van Veen grab from four study localities, sieved from sediment with 2 mm mesh screens, and selected for radiometric and aspartic acid racemization dating (for details, refer to Kowalewski et al. 2002; Krause et al. 2010) (Fig. 2). This study incorporates 136 *S. casali* and 128 *B. rosea* valves from four study sites. Total sample sizes from each station are presented in Table 1, broken down by host identity. The maximum growth dimension (length) of each valve was measured to the nearest 0.1 mm using electronic calipers. The range of bivalve and brachiopod shell sizes found at each site is shown in Figure 3. While the range of sizes overlap considerably and pooled valve lengths do not differ significantly between brachiopods and bivalves using a Wilcoxon 2-sided test ($Z = -1.485, p = 0.138$), significant differences are observed between bivalves and brachiopods at Station 1 ($Z = 3.0784, p = 0.0021$), Station 3 ($Z = 5.011, p < 0.0001$), and Station 5 ($Z = -4.9143, p < 0.0001$).

In order to standardize encrustation measurements as a function of shell surface area, twenty specimens of varying length were selected to construct a length-area model, evenly divided between taxa. Most dimensional measurements of size correlate with maximum valve length, making it a simple metric invoking few additional assumptions about shell size. For *S. casali*, both left and right valves were selected, while dorsal (brachial) and ventral (pedicle) valves were measured separately for *B. rosea*. Surface area measurements were obtained for both interior and exterior surfaces by impressing a mold of each valve on a piece of plastic wrap draped over modeling clay, and tracing the outline of the valve on the plastic wrap with a fine felt-tip pen. The plastic wrap was then extricated and the area within the outline measured by hand, counting intersections on 1 mm \times 1 mm graph paper. Interior, exterior, and total surface areas for each valve were graphed in relationship to measured valve length, and a variety of regression models were explored

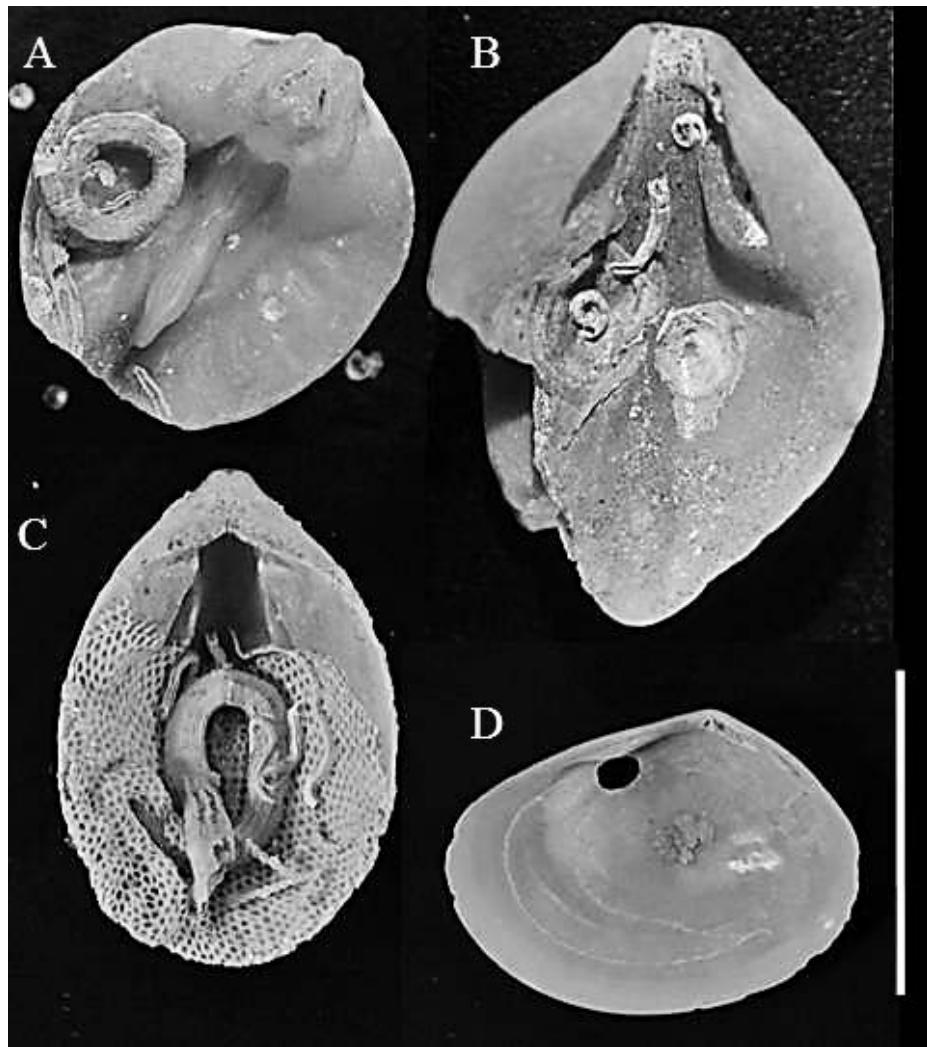


FIG. 2.—Encrusted examples of *Bouchardia rosea* and *Semele casali*. Scale bar = 1 cm. A) *B. rosea*, dorsal (brachial) valve. B, C) *B. rosea*, ventral (pedicle) valves. D) *S. casali*, right valve.

to determine the best fit equation relating length to area for each valve type. These equations were used to approximate surface area for all other valves in this study.

Commonly used encrustation and bioerosion metrics range from the area percent cover of a host (e.g., Lescinsky et al. 2002), to colonization frequency (e.g., Rodland et al. 2004), to the number of sclerobionts per unit area (e.g., Bordeaux and Brett 1990). Colonization frequency (the fraction of sampled valves colonized by sclerobionts) and area percent cover are emphasized in studies of host taphonomy that focus on the degree of alteration of the original shell, but when coupled to measurements of shell size, area metrics may also provide an estimate of epibiont biomass. In contrast, abundance and diversity metrics are often favored for paleoecological studies of sclerobionts. This study employs abundance (the number of sclerobionts on a valve) and diversity (generic richness; the number of different genera per valve) as they are easy to count and contain a wealth of ecological information. Abundance is distinct from areal cover measurements in that it does not address the relative size of individuals, nor their success in competitive interactions. Abundance also differs from colonization frequency insofar as the percentage of shells colonized provides no insight into the number of colonists. Instead, abundance relates to the number of colonization events during the exposure history of the valve under consideration.

Each specimen was examined under a binocular dissecting microscope (capable of up to 70 \times magnification) to evaluate the sclerobiont fauna,

and each sclerobiont was assigned a morphotype that was later identified to genus level when possible (Appendix 1, see Acknowledgments). The position and abundance of each genus was recorded, and used to compute the overall taxonomic richness for each valve. To keep diversity estimates conservative, if preservation did not allow genus-level identification, it was only included in estimating taxonomic richness for that valve if there were no other representatives of the same higher taxon present. As an example, all unidentifiable bryozoan colonies on a valve were considered to belong to one of the identified bryozoan genera for diversity estimates, unless none of them could be identified. In that case, all unidentified colonies were grouped together as one bryozoan genus of unknown identity. For evaluating abundance, unidentifiable taxa were always considered as individuals of one unidentified genus within the appropriate higher taxon.

In computing abundance, the focus is on the number of epibiont larvae which successfully colonize the substrate, without regard to biomass. Because of the focus on colonization and larval arrival, colonial organisms are regarded as single individuals, while multiple colonies on a valve are counted as separate individuals. In this sense, colonial organisms are simply treated as modular, iterative organisms. Sclerobiont abundance may be a proxy for productivity (e.g., Bambach 1993), but the precise interplay between encrustation and various measures of productivity requires further investigation.

In order to assess the effect of time averaging upon sclerobiont communities colonizing *S. casali* and *B. rosea*, encrustation and

TABLE 1.—Sclerobiont abundance and valve abundance at each site.

	Station 1	Station 3	Station 5	Station 9	All stations
# of shells					
<i>Bouchardia rosea</i>	32	40	15	41	128
<i>Semele casali</i>	30	25	43	38	136
combined	62	65	58	79	264
# encrusted					
<i>Bouchardia rosea</i>	27	30	13	41	111
<i>Semele casali</i>	10	17	16	34	77
combined	37	47	29	75	188
% encrusted					
<i>Bouchardia rosea</i>	84.4	75	86.7	100	86.7
<i>Semele casali</i>	33.3	68	37.2	89.5	56.6
combined	59.7	72.3	50	94.9	71.2
# epibionts					
<i>Bouchardia rosea</i>	58	141	41	317	557
<i>Semele casali</i>	27	59	50	209	345
combined	85	200	91	526	902
# bioeroded					
<i>Bouchardia rosea</i>	30	35	14	35	114
<i>Semele casali</i>	28	21	3	7	59
combined	58	56	17	42	173
% bioeroded					
<i>Bouchardia rosea</i>	93.8	87.5	93.3	89.7	89.1
<i>Semele casali</i>	93.3	84	6.98	18.4	43.3
combined	93.5	86.2	29.3	53.2	65.5
# endobionts					
<i>Bouchardia rosea</i>	52	63	15	67	197
<i>Semele casali</i>	29	26	3	9	67
combined	81	89	18	76	264
mean epibiont abundance per valve					
<i>Bouchardia rosea</i>	1.81	3.53	2.73	7.73	4.35
<i>Semele casali</i>	0.9	2.36	1.16	5.5	2.54
combined	1.37	3.08	1.57	6.66	3.42
mean epibiont abundance per encrusted valve					
<i>Bouchardia rosea</i>	2.15	4.7	3.15	7.73	5.02
<i>Semele casali</i>	2.7	3.47	3.13	6.15	4.48
combined	2.3	4.26	3.14	7.01	4.8
mean endobiont abundance per bored valve					
<i>Bouchardia rosea</i>	1.73	1.8	1.07	1.91	1.73
<i>Semele casali</i>	1.03	1.24	1	1.29	1.14
combined	1.4	1.59	1.06	1.81	1.53

bioerosion were evaluated using a subset of 146 individually dated valves. The age of these valves was determined using radiocarbon-calibrated aspartic acid racemization (for full details see Krause et al. 2010). A total of 69 specimens were selected from Station 1 (37 bivalves, 32 brachiopods) and 77 specimens from Station 9 (38 bivalves, 39 brachiopods), for a total of 75 bivalves and 71 brachiopods. Ages determined for each valve apply only to the host, and not the sclerobiont community, but this data makes it possible to evaluate changes in the encrustation and bioerosion of valves over time, and assess how much time is required for maximum abundance and diversity to stabilize (Rodland et al. 2006).

