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Changes in shell durability of common marine taxa through the Phanerozoic: evidence for biological rather than taphonomic drivers

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Abstract.—Phanerozoic trends in shell and life habit traits linked to postmortem durability were evaluated for the most common fossil brachiopod, gastropod, and bivalve genera in order to test for changes in taphonomic bias. Using the Paleobiology Database, we tabulated occurrence frequencies of genera for 48 intervals of ~11 Myr duration. The most frequently occurring genera, cumulatively representing 40% of occurrences in each time bin, were scored for intrinsic durability on the basis of shell size, reinforcement (ribs, folds, and spines), life habit, and mineralogy.

Shell durability is positively correlated with the number of genera in a time bin, but durability traits exhibit different temporal patterns across higher taxa, with notable offsets in the timing of changes in these traits. We find no evidence for temporal decreases in durability that would indicate taphonomic bias at the Phanerozoic scale among commonly occurring genera. Also, all three groups show a remarkable stability in mean shell size through the Phanerozoic, an unlikely pattern if strong size-filtering taphonomic megabiases were affecting the fossil record of shelly faunas. Moreover, small shell sizes are attained in the early Paleozoic in brachiopods and in the latest Paleozoic in gastropods but are steady in bivalves; unreinforced shells are common to all groups across the entire Phanerozoic; organophosphatic and aragonitic shells dominate only the oldest and youngest time bins; and microstructures having high organic content are most common in the oldest time bins.

In most cases, the timing of changes in durability-related traits is inconsistent with a late Mesozoic Marine Revolution. The post-Paleozoic increase in mean gastropod reinforcement occurs in the early Triassic, suggesting either an earlier appearance and expansion of durophagous predators or other drivers. Increases in shell durability hypothesized to be the result of increased predation in the late Mesozoic are not evident in the common genera examined here. Infaunal life habit does increase in the late Mesozoic, but it does not become more common than levels already attained during the Paleozoic, and only among bivalves does the elevated late Mesozoic level persist through the Holocene.

These temporal patterns suggest control on the occurrence of durability-related traits by individual evolutionary histories rather than taphonomic megabiases. Our findings do not mean taphonomic biases are absent from the fossil record, but rather that their effects apparently have had little *net* effect on the relative occurrence of shell traits generally thought to confer higher preservation potential over long time scales.

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Introduction

The intrinsic durability of a shelly exoskeleton, which determines the ability of a living animal to withstand physical, chemical, and biological assaults, also affects the shell's probability of surviving destructive postmortem processes and in turn has direct bearing on the likelihood of the individual's becoming a fossil. In parallel, the intrinsic durability of a taxon (or other biological entity, such as an age-class or functional group), which we define as the resistance to postmortem destruction conveyed by group-specific morphologic traits of the living organism, clearly figures prominently in whether the group is represented in the fossil record. For example, it is well known that the fossil records of soft-bodied groups contain larger gaps than do those of groups with mineralized or otherwise refractory tissues. Within the range of durability represented by shelled organisms that constitute the majority of the Phanerozoic marine record, what is the impact of variation in intrinsic durability on through-time trends in this record? Because changes in shell durability could result in taphonomic megabiases relating to preservation of more versus less durable taxa, understanding factors that control long-term changes in shell durability is essential to evaluating macroevolutionary patterns and processes that are commonly assumed to be biological in origin.

Taphonomic "megabiases" in large-scale paleobiological patterns (term of Behrensmeyer and Kidwell [1985]; concept first hypothesized by Efremov [1940]) could result from broad-scale changes in the *intrinsic* preservation potential of different organisms, including durability, and/or the *extrinsic* environmental controls on preservation. Studies at a range of scales suggest that some portion of the observed variability in Phanerozoic diversity reflects preservational artifacts rather than purely biological changes in taxonomic richness or ecological dominance (e.g., Peters 2005; Cherns and Wright 2009; Hendy 2009; Kosnik et al. 2009; Sessa et al. 2009). Such postulated long-term changes in preservability due to escalation are a key component of the Mesozoic Marine Revolution (Vermeij 1977, 2002). There also has a been a long-standing debate on the extent to which taphonomic biases based on body type might affect observed paleontologic patterns of taxonomic richness and abundance at various scales (e.g., Efremov 1940; Behrensmeyer and Kidwell 1985; Kidwell and Baumiller 1990; Greenstein 1991; Allison and Briggs 1993a,b; Kidwell and Brenchley 1994, 1996; Kowalewski and Flessa 1996; Harper et al. 1997; Schubert et al. 1997; Cherns and Wright 2000, 2009; Alroy et al. 2001, 2008; Wright et al. 2003; Behrensmeyer et al. 2000, 2005; Cooper et al. 2006; Kowalewski et al. 2006; Kosnik et al. 2007, 2009; Hendy 2009; Sessa et al. 2009).

