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Author(s): David L. Rodland, Michał Kowalewski, Monica Carroll, and Marcello G. Simões

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The Temporal Resolution of Epibiont Assemblages: Are They Ecological Snapshots or Overexposures?

David L. Rodland, Michał Kowalewski,[1] *Monica Carroll,*[2] *and Marcello G. Simões*[3]

Bio-INCREMENTS Group, Institute for Geology and Paleontology, Johann Wolfgang Goethe University–Frankfurt am Main, Senckenberganlage 32, 60325 Frankfurt am Main, Germany
(e-mail: d.rodland@em.uni-frankfurt.de)

ABSTRACT

The effects of time averaging on the fossil record of soft-substrate marine faunas have been investigated in great detail, but the temporal resolution of epibiont assemblages has been inferred only from limited-duration deployment experiments. Individually dated shells provide insight into the temporal resolution of epibiont assemblages and the taphonomic history of their hosts over decades to centuries. Epibiont abundance and richness were evaluated for 86 dated valves of the rhynchonelliform brachiopod *Bouchardia rosea* collected from the inner shelf. Maximum abundance occurred on shells less than 400 yr old, and maximum diversity was attained within a century. Taphonomic evidence does not support models of live-host colonization, net accumulation, or erasure of epibionts over time. Encrustation appears to have occurred during a brief interval between host death and burial, with no evidence of significant recolonization of exhumed shells. Epibiont assemblages of individually dated shells preserve ecological snapshots, despite host-shell time averaging, and may record long-term ecological changes or anthropogenic environmental changes. Unless the ages of individual shells are directly estimated, however, pooling shells of different ages artificially reduces the temporal resolution of their encrusting assemblages to that of their hosts, an artifact of analytical time averaging.

Online enhancements: appendixes.

Introduction

Hard-substrate benthic marine assemblages present a wealth of data for the analysis of ecological interactions and taphonomic patterns in the fossil record (e.g., Taylor and Wilson 2003; Leighton 2004). Encrusting organisms are effectively fixed in place after they colonize a substrate, producing assemblages with unparalleled spatial resolution and often preserving relative age relationships through overgrowth patterns. By contrast, fossil assemblages preserved in soft substrates are subject to spatial mixing and time averaging: hard skeletal elements collected from the same bed may be reworked across considerable distances and may differ in age by centuries or millennia (e.g., Walker and Bambach 1971; Kowalewski et al. 1998). Because individual skeletal elements are essentially independent of one another after disarticulation, they may experience different taphonomic processes within the same environment before final burial. The taphonomic histories of shell-encrusting organisms, or epibionts (episkeletobionts sensu Taylor and Wilson 2002), combine aspects of both hard- and soft-substrate fossil assemblages: epibionts on a specific host are fixed in space to a common frame of reference that is subject to transport and time averaging.

While processes and patterns of time averaging have been investigated through techniques ranging from experimental taphonomy and deployment studies (e.g., Parsons-Hubbard et al. 1999) to direct dating of individual shells (e.g., Kowalewski et al. 1998; Carroll et al. 2003; Simões et al. 2004*a*), the

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[1] Department of Geosciences, 4044 Derring Hall, Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24060, U.S.A.

[2] Department of Geology, University of Georgia, Athens, Georgia 30602, U.S.A.

[3] Instituto de Biociências, Universidade Estadual Paulista, Distrito de Rubião Junior, C.P. 510, 18.610-000, Botucatu, São Paulo, Brazil.

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temporal resolution of epibiont assemblages remains unclear. By documenting selective patterns of attachment and growth, it is possible to demonstrate or infer preferential settlement patterns and the existence of interactions (commensalism, parasitism, etc.) among epibionts or between them and their living hosts (e.g., Bordeaux and Brett 1990; Alexander 1994; Fagerstrom 1996; Lescinsky 1997). However, it can be difficult or impossible to distinguish between live-host colonization and postmortem occupation of skeletal surfaces exposed during life, and similar issues arise in identifying competitive overgrowth among epibionts. Among gastropods, hermit crabs can pass reoccupied shells among multiple hosts, so the interpretation of live-dead interactions in the fossil record is complicated at best. Postmortem encrustation may occur at any time within a "colonization window," during intervals when the host is exposed above the sediment-water interface before permanent burial or shell destruction. Because rates of sedimentation, bioturbation, and the depth and frequency of erosive events vary, multiple episodes of burial and exposure are possible (e.g., Parsons-Hubbard et al. 1999; Lescinsky et al. 2002); this process would "overexpose" a shell to surface taphonomic processes such as encrustation.

The number and duration of exposure events may be difficult or impossible to determine, but the potential duration of the colonization window is also influenced by the durability of the host shell. Terebratulid shells can degrade rapidly in marine settings (Emig 1990), and tumbler experiments suggest that *Bouchardia* are generally less durable than many co-occurring bivalve molluscs, despite being robust and thick-shelled for brachiopods (Torello et al. 2002). The fragility of brachiopod shells has led to the suggestion that their encrustation must occur during the life of the host or within decades after its death (e.g., Lescinsky 1997). If so, then the temporal resolution of encrusting assemblages should be excellent and should provide ecological "snapshots" of coexisting epibionts in the fossil record. This view is supported by experiments demonstrating the rapid colonization of deployed mollusc shells by epibionts (e.g., Parsons-Hubbard et al. 1999; Lescinsky et al. 2002). However, recent evidence indicates that modern brachiopods experience time averaging over centuries or millennia, with an age structure similar to that of bivalves, and apparently share similar taphonomic histories (Carroll et al. 2003). Over such long intervals, epibionts found on the same shell might differ in age by centuries, and epibiont assemblages may represent multiple protracted episodes of exposure to colonizing larvae.