RESULTS

Host Valve Size

Observed valve sizes occupied similar ranges for both brachiopods and bivalves among the studied sites regardless of sediment grain size or water depth (Appendix 1). The size range observed for *S. casali* and *B. rosea*

overlaps extensively at each station, but *S. casali* is, on average, slightly longer at each site except Station 9 (Fig. 3). Valve surface area is correlated with valve length, but different correlations apply for each species due to differences in valve morphology. Because of this, greater total surface area is provided by sampled specimens of *B. rosea* at each site, except for Station 3 (Table 2). Given that bivalve and brachiopod valves of equal lengths have dissimilar surface area, maximum valve length may not be the most appropriate estimator of size.

Colonization Frequency

A total of 902 epibionts colonized 188 out of 264 valves examined from four stations, for an overall encrustation frequency of 71.2% (percent of valves encrusted) and a mean abundance of 3.42 epibionts per shell. However, a great degree of heterogeneity is present in the data, as can be seen in Table 1. Bivalves are encrusted less frequently than brachiopods collected from the same sites (Fisher's exact test, $p < 0.001$), but similar spatial patterns are observed: shells are encrusted most frequently at the nearshore Station 9 and less frequently offshore. Higher encrustation

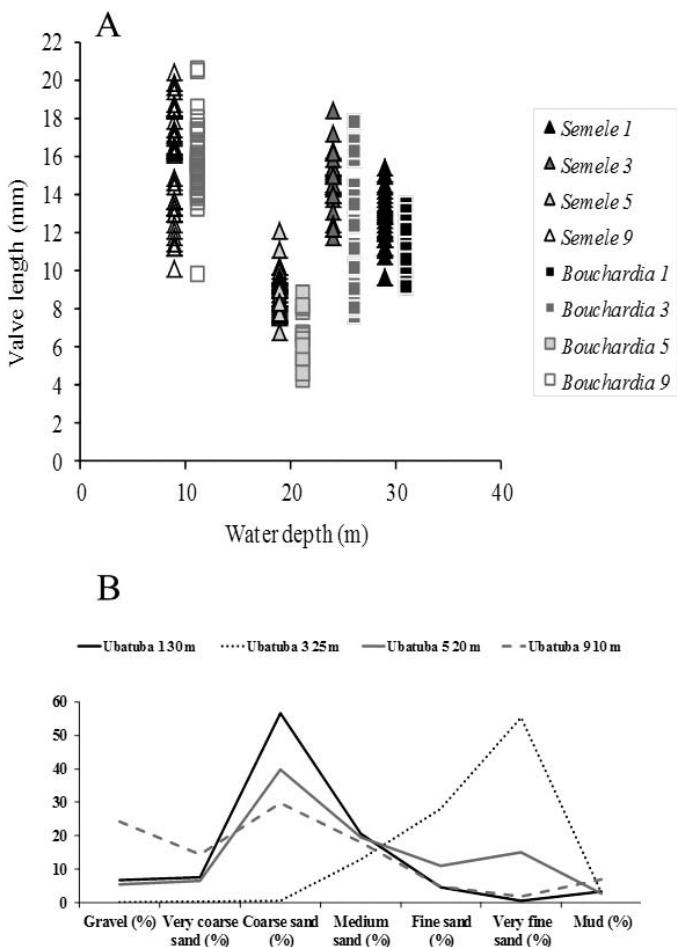


FIG. 3.—Grain size per site. A) Host valve length measured along maximum axis, plotted versus water depth. B) Sediment grain size distribution per site.

frequencies and epibiont abundance were observed on *B. rosea* than *S. casali* (Table 1, Fig. 4). Valve interiors are preferentially encrusted for all hosts except *S. casali* at Station 9 (Fig. 5). Figure 6 plots the mean shell size for each site against various measures of encrustation. Encrustation frequency increases with increasing size, and *B. rosea* is encrusted at higher frequencies than *S. casali*.

Similar results were obtained for the smaller subset of individually dated valves from Station 1 and Station 9. Every specimen of *B. rosea* was colonized by epibionts at the 10-m-depth Station 9 (100% encrustation frequency), compared to 84.4% for *S. casali*. The difference was more pronounced at Station 1, with 84.5% encrustation frequency observed for *B. rosea* while only 33.3% of *S. casali* were colonized. For individual clades of encrusters, the difference is more stark: at Station 9, brachiopod encrustation frequencies for polychaetes reached 84.6% and bryozoans were nearly ubiquitous at 97.4%, while only 21.9% of bivalves were colonized by either group. Station 1 results were similar: brachiopod encrustation frequencies reached 65.8% for bryozoans and 47.4% for polychaetes, but only 6.67% of bivalves were encrusted by either bryozoans or polychaetes. Overall, serpulids and bryozoans represented a greater proportion of the fauna colonizing *B. rosea*, while spirorbids, cirripedes, algae, and other taxa played a larger role on *S. casali*.

In contrast to encrustation frequencies, the highest frequencies of bioerosion were observed at the deepest water site, Station 1. For *B. rosea*, bioerosion frequencies remained in the range of 93.8%–87.5% across all four sites, but *S. casali* showed a generally decreasing trend toward shallow

waters except for Station 5, where only 3 specimens were bioeroded. The boring sponge *Cliona* was the most common endobiont for each population except Station 1 brachiopods, where *Caulostrepsis* borings produced by *Polydora* were more common, as were pits and microborings of unknown affinity. *Caulostrepsis* was not observed on *S. casali*.

Abundance

The number of sclerobionts present varies among sites, with the majority of epibionts colonizing either brachiopods or bivalves collected from Station 9, and decreasing in abundance offshore. This is not simply a sample-size bias: more than twice as many epibionts were counted at Station 9 than at Station 3, despite the two stations having nearly identical host numbers. However, this decrease was not uniform, as Station 5 (at 20 meters) has far fewer encrusters than Station 3 (at 25 meters), and less than Station 1 (at 30 meters).

Brachiopod encrusters are more abundant than bivalve encrusters at all sites except Station 5, where *S. casali* specimens outnumber *B. rosea* by nearly 3:1, and mean epibiont abundance per shell is greater for brachiopods than for bivalves at all sites (Wilcoxon two-sided test, $Z = 5.659$, $p < 0.0001$). The abundance of epibionts increases with valve surface area in a consistent manner for each site, whether plotted as the absolute number of epibionts, the number per shell, or the number per encrusted shell (Fig. 6).

In order to further evaluate the relationship between valve size at each station and measures of encrustation, data was pooled from all sites for size trend analyses. The wide scatter in this dataset is not unexpected: the number of epibionts landing on a shell should have a random component, but abundance should be proportional to valve area and time exposed at the sediment–water interface (SWI). Another complicating factor in analyzing epibiont abundance is the gregarious settlement tendencies of some taxa. Serpulids and foraminifera appear to be gregarious, and account for much of the variation in epibiont abundance. A weak increase in the mean abundance for a given size class can be seen for both *B. rosea* and *S. casali*, although the small number of samples at the upper and lower extremes of the size range may bias this pattern (Fig. 6B).

Because sclerobionts are not evenly distributed among valves collected at each site, variation in colonization frequency (either between sites or among taxa) influences estimates of abundance. Among individually dated valves from Stations 1 and 9, *B. rosea* demonstrates a higher pooled number of epibionts (58 and 302 epibionts, for a mean value of 1.81 and 7.74 per valve collected, respectively) than *S. casali* (28 and 210 epibionts, for mean values of 0.93 and 5.53 per valve collected, respectively). However, infaunal bivalves are less exposed to colonization than epifaunal brachiopods, and these metrics are therefore influenced by encrustation frequency. Comparison of mean values per valve for all potential hosts evaluates overall availability for colonization as well as potential host preferences among colonists. Comparisons of sclerobiont abundance must be restricted to colonized valves in order to address host preferences independently from differences in host colonization frequency. In contrast to the results above, mean epibiont values per colonized valve (those hosting one or more epibiont) at each site do not show a uniform preference: mean epibiont abundance per colonized valve is higher for *S. casali* than *B. rosea* at Station 1 (2.80 versus 2.15) but reversed for Station 9 (6.18 versus 7.74 respectively), and neither is significantly different from the combined values for both taxa. Despite low encrustation frequencies for *S. casali* at Station 1 (33.3%), when they are colonized, they achieve higher population densities per valve than for *B. rosea* at this site, but as data on epibiont size was not collected, it is not possible to determine whether this difference is driven by differences in the mean size of colonists of either host species.