The temporal resolution of epibiont assemblages therefore depends on a variety of factors, including the age of a host shell (in terms of both ontogeny, for live-host colonization, and time since death, for postmortem colonists), its exposure history, its durability, and the rate of colonization. However, these factors have direct effects on the number and diversity of epibionts colonizing each shell. Evaluation of encrustation as a function of the age of host shells provides insight into the temporal resolution of these faunas. This study evaluates the encrustation of 86 brachiopod valves placed in chronological order using ages determined with ^{14}C-calibrated amino acid racemization rates. While the age of individual epibionts cannot be determined from such a study, it is possible to determine whether epibiont diversity and abundance is higher on older valves than on younger hosts. This provides insight into the ecological dynamics of epibiont assemblages, including the extent to which encrusting organisms coexist and compete for resources on the same substrates. The taphonomic history of the host can also be evaluated, because shell colonization occurs only while the valve is exposed at the sediment-water interface.

Study Area, Materials, and Methods

Shells of the rhynchonelliform brachiopod *Bouchardia rosea* were collected from the near-coastal inner shelf of the southeast Brazilian Bight, in the vicinity of Ubatuba along the northeastern coast of São Paulo state. Brachiopods were collected from the upper 10 cm of sediment using a Van Veen grab sampler (1/40 m^2) from four localities (Carroll et al. 2003). Specimens from locality 1 were collected from 6-m-deep water in Ubatumirim Bay, while those from locality 2 were collected from a depth of 23 m. Locality 3 is located near Ilha das Couves (at 16 m deep), and locality 4 specimens were collected from 9 m deep in Ubatuba Bay (this site is Ubatuba Station 9 in Rodland et al. 2004). The specifics of the study area are addressed in more detail elsewhere (Kowalewski et al. 2002; Carroll et al. 2003; Rodland et al. 2004; Simões et al. 2004*b*).

A total of 86 brachiopod valves larger than 1 cm in maximum length were selected at random from specimens collected from these four sites, using numerical assignments for each and a random number generator. Approximately 20 individuals were selected per site in order to provide statistically robust age frequency distributions and to compare results among sites. Ages were determined by cal-

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culating A/I (alloisoleucine/isoleucine) ratios for each shell and calibrating these values against ages derived from ^{14}C ratios measured in five specimens selected across a broad range of A/I ratios (Carroll et al. 2003). Statistical comparisons and analyses of host size and the abundance and diversity of epibiont assemblages were performed using SAS, version 8.12, and assume $\alpha = 0.05$.

Each specimen was measured to the nearest 0.1 mm with electronic calipers and examined under a binocular microscope to evaluate the encrusting fauna. Epibionts were distinguished at the morphospecies level, when possible, and grouped to higher taxonomic levels (e.g., serpulid worms, bryozoans, foraminifera) commonly used in taphonomically oriented encrustation studies (e.g., Lescinsky 1997; Best and Kidwell 2000*a*, 2000*b*; Lescinsky et al. 2002). The epibiont assemblage for each shell was described in terms of abundance and richness (the number of morphospecies present), metrics that are easily measured, easily evaluated from a statistical point of view, and directly relevant to the issue of colonization rates. By contrast, area cover measurements reflect growth and resource utilization and are therefore not suitable for this kind of study.

Because the abundance and diversity of epibiont assemblages are affected by the size of the host (Rodland et al. 2004), comparison studies require shells of equivalent size or must use a shell size model for standardization. All specimens used here were restricted to the size class between 1.0 and 2.0 cm. Shell size was estimated by measurements of the anterior-posterior axis (the longest axis).

Results

Age Distributions. A total of 866 epibionts were counted on 86 valves, primarily recording postmortem encrustation (77 interior surfaces encrusted, with only 36 specimens colonized on the exterior). Host shells range in age from the present day to more than 3000 yr old (app. A, available in the online edition or from the *Journal of Geology* office). Age values due to A/I variation and analytical imprecision produce age value errors ranging from $\pm$<50 yr for young shells to $\pm$300 yr for older shells, with a mean of $\pm$150 yr (Carroll et al. 2003), suggesting that age bins narrower than 50-yr duration are inappropriate. The age distribution of host valves is strongly right-skewed, and few valves older than 500 yr provided age estimates within one century of one another. Host age frequency distributions for all sites pooled together are shown in figure 1, and mean values calculated for age bins of one century are presented in figure 2. Localities 1 and 2 are dominated by young shells, while localities 3 and 4 show a bimodal distribution of shell ages, with peaks at less than 200 and between 300 and 400 yr of age (Carroll et al. 2003).

For statistical comparisons among shells of differing ages, the shells were divided into three age clusters. Because of their rarity, the 15 host valves exceeding 500 yr in age were excluded from statistical comparisons with younger shells, although data collected from them are presented for illustrative purposes. For the remaining 71 shells, the median age of 120 yr was used to separate "young" and "old" shell categories. The median was chosen because it allows approximately equal numbers of host valves to be used for both age classes.

Size, Abundance, and Diversity. Mean shell length does not differ a great deal between older and younger shells measured for this study: hosts less than 120 yr of age were 16.2 mm long on average, while a mean of 14.7 mm was recorded for older shells. The size ranges and overall size distribution for both groups are very similar, allowing direct comparison without correction for shell surface area (fig. 3).