For endobiont abundance, when only bioeroded shells are considered, the average number of endobionts per brachiopod ranges from 1.91 at

TABLE 2.—Host size and encrustation metrics, per site. All area measurements are in mm², estimated from length-area models derived independently for each species.

	Station 1	Station 3	Station 5	Station 9	All stations
Mean valve area					
<i>Bouchardia rosea</i>	305	254	135	500	331
<i>Semele casali</i>	203	282	106	351	229
all shells	256	264	114	428	279
Pooled valve area per site					
<i>Bouchardia rosea</i>	9,760	10,160	2,025	20,500	42,368
<i>Semele casali</i>	6,090	7,050	4,558	13,338	31,144
all shells	15,872	17,160	6,612	33,812	73,656
Valve area available per epibiont					
<i>Bouchardia rosea</i>	168	72	49	65	76
<i>Semele casali</i>	226	119	91	64	90
all shells	187	86	73	64	82
Pooled area, encrusted shells					
<i>Bouchardia rosea</i>	8,235	7,620	1,755	20,500	36,741
<i>Semele casali</i>	2,030	4,794	1,696	11,934	17,633
all shells	10,265	12,414	3,451	32,434	54,374
Valve area per epibiont, encrusted shells					
<i>Bouchardia</i>	142	54	43	65	66
<i>Semele</i>	75	81	34	57	51
all shells	121	62	38	62	60
Mean epibiont density per cm ²					
<i>Bouchardia rosea</i>	0.59	1.39	2.02	1.55	1.31
<i>Semele casali</i>	0.44	0.84	1.1	1.57	1.11
all shells	0.54	1.17	1.38	1.56	1.22
Area ratio (<i>Semele/Bouchardia</i>)	1.34	1.66	1.85	0.99	1.19
Area ratio, encrusted shells (S/B)	0.53	1.5	0.79	0.88	0.77
Epibiont abundance ratio (S/B)	0.47	0.42	1.22	0.66	0.62

Station 9 to 1.07 at Station 5, while bivalves range from 1.29 to 1.00 endobionts per shell respectively. In all cases, *S. casali* endured lower measures of bioerosion at each site than co-occurring *B. rosea*.

Diversity

Brachiopod and bivalve shells vary significantly between one another and among the studied sites in terms of the composition and diversity of sclerobiont assemblages (Table 3). Comparison of the abundance structure of epibionts at class level taxonomic resolution (numbers of polychaetes versus bryozoans versus bivalves, etc.) between *S. casali* and *B. rosea* shows significant differences in encrusting faunas (Chi square test, 7 degrees of freedom, χ^2 value = 355, $p < 0.0001$). By contrast, endobiont assemblages were limited to the drilling trace *Oichnus*, borings of the polychaete *Polydora*, the sponge *Cliona*, and microborings of uncertain affinity. The most diverse epibiont assemblage was found at Station 9, followed by Station 3. A total of 30 epibiont genera were identified across these four sites: seven were observed only on *B. rosea*, while three were only seen on *S. casali*. A larger number of epibiont genera occur on brachiopods at each site. Of these, some taxa show distinct preferences: anomiid bivalves were much more common on *B. rosea*, while barnacles were more common on *S. casali*, although potential causes for these preferences remain unexplored.

Epibiont diversity (richness) appears to show trends correlating with measures of valve size (Fig. 6). While the mean diversity of epibionts on *S. casali* is lower than the mean diversity encrusting *B. rosea* for any given length (Fig. 7), diversity increases at the same rate as a function of calculated surface area for both hosts. Mean epibiont species richness for any given size class increases as a power function of valve length, consistent with the apparently linear trend seen relative to surface area.

Taphonomy and Age Structure

Most epibiont taxa observed in this study exhibit a preference toward cryptic habits, settling on concave or grooved surfaces (with some exceptions; for example, barnacles were not observed on shell interiors). As a result, valve interiors are colonized much more frequently than valve exteriors (Fig. 5). As these surfaces are not exposed during the life of the animal, these events reflect postmortem colonization. Bivalve exteriors are colonized more frequently than interiors only at one location: Station 9, where epibionts are most abundant and diverse. Brachiopod valve interiors are encrusted more often than valve exteriors at each of the four sites in this study.

Age spectra for each site and species have been reported previously, with both taxa showing incomplete and typically right-skewed age distributions, ranging up to 8118 years for *B. rosea* and up to 4437 years for *S. casali* (for detailed discussion, see Krause et al. 2010). No significant trends were identified in host size over the time period represented (Fig. 8), nor in epibiont abundance or diversity (Figs. 9–10). *S. casali* records mean host ages of 1063 years at Station 1 and 972 years at Station 9, while mean host ages determined for *B. rosea* were 4299 years (Station 1) and 1064 years (Station 9) respectively. The median ages were typically lower: at Station 9, median valve ages ranged from 100 years for *S. casali* to 544 years for *B. rosea*, while at Station 1, the median for *S. casali* was 797 years, compared to 4911 years for *B. rosea*—the only case where a median exceeded the mean. The majority of encrustation occurred before the mean or median age of host valves: at Station 9, 50% of epibiont abundance occurs on *B. rosea* 650 years old or less, and on shells dated to the past 79 years for *S. casali*. At Station 1, 50% of epibionts occur on *B. rosea* valves 3990 years old or less, and 157 years or less for *S. casali*. When compared to mean host valve age, only three

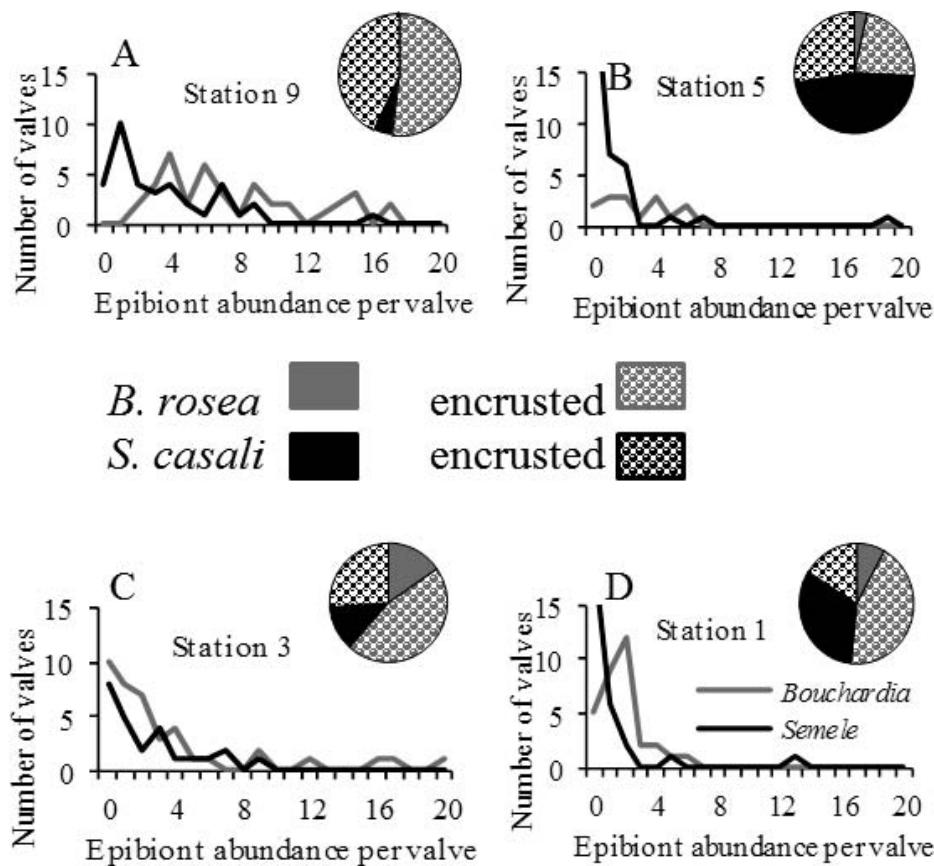


FIG. 4.—Encrustation frequency and epibiont abundance (plotted as frequency distributions) for each station. Black lines represent the number of bivalves encrusted for any given number of epibionts, while gray lines represent the number of brachiopods encrusted. Pie charts indicate the proportion of bivalves (black) and brachiopods (gray) in each sample, and the frequency of encrustation for each (patterned wedges). A) Station 9: 10 m water depth. B) Station 5: 20 m water depth. C) Station 3: 25 m water depth. D) Station 1: 30 m water depth.

additional epibionts out of a total of 28 accrue onto older specimens of *S. casali* at Station 1, and only 30 additional specimens accrue (of 210) to older bivalves from Station 9. The same is seen for *B. rosea* at Station 9: 116 of 302 specimens (38.4%) accumulate on valves older than the mean, although at Station 1, 28 out of 58 epibionts (48%) are found on older hosts. In a similar vein, 24 of 28 epibionts on *S. casali* encrust valves below the median age of their hosts at Station 1, and 142 of 210 (67.6%) at Station 9 occur on valves below the median host age. For *B. rosea*, 34 of 58 (58.6%) of encrusters colonize hosts below the median age at Station 1, but at Station 9, 119 of 302 (39.4%) epibionts occur on valves below the median host age, and 60.6% on valves older than the median.