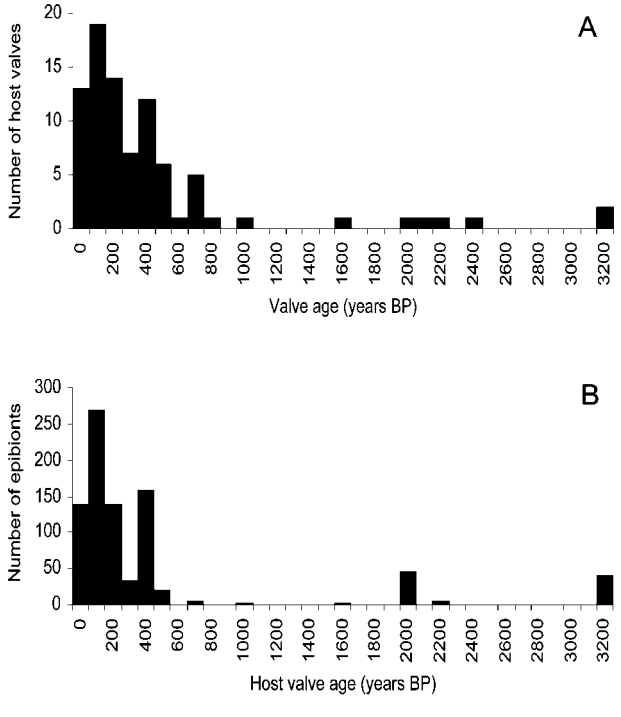

Figure 1. Host shell age distributions pooled for all sites. *A*, Age distributions of brachiopod shells. *B*, Frequency distribution of epibionts as a function of host shell age.

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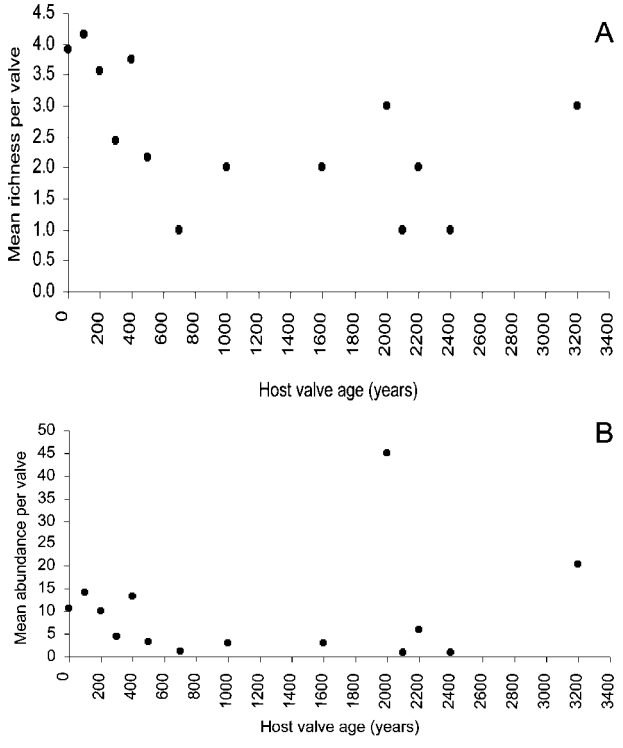

Figure 2. Mean abundance and diversity of epibionts per shell as a function of host age. Age categories older than 500 yr are represented by fewer than five shells. *A*, Mean number of epibiont taxa per shell. *B*, Mean epibiont abundance per shell.

The majority of epibionts (467) were calcareous tube-dwelling polychaetes (represented by five morphospecies), primarily serpulids, followed by 208 bryozoan colonies (13 morphospecies) and 131 foraminifera (three morphospecies), as well as one species of anomiid bivalve and several varieties of soft-bodied algae unlikely to be preserved in the fossil record. The abundance of epibionts on hosts in a given age range shows a distribution similar to the age distribution of their hosts (fig. 1). Epibiont abundance does not increase with the age of the host: 424 epibionts were counted on 35 valves dated at less than 120 yr of age, while 336 epibionts were observed on 36 hosts between 120 and 500 yr of age.

The epibiont abundance distribution for each age group is illustrated in figure 4. Six of the 10 shells with the highest epibiont abundance exceed the median 120 yr of age, but this is outweighed by much higher numbers of shells hosting 10 or more epibionts in the youngest age class. As a result, the mean number of epibionts per valve is higher on younger hosts (12.1 epibionts per valve) than on older hosts (9.3 epibionts per valve). Similarly, the 15 hosts older than 500 yr bear a total of 106 epibionts, with a mean value of 7.1 epibionts per valve, and show a frequency distribution much like that of 120–500-yr-old hosts. However, the frequency distribution of epibionts on dated shells is, like the distribution of their hosts, strongly right-skewed (fig. 1). Thus, the apparent decrease in mean epibiont abundance with increasing host age could be influenced by decreasing sample sizes for older age bins.

No taxonomic group shows consistent trends in abundance as a function of host age, suggesting that all groups have a similar taphonomic history. The number of epibiont taxa colonizing individual valves is presented in appendix B, available in the online edition or from the *Journal of Geology* office, broken down by major taxonomic groups and or-