DISCUSSION

Sediment Characteristics

The grain size and character of sediment at each site may influence the abundance of sclerobionts and the resulting patterns of encrustation and bioerosion. Fine mud may impede feeding and respiration in filter feeding benthos, clogging gills and lophophores, and thus limiting the survival potential of both hosts and epibionts. Sediment composition may also play a role. On the outer shelf, *B. rosea* is only found on sediments composed of more than 40% carbonate by weight (Kowalewski et al. 2002). In addition, the presence of dissolved organic matter may influence local productivity or even serve as a subsidiary source of nutrition. Brachiopods, at least, can absorb dissolved organic matter directly through the lophophore (McCammon 1969; Steele-Petrovic 1976), and

similar nutrient uptake might be favored by bryozoans. None of these potential influences seems to relate directly to the abundance of epibionts at each site, although Station 9 is characterized by a higher percentage of organic matter in the sediment. Finer grained sediments occur only at Station 3, characterized by intermediate encrustation frequencies. The sediment size and composition at Station 9 and Station 1 are nearly

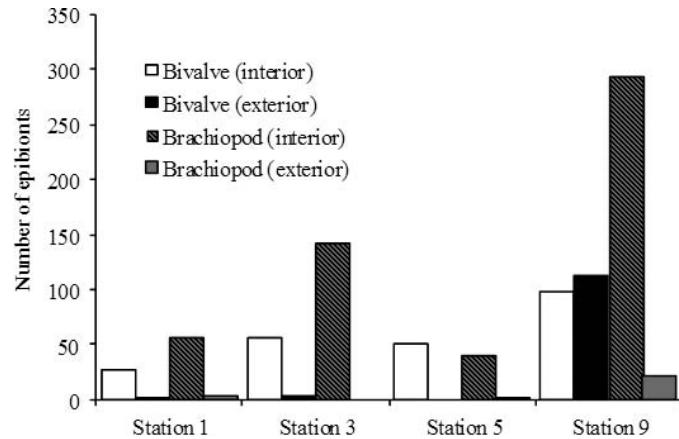


FIG. 5.—Total epibiont abundance as a function of sample location for both *B. rosea* and *S. casali*, with interior and exterior surfaces plotted independently for each.

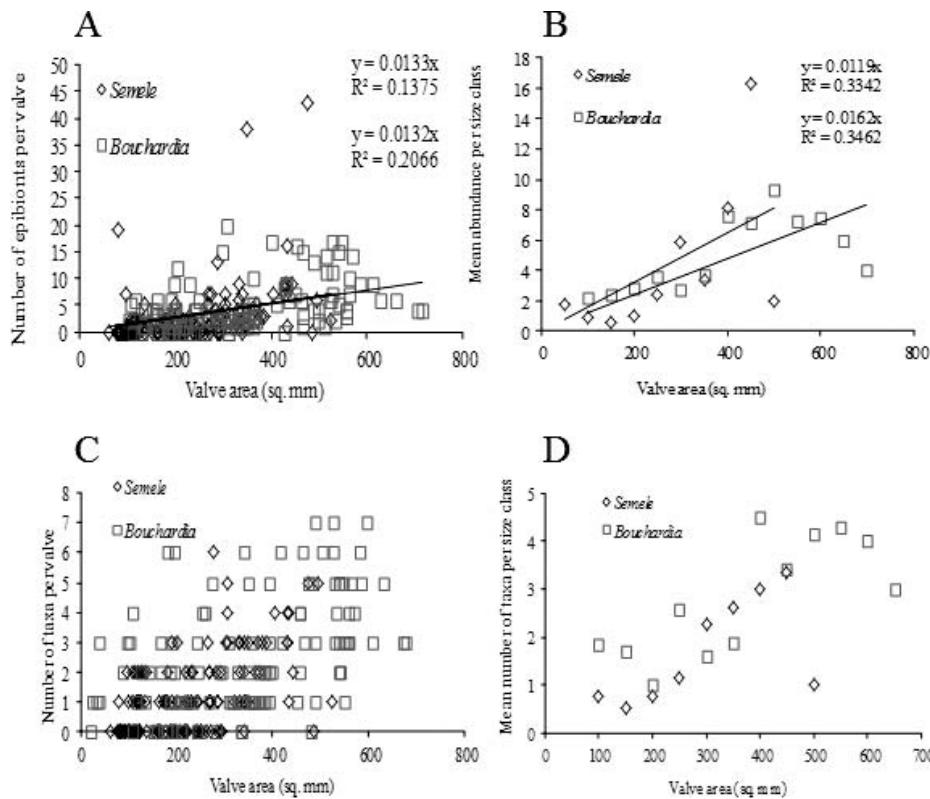


FIG. 6.—Measures of encrustation at each station, plotted as a function of modeled valve area. A) Epibiont abundance. B) Mean epibiont abundance per valve, plotted independently per size class. C) Epibiont diversity (species richness). D) Mean richness per valve, plotted independently per size class.

identical, so variations in epibiont and endobiont assemblages must reflect environmental parameters other than sediment alone.

Colonization Frequencies

Encrustation frequencies may vary greatly between brachiopod genera collected from the same sedimentary units (e.g., Alexander and Scharpf 1990; Bordeaux and Brett 1990) or from the same sites in modern oceans (e.g., Rodland et al. 2004). However, there has been little work done to compare encrustation and bioerosion of co-occurring bivalves and brachiopods. While the results reported here are limited to two genera, they demonstrate differences in hard-substrate faunas on naturally co-occurring shells representing equivalent size and temporal ranges. Caution is required in interpretation of these results, as these differences among host taxa may reflect differences in surface area or burial history rather than indicating substrate selectivity.

B. rosea is unusual for modern rhynchonelliform brachiopods in that it is free-living on soft substrates, and may be epifaunal to semi-infaunal. The posterior portion of the dorsal (brachial) valve is heavily calcified, counterweighting the shell so that the commissure is elevated above the substrate, and its pedicle can push the animal forward by retracting and extending from the foramen, using its projecting branches as a ratchet to push against the sediment (Richardson 1997; Simões et al. 2007). Like other articulate brachiopods, *B. rosea* is a suspension feeder. By contrast, the bivalve *S. casali* is infaunal, feeding from suspended food particles as well as from nearby surface sediments using an extensible siphon. While *B. rosea* is less resistant to abrasion than many bivalves (Torello et al. 2002), it is robust with respect to compaction: anecdotally, a few valves showed damage after airmail shipment, but samples of the thin-shelled bivalve *S. casali* shipped in identical packaging suffered a fragmentation rate of 100% (see Flessa et al. 1992, for similar work on postcollection taphonomy).

TABLE 3.—Epibiont diversity at each site.

	Station 1	Station 3	Station 5	Station 9	All stations
# epibiont taxa					
<i>Bouchardia rosea</i>	11	13	9	26	27
<i>Semele casali</i>	5	9	6	17	20
mean # epibiont taxa per valve					
<i>Bouchardia rosea</i>	1.37	1.78	1.80	4.22	2.46
<i>Semele casali</i>	0.50	1.44	0.53	2.11	1.13
mean # epibiont taxa per encrusted valve					
<i>Bouchardia rosea</i>	1.63	2.37	2.08	4.22	2.84
<i>Semele casali</i>	1.50	2.12	1.44	2.35	2.00

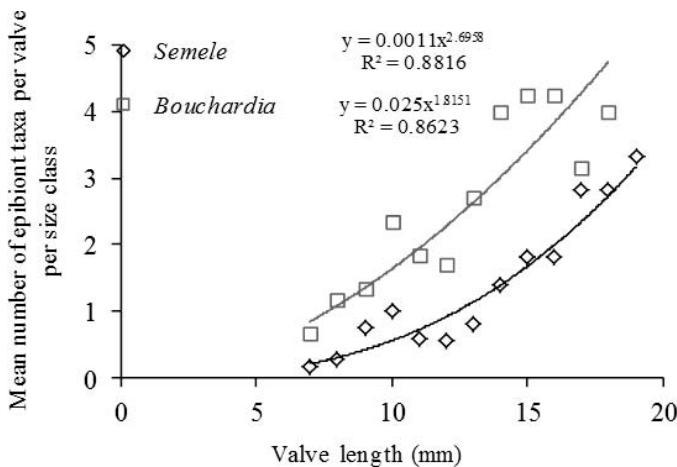


FIG. 7.—Mean epibiont richness per size class plotted as a function of valve length rather than surface area. Mean epibiont richness values per size class show strongest correlation with power functions of valve length: for *Bouchardia* ($y = 0.025x^{1.8151}$) and for *Semele* ($y = 0.0011x^{2.6958}$).

For individually dated shells, epibionts colonized *B. rosea* more frequently (87%) than *S. casali* (57%). While these results may reflect epibiont selectivity on the basis of host mineralogy or similar factors, differences in life habit and exposure history must be considered. The epifaunal brachiopod *B. rosea* is exposed during life and may remain above the sediment–water interface postmortem if not buried, while the infaunal bivalve *S. casali* can only be colonized after it is exhumed from the sediment by currents, wave action, bioturbation, or other mechanisms. Because buried valves of *B. rosea* are subject to the same mechanisms of exhumation, the brachiopod has a greater exposure potential, even though most encrustation takes place after the death of the host.

As colonization occurs only at the sediment–water interface, total colonization frequencies (the percentage of potential hosts colonized by any sclerobiont) for *S. casali* provide an estimate of the minimum percentage of valves exhumed postmortem. Changes in colonization frequency for host valves as a function of host age may then be used to evaluate exhumation rates over time. On a similar note, the difference in colonization frequencies between infaunal and epifaunal taxa may be used as an estimate of the proportion of infaunal valves that are never exhumed, if all other factors are equal. In combination with estimates of siphon length and depth of life position, the minimum depth and frequency of reworking events within the taphonomically active zone (TAZ) may be evaluated. Given the size range evaluated in this study, *S. casali* was likely restricted to the uppermost 5 cm of the TAZ.

While encrustation frequencies for both hosts were higher in shallow water, the results differ for endobionts. Except for Station 5, endobiont colonization of *B. rosea* remains relatively constant across the depth spectrum, while a general preference is observed for colonization of *S. casali* in deeper settings. The boring polychaete *Polydora* appears limited to *B. rosea*, as its associated trace *Caulostrepis* was not observed on *S. casali*. *Polydora* is known to colonize the anterior margins of *B. rosea* during life, acting as a kleptoparasite (Rodrigues et al. 2008), but the infaunal habit of *S. casali* may deter colonization in life.

The sclerobiont colonization frequency (percentage of shells colonized by either encrusting or boring taxa) observed for *S. casali* at each site serves as a minimum estimate of the frequency of exhumation, as postmortem colonization of infaunal taxa occurs at the sediment–water interface. Given the age of each valve, frequencies can then be turned into rates (colonization events per unit time). Within the age spectra of local shells, a minimum of 89.5% of all valves at Station 9 were exhumed by

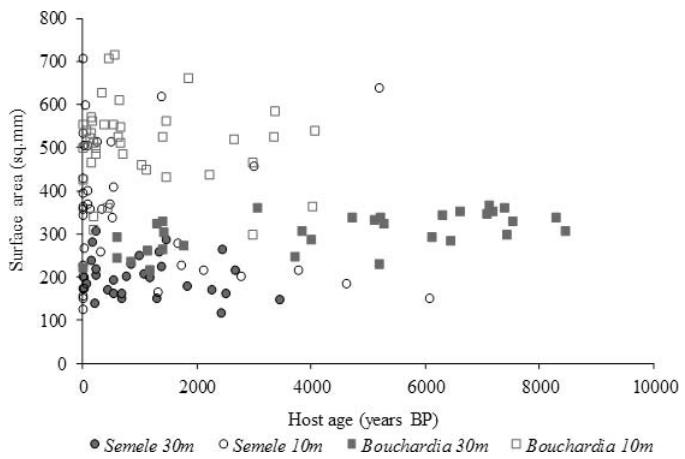


FIG. 8.—The relationship between host valve size and calibrated age.

bioturbation, predation, storms or currents, as indicated by encrustation frequency, and a minimum of 93.3% of shells were exhumed in the deeper water Station 1, given the frequency of bioerosion. For Station 9, the infaunal bivalve *S. casali* has an 89.5% colonization frequency (and thus a 10.5% chance of remaining buried after death), while every specimen from Station 1 was either bioeroded or encrusted, if not both. While it has long been established that many marine shell beds are well mixed from a perspective of time averaging (e.g., Carroll et al. 2003), the high frequency of recent infaunal bivalves colonized by sclerobionts after death confirm that physical mixing of shells occurs between the sediment surface and subsurface within timescales of decades to centuries.

Station 9 is likely to experience higher wave energy, more frequent storm events, and thus a deeper taphonomically active zone below the sediment–water interface, compared to the deeper-water Station 1. However, the observed frequency of colonization by endobionts suggests that the frequency of exhumation varies in site-specific microenvironmental factors other than just water depth, or proximity to shore. Borings at Station 1 indicate that the vast majority of shells experienced postmortem exhumation and exposure to surface currents, despite the lower encrustation frequencies observed for both host species. This may reflect a preference for shallow water among epibiont taxa or for slightly deeper waters among endobionts, or may indicate competitive displacement between the two groups. Shallower, warmer waters are likely to host larger plankton concentrations and thus provide more food for suspension-feeding sclerobionts, while colder waters would favor lower metabolic rates and lower carbonate saturation states, which could make bioerosion more efficient than carbonate secretion.

The limited percentage of bored bivalve shells from Station 9, compared to the high percentage encrusted (18.4% versus 89.5%), is difficult to interpret, although it may reflect a degree of competitive exclusion. Duration of exposure might play a role, as infaunal bivalve shells might remain in the sediment for extended periods before exhumation and exposure to colonization. However, this is probably not the case here. While the youngest bivalve demonstrating bioerosion at Station 9 was dated to 313 years BP (21 of the 38 dated valves from this site were younger), 20 out of 67 brachiopod endobionts from Station 9 were observed in the same age range.

Difficulties with radiocarbon calibration make it impossible to determine the ages of the most recent specimens definitively, beyond postdating the onset of widespread atmospheric nuclear bomb testing, but soft tissues associated with epibionts in some specimens suggest that some of these were live collected. Exhumation and colonization may occur within years or decades: 9 out of 12 specimens of *S. casali* from Station 9

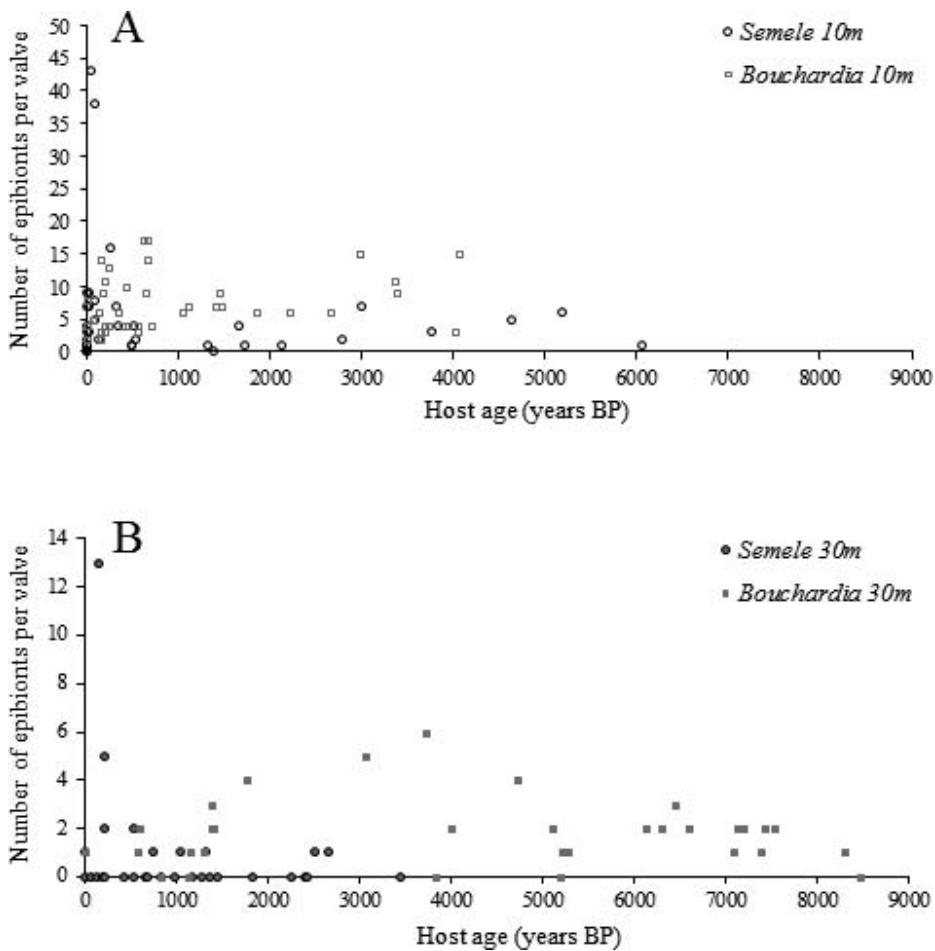


FIG. 9.—The relationship between epibiont abundance and calibrated age. A) Station 9: 10 meters water depth. B) Station 1: 30 m water depth.

dated to the time of collection were colonized by a total of 29 epibionts (encrustation frequency: 75%). Only one specimen of *S. casali* from Station 1 was dated to the time of collection, but it was also colonized by a single epibiont. Given the temporal structure of the sample, observed differences in sclerobiont colonization frequency between *S. casali* and *B. rosea* may have less to do with taphonomic history, and owe more to differences in the life position of the host.

Abundance and Diversity

The diversity and number of sclerobionts present on brachiopods and bivalves varies significantly among all the sites studied. Variation in encrustation at each site appears to be controlled primarily by the size of shells available to colonize at each site, rather than due to sediment composition, water depth, or other environmental factors. Even though the same shell size range is occupied by both *S. casali* and *B. rosea* at each site, the difference in surface area between bivalves and brachiopods of equal length produce differences in encrustation patterns despite similar rates of colonization per valve and similar host-valve age structures.