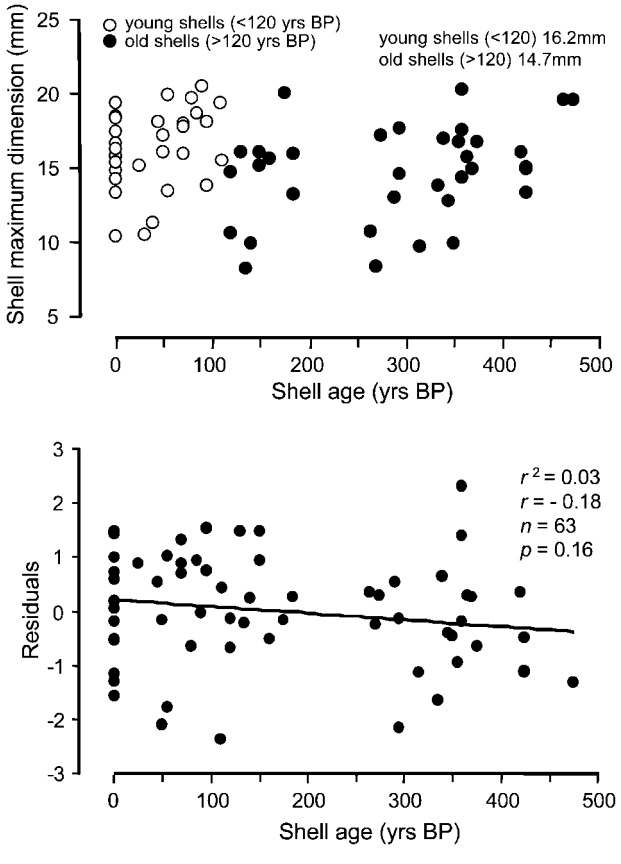

Figure 3. Shell size as a function of age. *Top*, Length of maximum shell dimension (in mm) versus measured shell age. Open circles correspond to shells younger than the median age of 120 yr, while filled circles represent shells older than the median. *Bottom*, Residuals from the epibiont abundance–host size relationship as a function of host age.

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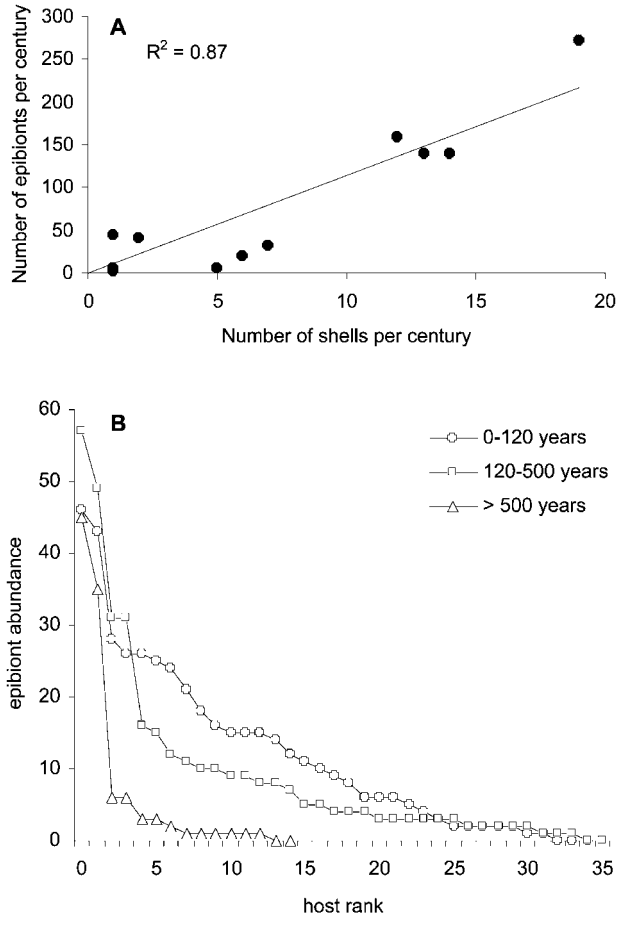

Figure 4. Epibiont abundance as a function of host age. *A*, Relationship between the number of epibionts and the number of host valves per century. This correlation suggests that the apparent decrease in mean epibiont abundance with increasing host age is an artifact of decreasing sample sizes for older age bins. *B*, Epibiont abundance distributions for each age group. Each shell in each age group has been ranked by epibiont abundance to illustrate differences in abundance structure between age categories.

dered by age. Figure 2 plots mean epibiont abundance and diversity (richness, or the number of epibiont morphospecies) per valve as a function of host age, divided into century-long age bins. As with epibiont abundance, mean richness does not appear to increase on older hosts. Host abundance, epibiont abundance, the number of epibionts per valve, and the mean diversity per valve are presented in century-long age bins in appendix C, available in the online edition or from the *Journal of Geology* office.

Just as the abundance of epibionts in any given age bin is dependent on the number of hosts, the number of epibiont taxa colonizing any given valve depends on the number of epibionts (fig. 4). As with many fossil assemblages, diversity increases logarithmically with abundance (e.g., Powell and Kowalewski 2002). No directional trend is apparent for residuals as a function of host age, but there is an apparent decrease in variability with increasing age (fig. 5).

Differences of mean and total abundance and diversity of epibiont taxa by age group are shown in table 1. The total number of epibionts, the mean number of epibionts per host, and the number of taxa per host are highest for hosts younger than 120 yr, but equal numbers of taxa (24 distinguishable morphospecies) were observed in both groups.

Epifaunal Composition. Notable differences appear in the relative abundance of major groups of epibiont taxa as a function of age (fig. 6), and common trends are seen at each of the studied sites. When each site is evaluated separately, significant differences between young and old faunas can be distinguished via *G*-tests (in order from sites 1 through 4: $G = 33.8, 19.4, 19.8, 27.3$; $p < 0.0001$, $p = 0.0002$, $p = 0.0002$, $p < 0.0001$). In all cases, younger hosts were colonized by a greater proportion of serpulids, while older hosts were colonized by a greater proportion of bryozoans. At sites 3 and 4, foraminifera occur only on young shells, despite a large number of potential hosts exceeding 120 yr of age.