Area available for colonization plays an important role in the regulation of diversity in the theory of island biogeography (e.g., MacArthur and Wilson 1967). Greater surface area increases the chance of settlement and reduces the possibility of extinction through competition or predation. When calculated surface area is plotted versus epibiont abundance per valve, both *B. rosea* and *S. casali* plot within the same field, and linear regressions plotted through the origin yield practically identical slopes (*B. rosea* $y = 0.0132x$, $r^2 = 0.2066$; *S. casali* $y = 0.0133x$, $r^2 = 0.1375$). Total shell area per site (the mean valve size per site multiplied by the number of

shells at that site) provides similar results. By dividing this proxy by the number of epibionts at each station, the mean area occupied by each epibiont can be found (this is the inverse of epibiont population density). By this measure, *B. rosea* is the preferred substrate for epibionts at all stations except Station 9, where the two host species are equivalent. Colonists of *S. casali* have half the population density of epibionts on *B. rosea* (Table 2), and *B. rosea* demonstrates greater diversity per valve when surface area and colonization frequency are taken into account (Table 3).

This estimate assumes similar exposure histories, but may be biased by the infaunal life habits of *S. casali*. Again, as with epibiont frequency distributions above, this problem can be circumvented by restricting consideration to encrusted shells. The assumption here is that any shell that is encrusted at least once has had the same exposure to colonization that any other encrusted shell has had. An estimate of the shell surface area colonized by epibionts can be derived for both hosts at each site by multiplying the surface area available for each shell per site by the encrustation frequency for each site.

Estimates from each site except Station 3 support a preference for colonizing *B. rosea*: overall, encrusters of *S. casali* have 1.29 times the surface area available than epibionts have on *B. rosea*. Complications stemming from the partial burial or exhumation of a shell have not been investigated, but are worth future consideration.

Epibionts may be sensitive to fundamental differences that exist between *S. casali* and *B. rosea*, beyond taphonomic history and other environmental factors. Three main differences probably affect epibiont colonization patterns. For one, the mineral composition of a valve may affect the ability of epibionts to attach their own exoskeletons to the substrate. *B. rosea*, like all articulate brachiopods, is composed of low-

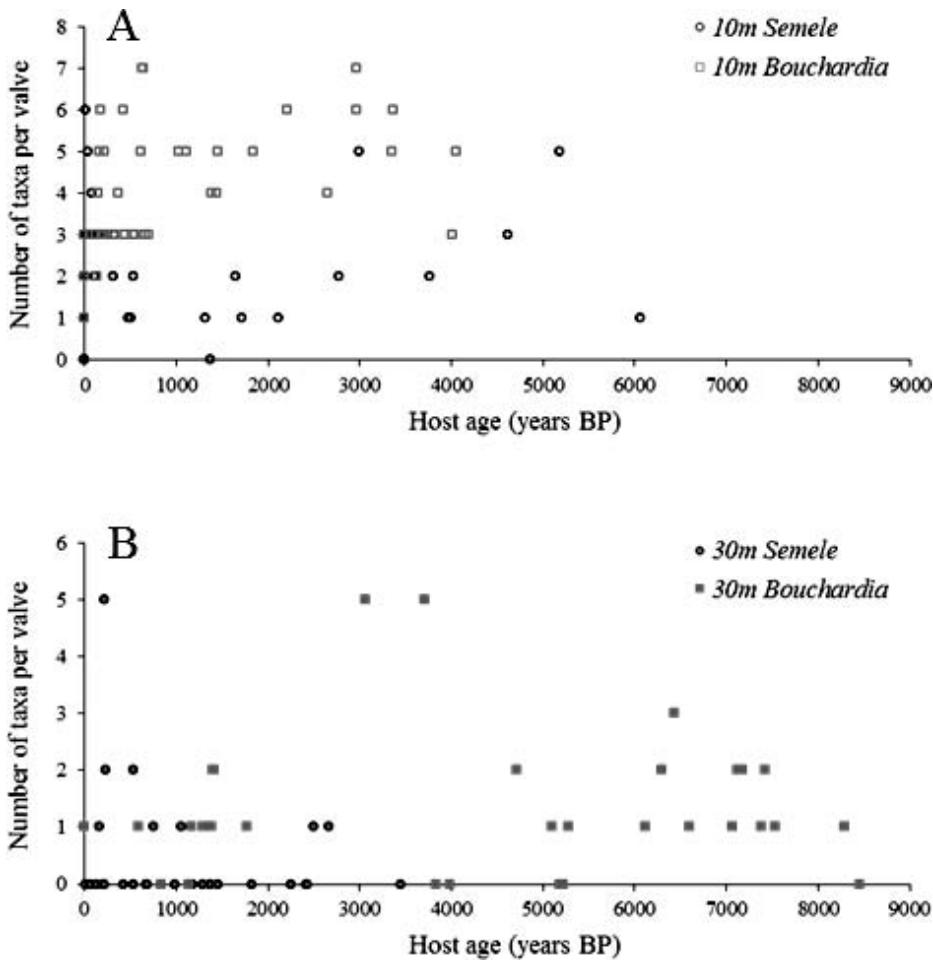


FIG. 10.—The relationship between epibiont diversity (taxonomic richness) and calibrated age. A) Station 9: 10 meters water depth. B) Station 1: 30 m water depth.

magnesium calcite, and calcitic epibionts like bryozoans and anomids colonize it more often than the aragonitic bivalve *S. casali*. A second major difference may be the composition of shell periostracum, which might influence the encrustation of valve exteriors, and provide a partial explanation for the preference of epibionts for valve interiors. However, strong cryptic tendencies are noted for most epibionts, and the grooves and ridges on the valve exterior of *S. casali* appear to foster exterior colonization by foraminifera. A third difference is the life position of the host; because *S. casali* is infaunal, it may have less exposure to colonization than *B. rosea* does. However, the greater number of epibionts per unit area on encrusted *B. rosea*, relative to encrusted specimens of *S. casali*, indicates that this does not account for all the differences observed.

Taphonomic Implications

The availability of age data for individual host valves provides deeper insight into the ecology and preservation of hard-substrate assemblages than simple faunal metrics alone, and provides insight into the taphonomic history of their hosts as well. The results seen here support previous studies (Carroll et al. 2003; Rodland et al. 2006) which reported little taphonomic difference between host valves dated to the recent versus those with estimated ages measured in millennia, and observed few differences in the faunal assemblage colonizing those shells. While the endobiont *Polydora* preferentially colonizes live *B. rosea* (Rodrigues et al. 2008), the epibiont assemblage encrusts the interior surfaces of valves after the death of the host. For the epifaunal brachiopod *B. rosea*, the

lack of long-term change in encrustation over hundreds to thousands of years is interpreted as indicating initial colonization followed by rapid valve burial and passage through the taphonomically active zone (TAZ) to the depth of final burial (DFB, *sensu* Olszewski 2004) at a depth where subsequent storms, currents, or bioturbation could no longer return valves to the surface (Olszewski 2004; Rodland et al. 2006). However, similar results observed for the infaunal bivalve *S. casali* complicate this interpretation. *S. casali* must be exhumed in order for encrustation or bioerosion to occur at the sediment–water interface (SWI), and the high colonization frequencies noted for recent hosts indicate that this occurs very rapidly.

It is difficult to reconcile these two observations via abiotic mechanisms. While a shallow TAZ would allow rapid cycling between the sediment surface and subsurface, host valves could be recolonized repeatedly over millennia due to frequent exhumation events and/or bioturbation. While this may still be true, these results require biological selectivity on the part of the sclerobiont assemblage, preferentially colonizing the interiors of very recently dead hosts (perhaps attracted to chemical biomarkers of decay), but then avoiding them thereafter (the “fresh shell syndrome” of Brett et al. 2011). Alternatively, accumulated epibiont abundance and diversity on older shells could be eliminated through taphonomic mechanisms (abrasion, dissolution, etc.) at exactly the rate new colonists arrive, balancing arrival versus loss of taxa (a process analogous to the production of palimpsests) as discussed in the erasure model of Rodland et al. (2006). However, there is no positive association between encrustation and taphonomic damage scores (Carroll et al. 2003); the presence and abundance of many epibiont taxa can be

observed after extensive damage, even when their identity is difficult to ascertain; and no increase in the proportion of unidentifiable epibionts was observed as a function of age, as would be predicted by the erasure model.

One consequence is the recognition that hard-substrate faunal assemblages would be true ecological snapshots, and not overexposures. This reinforces the utility of long-term taphonomic deployment experiments such as the Shelf and Slope Experimental Taphonomy Initiative (SSETI) (e.g., Parsons-Hubbard et al. 1999, 2011): despite the short timescales covered relative to the measured age spectra of mollusks and brachiopods, our conclusions suggest that the duration of these experiments is sufficient to capture the signals they were designed to study.

Paleoecological Implications

Additional comparative studies of the encrustation of other bivalve and brachiopod taxa would help to determine whether the differences observed in this study are unique to these two genera, or are generally applicable to the encrustation of bivalves and brachiopods. There are a variety of reasons why this avenue of study is worth pursuing. Hard substrate communities were common by the early Paleozoic (e.g., Kobluk and James 1979; Kobluk 1981a, 1981b, 1985; Brett et al. 1983), and rhynchonelliform brachiopods were among the most abundant shell-producing benthic organisms in open marine settings during this critical phase of evolution. Bivalves were often confined to marginal, nearshore settings during the Paleozoic (e.g., Ziegler et al. 1968; Olszewski and Patzkowski 2001; but see Cherns and Wright 2000, and Wright et al. 2003 for alternative interpretations), but radiated rapidly in the aftermath of the end-Permian extinction, quickly dominating level bottom communities in the Mesozoic (e.g., Schubert and Bottjer 1995). Major changes have taken place in the relative roles of bivalves and brachiopods in fossil communities through time or between environments, with repercussions for the substrates available for shell-encrusting organisms. If epibionts and bioeroders are sensitive to shell identity, then the evolution of hard-substrate faunas through geologic time cannot be understood outside of the context of their hosts. Even if host life position is the primary controlling factor, the increasing infaunalization of the marine benthos during the Phanerozoic would tend to restrict substrate availability for sclerobionts over time.

Further problems arise in the use of epibionts and bioeroders to study paleoenvironmental questions. Several authors have suggested that encrusters could be useful proxies for planktonic productivity in the fossil record (e.g., Vermeij 1995) and encrustation has been correlated with primary productivity for shells in deployment experiments, once sedimentation rates are taken into account (Lescinsky et al. 2002). Our results suggest that caution must be taken before any attempt is made to use epibionts for this purpose. Since the encrustation and bioerosion of shells at a given site vary between hosts, such assessments should be restricted to single host taxa when possible, or should evaluate differences among hosts from site to site. Furthermore, since encrustation varies as a function of shell size, some form of standardized measurements must be used to evaluate the size of each host. Other factors, such as valve topography, rugosity, mineralogy, and infaunal life habits, must also be considered, although our results suggest that, at least for inner shelf settings, exhumation of infaunal hosts occurs very rapidly relative to the age spectra of host valves.

On the bright side, encrustation might be a useful measure of factors such as productivity once these factors are taken into account. Water depth does not appear to be directly linked to the degree of encrustation and bioerosion at any given site, although the decrease in encrustation frequencies between inner and outer shelf *B. rosea* suggests a linkage to factors related at least in part to water depth. The encrustation of modern

mollusks is higher in eutrophic than in mesotrophic sites in the epeiric Java Sea (Lescinsky et al. 2002). Encrustation may be a measure of productivity in the sense that shells of a given, measurable size accumulate larvae settling from the plankton within a limited interval of exposure. Therefore, estimates of colonization frequency (as the probability of a host valve being colonized), abundance (as individual colonization events), and sclerobiont diversity may be useful in evaluating the planktonic productivity of a given site. Epibiont size and biomass might also prove to be useful in this regard, although they may also be affected by host-valve taphonomy. If changes in the rate of increase in mean epibiont diversity per size class record some measure of competition, then the relative degree of space and nutrient utilization may also be estimated.

The sclerobiont fossil record, modern or ancient, possesses extraordinary spatial resolution from which a great wealth of ecological information can be obtained. We have spent decades looking at encrustation and bioerosion as taphonomic processes, but have only begun to look at encrusted and bioeroded shells as paleocommunities in their own right. Abundance and diversity dynamics can be resolved at a scale of millimeters, but the substrate selectivity of sclerobionts results in differing patterns on different host taxa collected from the same sites. While studies of hard-substrate faunas have great potential, they require careful evaluation of colonization patterns and the microenvironmental context of the shells they inhabit before large-scale patterns can be inferred.

CONCLUSIONS

The following points briefly summarize the results and implications of this study:

1. Measures of encrustation and bioerosion vary among sites in a consistent manner for both the bivalve *Semele casali* and the brachiopod *Bouchardia rosea*, but water depth, sediment grain size, and sediment composition do not account for this variation.
2. Host shell size, particularly surface area, appears to play a primary control on measures of the abundance and diversity of sclerobionts. Differences in the surface area of different taxa, or between shells collected from different sites, should be taken into account when comparing results between them.
3. At each station, *B. rosea* is encrusted more frequently and by a larger number of epibionts than *S. casali*. If only encrusted valves are considered, *B. rosea* is still colonized by a larger number of epibionts than *S. casali*, but mean per-valve abundance values are equivalent when standardizing for surface area.
4. Colonization metrics from individually dated shells indicate that exhumation of infaunal bivalves occurs rapidly (on timescales of decades) relative to the age structure of the overall population. Infaunal life habits influence the probability of a host valve becoming colonized, but once exposed, encrustation patterns for both bivalves and brachiopods are roughly the same.
5. The majority of epibionts are observed on valves younger than the mean host age measured for each species at each site, but colonization frequency, abundance, and diversity of sclerobiont assemblages do not appear to increase as a function of host age. These results indicate that the taphonomic history of host valves has little effect on encrustation and bioerosion over timescales of centuries to millennia, and suggest a selective preference exists among sclerobiont taxa for recently deceased hosts. Thus, the temporal resolution of sclerobiont faunas is closer to an ecological snapshot than a long-duration exposure, and multiyear deployment experiments are likely to capture the full range of variation in colonization.
6. The number of epibionts on any given valve is largely random, but the mean number of epibionts per shell in a given size class increases with

- size. The mean number of epibiont taxa in a given size class increases as a function of valve surface area for both *S. casali* and *B. rosea*.
7. Estimates of epibiont diversity as a function of host size are sensitive to the method of size determination: mean values per size class are consistently higher for *B. rosea* than *S. casali* for any given maximum linear dimension (length). Length measurements correlate with surface area, and this correlation can be used to provide area estimates based on length measurements alone, but the relationship between the two must be established separately for each taxon and for each valve type.
 8. When differences in surface area as a function of valve length are taken into account for each species and valve type, abundance and diversity metrics for both species overlap substantially.
 9. Two different host substrates collected from the same locations may differ significantly in terms of encrustation and bioerosion patterns. Therefore, attempts to interpret the ecology or paleoecology of hard substrate communities must account for the identity, structure, shape, ecology, and surface area of the hosts under consideration.