Bioerosion. The condition of the shells was evaluated for abrasion, bioerosion, fragmentation, and other factors as part of a previous study (Carroll et al. 2003). While no correlation between age and taphonomic score was observed, bioerosion may provide additional insight into the preservation of encrusting assemblages.

A total of 59 shells also exhibited bioerosion: 40 with clionid sponge borings, 26 with U-shaped tubes attributed to the polychaete *Polydora*, 10 with microborings, and one showing surficial scratches interpreted as radular grazing marks. Mean frequencies of bioerosion decrease with increasing valve age: 75.7% of young valves (<120 yr) were bioeroded, in contrast to 67.6% of old (120–500 yr) shells and 53% of shells more than 500 yr of age.

Discussion

Individual shell dating provides a long-term temporal dimension for the study of encrustation that has not been available through taphonomic deployment studies. Older shells do not host more abundant or diverse epibiont assemblages than young shells, despite the potential for centuries of

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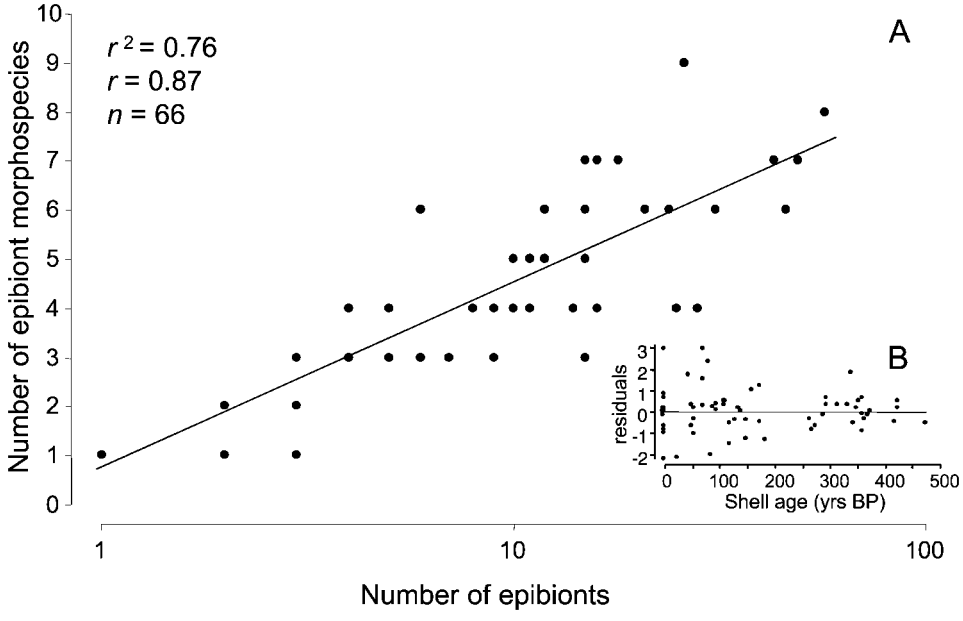

Figure 5. Relationship between epibiont abundance and diversity. *A*, Normal log plot of the number of epibiont taxa versus number of epibionts for individual valves. *B*, Residuals versus shell age, showing decreasing variability in the number of taxa present for any given number of epibionts as host age increases.

epibiont accretion on older hosts. In fact, younger shells host a larger number of epibionts per host shell than older shells do, presenting a conundrum. The simplest interpretation of this data is that diverse and abundant epibiont assemblages develop on modern subtropical brachiopod hosts within the first century after death. If long-term epibiont accretion occurred on the studied shells, it has been counterbalanced by taphonomic loss of epibionts (erasure) or an increase in the rate of colonization in the recent past. However, there are multiple ways in which these epibiont assemblages could be produced. Several models are discussed below.

Live-Host Colonization. Encrustation can occur during the life of the host and can be documented by evidence for parasitism, mutualism, or other interactions between host and epibiont. Preferential colonization of live hosts would not result in the accretion of epibionts on older shells, and in this case, epibiont abundance and diversity would reflect colonization rates during the life of the host. Deployed taphonomy experiments show that shells can be rapidly buried in soft substrates, limiting the duration of the "colonization window" during which shells may be encrusted (e.g., Parsons-Hubbard et al. 1999; Best and Kidwell 2000*a*, 2000*b*; Lescinsky et al. 2002). Thus, external encrustation may occur primarily while the live host is able to maintain itself at or above the sediment-water interface (e.g., Lescinsky et al. 2002). In support of this model, a number of studies have demonstrated or inferred host-epibiont interactions and symbiosis in the fossil record (e.g., Alvarez and Taylor 1987; Fagerstrom 1996). However, the fossil record also shows that postmortem encrustation of Paleozoic brachiopods was common (e.g., Watkins 1981; Bordeaux and Brett 1990; Meyer 1990; Gibson 1992), and the prevalence of internal colonization requires this interpretation here (Rodland et al. 2004).

The live-host colonization model has simple assumptions and powerful implications for the ecology of epibionts and may describe other settings very well. Unfortunately, other taphonomic circumstances preclude its adoption here. Live-host colonists share a common taphonomic history with their hosts, but the studied specimens vary a great deal in taphonomically significant textural details.

Table 1. Comparison of Epibiont Abundance and Diversity between Young and Old Host Shells

	Young hosts (0–119 yr)	Old hosts (120–500 yr)
Number of brachiopods	35	36
Total epibiont abundance	424	336
Richness	24	24
Mean abundance per valve	12.1	9.3
Mean richness per valve	3.97	3.22

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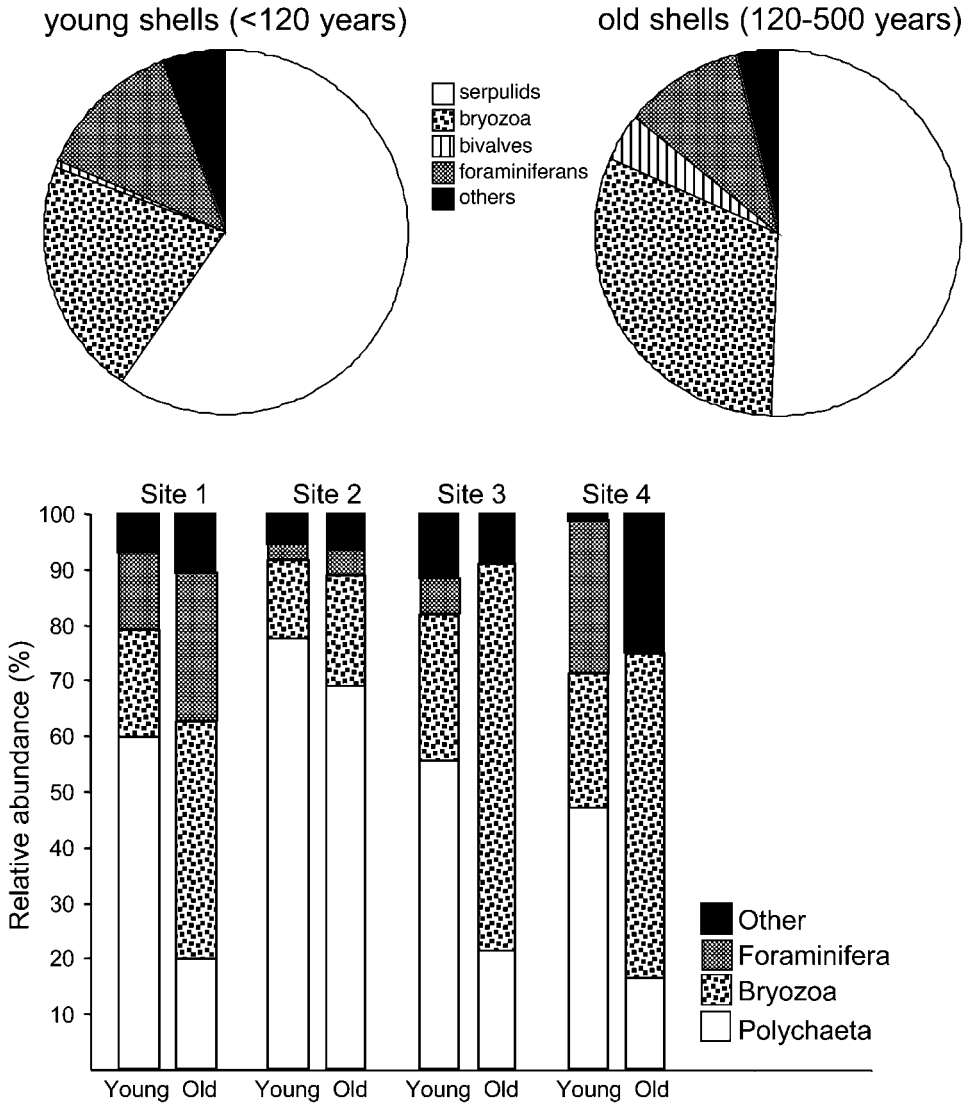

Figure 6. Relative abundance of epibiont taxa. Consistent differences are found between the epibiont faunas of young (0–120 yr) and old (120–500 yr) hosts at all sites studied. Changes in the relative abundance of taxa between young and old valves plotted separately per site.

Pristine shells have been observed as well as specimens displaying high degrees of bioerosion, abrasion, and corrosion, with little correlation between taphonomic state and shell age (Carroll et al. 2003; Simões et al. 2004*c*). In addition, valve interiors are characterized by higher epibiont abundance and encrustation frequencies than exteriors for modern *Bouchardia* collected from nearshore localities (Rodland et al. 2004). Because interior encrustation is inhibited by the presence of mantle tissue during the life of the host, this observation indicates that live-host colonization is not a viable model here.

Erasure. In an alternate model, epibionts may be removed from older shells (erasure) through taphonomic processes of shell abrasion and fragmentation or through bioerosion. Previous workers have noted reduced coverage and diversity of epibionts on heavily altered Paleozoic brachiopods (Bordeaux and Brett 1990), and similar results have been noted for modern reefs (Rasmussen and Brett 1985). In an erasure-dominated scenario, stable abundance and diversity patterns are achieved if epibiont removal balances colonization rates over a sufficient interval of time. If true, all of the epibionts on a shell would coexist within a narrow temporal window.

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The role of erasure is relatively easy to discern. If true, increasing taphonomic scores (measures of host damage) should show a negative correlation with epibiont abundance or diversity, because only taphonomically robust epibionts would be preserved. When evaluated versus taphonomic scores recorded for valve fragmentation, abrasion, and other shell damage (Carroll et al. 2003), epibiont abundance and diversity show very weak positive correlations with increasing damage ($r^2 = 0.06$ for abundance, 0.07 for diversity). These correlations are not significant and do not provide much support for the erasure model; rather, they are more consistent with the notion that encrustation increases on more heavily altered shells.