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REFERENCES

- ALEXANDER, R.R., 2001, Functional morphology and biomechanics of articulate brachiopod shells, in Carlson, S.J., and Sandy, M.R., eds., Brachiopods Ancient and Modern: A Tribute to G. Arthur Cooper: The Paleontological Society, Papers, v. 7, p. 145–169.
- ALEXANDER, R.R., AND SCHARPF, C.D., 1990, Epibionts on Late Ordovician brachiopods from southeastern Indiana: Historical Biology, v. 4, p. 179–202.
- BAMBACH, R.K., 1993, Seafood through time: changes in biomass, energetics, and productivity in the marine ecosystem: Paleobiology, v. 19, p. 372–397.
- BEST, M.M.R., AND KIDWELL, S.M., 2000a, Bivalve taphonomy in tropical mixed siliciclastic–carbonate settings: I. Environmental variation in shell condition: Paleobiology, v. 26, p. 80–102.
- BEST, M.M.R., AND KIDWELL, S.M., 2000b, Bivalve taphonomy in tropical mixed siliciclastic–carbonate settings: II. Effect of bivalve life habits and shell types: Paleobiology, v. 26, p. 103–115.
- BORDEAUX, Y.L., AND BRETT, C.E., 1990, Substrate specific associations of epibionts on Middle Devonian brachiopods: implications for paleoecology: Historical Biology, v. 4, p. 203–220.
- BRETT, C.E., LIDDELL, W.D., AND DERSTLER, K.L., 1983, Late Cambrian hard substrate communities from Montana/Wyoming: the oldest known hardground encrusters: Lethaia, v. 16, p. 281–289.
- BRETT, C.E., PARSONS-HUBBARD, K., WALKER, S.E., FERGUSON, C., POWELL, E.N., STAFF, G., ASHTON-ALCOX, K.A., AND RAYMOND, A., 2011, Gradients and patterns of sclerobionts on experimentally deployed bivalve shells: synopsis of bathymetric trends on a decadal time scale: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 312, p. 278–304.
- CARROLL, M., KOWALEWSKI, M., SIMÕES, M.G., AND GOODFRIEND, G.A., 2003, Quantitative estimates of time-averaging in brachiopod shell accumulations from a modern tropical shelf: Paleobiology, v. 29, p. 381–402.
- CHERNS, L., AND WRIGHT, V.P., 2000, Missing molluscs as evidence of large scale, early skeletal dissolution in a Silurian sea: Geology, v. 28, p. 791–794.
- DALEY, G.M., 1993, Passive deterioration of shelly material: a study of the recent eastern Pacific articulate brachiopod *Terebratalia transversa* Sowerby: PALAIOS, v. 8, p. 226–232.
- EMIG, C.C., 1990, Examples of post-mortality alteration in recent brachiopod shells and (paleo)ecological consequences: Marine Biology, v. 104, p. 233–238.
- FLESSA, K.F., KOWALEWSKI, M., AND WALKER, S.E., 1992, Post-collection taphonomy: shell destruction and the Chevrolet: PALAIOS, v. 7, p. 553–554.
- GIBSON, M.A., 1992, Some epibiont-host and epibiont–epibiont interactions from the Birdsong Shale Member of the Lower Devonian Ross Formation (west-central Tennessee, U.S.A.): Historical Biology, v. 6, p. 113–132.
- GOULD, S.J., AND CALLOWAY, C.B., 1980, Clams and brachiopods: ships that pass in the night: Paleobiology, v. 6, p. 383–396.
- JACKSON, J.B.C., 1977, Competition on marine hard substrata: the adaptive significance of solitary and colonial strategies: American Naturalist, v. 111, p. 743–767.
- KNOLL, A.H., BAMBACH, R.K., CANFIELD, D.E., AND GROZINGER, J.P., 1996, Comparative earth history and the Late Permian mass extinction: Science, v. 273, p. 452–457.
- KOBLUK, D.R., 1981a, The record of early cavity-dwelling (coelobiontic) organisms in the Paleozoic: Canadian Journal of Earth Science, v. 18, p. 181–190.
- KOBLUK, D.R., 1981b, Earliest cavity-dwelling organisms (coelobionts), lower Cambrian Poleta Formation, Nevada: Canadian Journal of Earth Science, v. 18, p. 669–679.
- KOBLUK, D.R., 1985, Biota preserved within cavities in Cambrian *Epiphyton* mounds, upper Shady Dolomite, southwestern Virginia: Journal of Paleontology, v. 59, p. 1158–1172.
- 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.
- KOSNIK, M.A., ALROY, J., BEHRENSMEYER, A.K., FURSICH, F.T., GASTALDO, R.A., KIDWELL, S.M., KOWALEWSKI, M., PLOTNICK, R.E., ROGERS, R.R., AND WAGNER, P.J., 2011, Changes in shell durability of common marine taxa through the Phanerozoic: evidence for biological rather than taphonomic drivers: Paleobiology, v. 37, p. 303–331.
- KOWALEWSKI, M., SIMÕES, M.G., CARROLL, M., AND RODLAND, D.L., 2002, Abundant brachiopods on a tropical, upwelling-influenced shelf (southeast Brazilian Bight, South Atlantic): PALAIOS, v. 17, p. 277–286.
- KOWALEWSKI, M., HOFFMEISTER, A.P., BAUMILLER, T.K., AND BAMBACH, R.K., 2005, Secondary evolutionary escalation between brachiopods and enemies of other prey: Science, v. 308, p. 1774–1777.
- KRAUSE, R.A., JR., BARBOUR-WOOD, S.L., KOWALEWSKI, M., KAUFMAN, D.S., ROMANEK, C.S., SIMÕES, M.G., AND WEHMILLER, J.F., 2010, Quantitative estimates and modeling of time averaging in bivalve and brachiopod shell accumulations: Paleobiology, v. 36, p. 428–452.
- LESCINSKY, H.L., 1997, Epibiont communities: recruitment and competition on North American Carboniferous brachiopods: Journal of Paleontology, v. 71, p. 34–53.
- LESCINSKY, H.L., EDINGER, E., AND RISK, M.J., 2002, Mollusc shell encrustation and bioerosion rates in a modern epeiric sea: taphonomy experiments in the Java Sea, Indonesia: PALAIOS, v. 17, p. 171–191.
- MACARTHUR, R.H., AND WILSON, E.O., 1967, The Theory of Island Biogeography: Princeton, New Jersey, Princeton University Press, 203 p.
- MCCAMMON, H.M., 1969, The food of articulate brachiopods: Journal of Paleontology, v. 43, p. 976–985.
- OLSZEWSKI, T.D., 2004, Modeling the influence of taphonomic destruction, reworking, and burial on time-averaging in fossil accumulations: PALAIOS, v. 19, p. 39–50.
- OLSZEWski, T.D., AND PATZKOWSKI, M.E., 2001, Measuring recurrence of marine biotic gradients: a case study from the Pennsylvanian–Permian Midcontinent: PALAIOS, v. 16, p. 444–460.
- PARSONS-HUBBARD, K.M., CALLENDER, W.R., POWELL, E.N., BRETT, C.E., WALKER, S.E., RAYMOND, A.L., AND STAFF, G.M., 1999, Rates of burial and disturbance of experimentally-deployed molluscs: implications for preservation potential: PALAIOS, v. 14, p. 337–351.
- PARSONS-HUBBARD, K., BRETT, C.E., AND WALKER, S.E., 2011, Taphonomic field experiments and the role of the Shelf and Slope Experimental Taphonomy Initiative: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 312, p. 195–208.
- RICHARDS, R.P., 1972, Autecology of Richmonidian brachiopods (Late Ordovician of Indiana and Ohio): Journal of Paleontology, v. 46, p. 29–32.
- RICHARDSON, J.R., 1997, Biogeography of articulate brachiopods, in Kaesler, R.L., ed., Treatise on Invertebrate Paleontology, Part H, v. 1, Revised, Brachiopoda: Geological Society of America and University of Kansas, p. 463–472.
- RODLAND, D.L., KOWALEWSKI, M., SIMÕES, M.G., AND CARROLL, M., 2004, Colonization of a “Lost World”: encrustation patterns in modern subtropical brachiopod assemblages: PALAIOS, v. 19, p. 381–395.
- RODLAND, D.L., KOWALEWSKI, M., CARROLL, M., AND SIMÕES, M.G., 2006, The temporal resolution of epibiont assemblages: are they ecological snapshots or overexposures?: Journal of Geology, v. 114, p. 313–324.
- RODRIGUES, S.C., 2006, Tafonomia de moluscos bivalves e braquiópodes das enseadas de Ubatuba e Picinguaba, norte do Estado de São Paulo: implicações do uso de assinaturas tafonômicas no reconhecimento de gradientes ambientais [Ph.D. Dissertation]: Instituto de Geociências, Universidade de São Paulo, São Paulo, Brazil, 118 p.
- RODRIGUES, S.C., AND SIMÕES, M.G., 2010, Taphonomy of *Bouchardia rosea* (Rhynchonelliformea, Brachiopoda) shells from Ubatuba Bay, Brazil: implications for the use of taphonomic signatures in (paleo)environmental analysis: Ameghiniana, v. 47, p. 373–386.
- RODRIGUES, S.C., SIMÕES, M.G., KOWALEWSKI, M., PETTI, M.A., NONATO, E.F., MARTINEZ, S., AND DEL RIO, C., 2008, Biotic interaction between spongid polychaetes and bouchardiid brachiopods: paleoecological, taphonomic and evolutionary implications: Acta Palaeontologica Polonica, v. 53, p. 657–668.
- SCHUBERT, J.K., AND BOTTER, D.J., 1995, Aftermath of the Permo-Triassic mass extinction event: paleoecology of Lower Triassic carbonates in the western USA: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 116, p. 1–40.

- SIMÕES, M.G., KOWALEWSKI, M., MELLO, L.H.C., RODLAND, D.L., AND CARROLL, M., 2004, Recent brachiopods from the southern Brazilian shelf: palaeontological and biogeographical implications: *Palaeontology*, v. 47, p. 515–532.
- SIMÕES, M.G., RODRIGUES, S.C., AND KOWALEWSKI, M., 2007, Comparative analysis of drilling frequencies in recent Brachiopod–Mollusk associations from the Southern Brazilian Shelf: *PALAIOS*, v. 22, p. 142–151.
- SIMÕES, M.G., RODRIGUES, S.C., AND KOWALEWSKI, M., 2009, *Bouchardia rosea*, a vanishing brachiopod species of the Brazilian platform: taphonomy, historical ecology and conservation paleobiology: *Historical Biology*, v. 21, p. 123–137.
- STEELE-PETROVIC, H.M., 1976, Brachiopod food and feeding processes: *Palaeontology*, v. 19, p. 417–436.
- TAYLOR, P.D., AND WILSON, M.A., 2002, A new terminology for marine organisms inhabiting hard substrates: *PALAIOS*, v. 17, p. 522–525.
- TOMAŠOVÝCH, A., AND ROTHFUS, T., 2005, Differential taphonomy of modern brachiopods (San Juan Islands, Washington State): effect of intrinsic factors on damage and community-level abundance: *Lethaia*, v. 38, p. 271–292.
- TOMAŠOVÝCH, A., AND ZUSCHIN, M., 2009, Variation in brachiopod preservation along a carbonate shelf–basin transect (Red Sea and Gulf of Aden): environmental sensitivity of taphofacies: *PALAIOS*, v. 24, p. 697–716.
- TORELLO, F.F., SIMÕES, M.G., AND PASSOS, J.R.S., 2002, The taphonomic tumbling barrel: a methodological review to understand preservational biases in the fossil record, in First International Palaeontological Congress: The Geological Society of Australia, McPherson's Printing Group, Sydney, Abstracts, v. 68, p. 285–286.
- VERMEIJ, G.J., 1995, Economics, volcanoes, and Phanerozoic revolutions: *Paleobiology*, v. 21, p. 125–152.
- WATKINS, R., 1981, Epizoan ecology in the type Ludlow Series (upper Silurian), England: *Journal of Paleontology*, v. 55, p. 29–32.
- WESSEL, P., AND SMITH, W.H.F., 1998, New, improved version of the Generic Mapping Tools released: American Geophysical Union, *Eos, Transactions*, v. 79, p. 579.
- WRIGHT, P., CHERNS, L., AND HODGES, P., 2003, Missing molluscs: field testing taphonomic loss in the Mesozoic through early large-scale aragonite dissolution: *Geology*, v. 31, p. 211–214.
- ZIEGLER, A.M., COCKS, L.R.M., AND BAMBACH, R.K., 1968, The composition and structure of lower Silurian marine communities: *Lethaia*, v. 1, p. 1–27.

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