The taphonomy of epibionts themselves was not directly measured, but it can be analyzed indirectly by examining the proportion of epibionts that cannot be identified to morphospecies level because of abrasion and other taphonomic damage. No significant difference is observed in the ratio of identifiable to unidentifiable specimens between older and younger host shells (Pearson: $r = -0.01$, $p = 0.92$, $n = 57$; Spearman: $r = -0.14$, $p = 0.30$, $n = 57$). Therefore, the data presented here do not support the view that epibionts are preferentially removed from older hosts.

Another test for erasure is the evaluation of changes in bioerosion with host age. The colonization of shells by endobionts is likely to proceed in a manner similar to colonization by epibionts, but it is more difficult to eradicate evidence for bioerosion from a shell than it is to remove an epibiont skeleton. In contrast to expectations under the erasure model, bioerosion frequencies decrease with host valve age rather than increase. Thus, the increased abundance and richness observed in younger epibiont assemblages are not likely to reflect a preservational artifact. However, increasing frequencies of bioerosion and encrustation on younger shells could record a biological signal if the duration of shell exposure is limited.

Limited-Exposure Scenarios. The remaining interpretations suggest that shells are exposed to colonization by epibionts (and endobionts) for brief intervals after the death of the host. This is consistent with modern models of time averaging of soft-substrate assemblages (e.g., Flessa et al. 1993; Parsons-Hubbard et al. 1999; Carroll et al. 2003). The exposure history of a shell plays a critical role in its colonization history, at least where bioturbation produces a deep, taphonomically active zone.

One interpretation of the data is that shells were exposed briefly between the death of the host and burial and that hosts were never exhumed before collection. In this case, epibiont assemblages should be ecological snapshots with a temporal resolution encompassing no more time than the interval between death and burial. This scenario is fully consistent with the abundance and diversity data collected and provides the best explanation of the shifting abundance of taxa between younger and older hosts. One argument against this interpretation is the observation that infaunal bivalves from the same study area are frequently encrusted. This suggests that exhumation is not uncommon, and comparative study of bivalve and brachiopod encrustation is needed to answer some of the questions raised here.

It is worth noting that shells that are buried and exhumed repeatedly would be exposed to surface processes (encrustation, bioerosion, abrasion) more frequently than permanently buried shells. Despite a short initial window for epibiont colonization, shells could pass through this window repeatedly, accreting increasingly diverse and abundant epibiont assemblages over time. Even if these shells spend brief intervals at the sediment-water interface, multiple exposures complicate the interpretation of epibiont assemblages. In this case, mean epibiont abundance and diversity of older shells should exceed that of younger shells, so long as exhumation and reburial are independent of shell age. As the data presented here do not indicate higher mean values of abundance or diversity on older shells, this scenario is not consistent with the observed data.

Taphonomic processes may not destroy epibionts, but they could change the susceptibility of host valves to epibiont colonization. For instance, the primary layer of periostracum can deter colonization, because specialized structures in bivalve periostracum have been shown to impede boring organisms and influence epibiont colonization patterns (e.g., Bottjer and Carter 1980). Boring polychaetes have also been observed in commensal or parasitic relationships with *Bouchardia* maintained alive in aquaria, sometimes prefiltering the inhalant currents. Their feeding may inhibit epibiont settlement, as would the feeding processes of previous colonists or even the live host.

Exposure need not be a matter of burial, or even host death, because both live and dead individuals can be covered by soft-bodied epibionts (e.g., Rasmussen and Brett 1985). The development of biofilms and the action of bioeroders may further inhibit encrustation. However, the lack of meaningful correlation between altered shells and encrustation suggests that this has little effect.

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In short, the data appear to support a model in which epibiont colonization is limited to a brief interval during the life and shortly after the death of the host valve, even if shells pass through the taphonomically active zone on multiple occasions. One positive consequence of this is that it affirms the long-held notion that epibionts preserved on a shell can document interactions between and among coexisting live individuals and colonies rather than merely passive overgrowth (e.g., Jackson 1977; Buss and Jackson 1979; Lescinsky 1997). Whether this is the result of rapid burial or of rapid valve coverage by biofilms and unpreservable epibionts remains a matter for further investigation.

Faunal Changes. Some of the patterns observed in the abundance and diversity data may reflect natural or anthropogenic ecological changes in the epibiont assemblages studied over centuries to millennia. Such changes could occur in conjunction with the previously discussed taphonomic models but must be interpreted carefully, depending on the circumstances of their preservation. Consistent patterns occur among all sites observed: serpulids represent a greater proportion of the total epibiont fauna, relative to bryozoans and other taxa, in the past 120 yr. Because a taphonomic bias against serpulids seems unreasonable, this suggests a real sensitivity in the epibiont record to faunal changes over decades to centuries. The absence of foraminifera on older shells and their presence on younger shells at localities 3 and 4 (Ilha das Couves and Ubatuba Bay) provide further support for this idea and might record recent immigration of these taxa into localities where they were previously absent. The change in the faunal composition of these epibiont assemblages as a function of host age is most readily interpreted as changes in the epibiont fauna over time. This strengthens the argument that these assemblages represent ecological snapshots, despite the potential for long-term overexposure. If this is true, studies of encrustation of dated shells may have utility for tracking changes in productivity and the migration of taxa in the subfossil record and may provide evidence of anthropogenic environmental change (e.g., eutrophication).

The relationship between epibiont abundance and diversity is typical of benthic assemblages, but the apparent decrease in variability with increasing age is curious. This might be a sign of time averaging on individual shells: the longer the host is exposed, the closer its epibiont fauna comes to representing a long-term average of epibiont abundance and diversity. Such a pattern might even represent some form of ecological succession. However, the data do not support this interpretation, because older shells host fewer epibionts and less diverse assemblages.

This problem appears to be an artifact of sample size. Because there are fewer shells in each old cohort than in each young cohort, less variability is expected, from a statistical point of view. Because time averaging of faunas should result in more uniform epibiont assemblages, comparison of young and old assemblages by multidimensional scaling (MDS) can be used to test for this pattern. Removing fragile taxa that could be removed from host valves by taphonomic processes, MDS results do not support the assertion that older valves have more time-averaged epibiont faunas (young: dim1 Var = 1.09, dim2 Var = 0.85, total variance = 1.94; old: dim1 Var = 1.15, dim2 Var = 0.72, total variance = 1.87). This is consistent with the limited-exposure model, because there would be little chance for time averaging to occur on individual valves if colonization were limited to a brief window of opportunity.

Taphonomic Interpretations. The results of this study support previous suggestions (e.g., Lescinsky 1997) that epibiont assemblages on individual host shells have a temporal resolution in the range of weeks to decades, not centuries. In combination with shell-dating techniques, epibionts may allow the evaluation of long-term (decades to centuries) changes in modern benthic marine faunas and provide important clues about the taphonomic history of these shells. Encrustation can occur only at or above the sediment-water interface, and given that older shells do not have more abundant or diverse epibiont faunas, it appears that shells of different ages experience similar exposure histories. The fact that maximum epibiont diversity and abundance are reached quickly suggests that burial occurs within a matter of decades. Observations from taphonomic deployment experiments indicate that this period may be as short as months or weeks (e.g., Parsons-Hubbard et al. 1999).

Exhumation of shells by storms and bioturbation should influence the record of encrustation, and the presence of encrusted infaunal bivalves from the same sites indicates that this occurs on a regular basis. Older shells might be subject to more cycles of exhumation and might spend a greater length of time exposed at the surface. These reworked shells should be colonized by a greater number of epibionts and show higher frequencies of bioerosion. Because neither epibiont abundance nor bioerosion frequency increase with host age, posthumous exposure intervals may be so brief and uncommon that the record of encrustation is not affected. However, valve exhumation may be consistent with the

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data collected here if older shells are colonized much less frequently than young shells. It is worth stressing that the reasons for this are still unknown, but they may be related to the development of biofilms or other unpreserved epibionts, thin veneers of sediment coating the shell, the loss of periostracum, changes in microtexture due to bioerosion, or simple long-term burial.

Analytical Time Averaging. Unlike the epibiont assemblages encrusting them, modern *Bouchardia* experience time averaging on the order of centuries to millennia (Carroll et al. 2003). Because they show age distributions similar to those of modern bivalve assemblages (e.g., Kowalewski et al. 2000), these brachiopods are likely subjected to the same degree of reworking and encrustation as bivalves, despite being demonstrably more fragile (e.g., Emig 1990; Daley 1993; Torello et al. 2002). In consequence, time averaging of substrate shells still affects the temporal resolution of their epibiont assemblages. This artifact is an example of a phenomenon best described as "analytical time averaging."

The temporal resolution of epibiont assemblages on individual shells appears to be better than the error margins of the dating techniques used here, and individual encrusted shells provide ecological snapshots with a resolution of weeks or months. However, short-term changes in epibiont assemblages can be observed in the fossil record only if ages are determined for individual hosts. No matter how good the temporal resolution is for individual epibiont associations on individual shells, the resolution of pooled data from multiple shells is artificially time averaged unless the age of each shell is known. Individual snapshots provide insight into the moment they were taken, but ages for shells serve the same function as time stamps in photography, providing the temporal context integral to their interpretation as part of a longer time series.

Because individually dated shells cannot be obtained often, it appears that the temporal resolution of pooled epibiont assemblages in the fossil record can never be as good as the temporal resolution of assemblages on individual shells. When groups of encrusted shells are considered, the same virtues and perils of time averaging apply to epibiont assemblages as govern their hosts. This should not be a cause for despair, because it may improve some aspects of their utility in paleoecology. For instance, time averaging provides time-weighted averages of ecological conditions less subject to the vagaries of short-term population dynamics (e.g., Walker and Bambach 1971; Kowalewski et al. 1998), such as those noted in this study. The recognition of this phenomenon is vital to developing a thorough understanding of the importance of taphonomy in paleoecological studies of encrustation.

Conclusions

Comparison of epibiont abundance and diversity data obtained from 86 brachiopod with individual ages determined by ^{14}C-calibrated amino acid racemization rates (Carroll et al. 2003) suggests that epibiont colonization occurs during a brief interval after the death of the host. Despite extensive time averaging of the brachiopod hosts in a setting where shells are known to experience at least occasional exhumation, the abundance and diversity of epibionts per host valve reach maximum values within the first century. Differences in the relative abundance of taxa as a function of valve age suggest that burial takes place rapidly and that later exhumation does not result in significant recolonization of valves, although the reasons remain unclear. Thus, dated shells can be used to construct ecological records of epibiont assemblages over decades to centuries.

These results support evidence from experimental deployment studies (e.g., Parsons-Hubbard et al. 1999; Lescinsky et al. 2002) that encrustation takes place relatively rapidly. The exposure histories of the hosts appear to be similar, and the abundance and diversity of epibiont assemblages are not affected by the age of the host, even when the composition of these assemblages changes over time. Thus, epibiont assemblages on individual valves may represent ecological snapshots in the fossil record, providing both high temporal resolution and spatial resolution, and comparisons among shells are likely to provide consistent data. However, their host valves are still subject to time averaging, and pooling data from multiple shells without adequate age control will artificially reduce the temporal resolution of the whole assemblage. The temporal resolution of paleoecological data collected from assemblages of encrusted shells must therefore be interpreted with care.

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