Intrinsic megabias in preservability might arise from sweeping changes—some quite rapid—that occurred in marine organisms and communities during the Phanerozoic (e.g., Wagner et al. 2006). These include changes in intrinsic shell durability and infaunal versus epifaunal life habit. For example, evolutionary increases in shell size, shell reinforcement, and infaunality as expressions of escalation (e.g., Vermeij 1977, 2002) might increase the proportional richness or abundance of readily preserved genera. The fusion of bivalve mantle margins into siphons, permitting bivalves to maintain deeper and more completely infaunal habits, allowed the exploitation of new resources and provided refuge from predation (Stanley 1977) but probably also increased bivalve preservation potential, according to actualistic and fossil studies (Valentine 1989; Best and Kidwell 2000; Lazo 2004; Rivadeneira 2010; but see Valentine et al. 2006). Among gastropods, the reduction of the primitive double-gilled condition of early gastropods to the modern monopectinate state allowed elongate apertures, inhalant siphons, streamlined shapes, and perhaps smaller body sizes (Erwin 1990; Lindberg and Ponder 2001) that could reduce the average preservation potential of gastropods over the Phanerozoic. Shell mineralogy, which has changed in many groups, possibly in response to changing ocean chemistry (e.g., Harper et al. 1997; Stanley and Hardie 1998; Stanley 2006; but see Kiessling et al. 2008), should affect the relative preservation of genera via the solubility of shells on the seafloor and during diagenesis. In addition to changes in mineralogy, long-term changes in the relative proportion of organic and biomineral phases (''organic content'') of shells might affect intrinsic fossilization potential (e.g., Glover and Kidwell 1993; Harper 2000; but see Tomašových and Zuschin 2009), a mechanism suggested to explain the apparent Phanerozoic decline in the quality of the fossil record of lingulid brachiopods (Cusack and Williams 1996; Kowalewski and Flessa 1996; for other patterns see Kidwell and Brenchley 1996 and Kidwell 2005). Increasing metabolic rates and fecundity should increase the rate of shell supply and thus the overall abundance of fossils from those groups, as would evolutionary expansion into settings that are more favorable to preservation (e.g., Bambach 1993; Kidwell and Brenchley 1994, 1996). The effects of fecundity and range size will be discussed later in greater detail.

Possible extrinsic causes of megabiases include the frequency of recurring conditions that preserve soft-tissues (e.g., Allison and Briggs 1993b; Orr et al. 2003), the latitudinal distribution of paleocontinents (e.g., Allison and Briggs 1993a; Taylor and Allison 1998), the saturation state of oceans (e.g., Dickson 2002; Stanley 2006), the depth and intensity of bioturbation and associated early diagenesis (Thayer 1983; Droser and Bottjer 1989; Sepkoski et al. 1991; James et al. 2005), evolutionary increases in durophagous predation (e.g., Vermeij 1977, 2002, 2008), changes in replacement and lithification (Schubert et al. 1997; Kowalewski et al. 2006; Sessa et al. 2009; Hendy 2009), and the geological survival or exposure in outcrops of fossil-bearing rocks (Raup 1976; Peters and Foote 2001; Peters 2005; McGowan and Smith 2008). A priori, the effects of extrinsic factors on fossil preservation might amplify trends in biological evolution but might also counteract or even swamp them (Behrensmeyer and Kidwell 1985; Kidwell and Brenchley 1994, 1996). For example, increasing depth and intensity of bioturbation over the Phanerozoic should increase time-averaging, but time-averaging could decrease if the promotion of porewater acidification hastens shell loss or if advective burial of shells is accelerated. Similarly, increasing predation might improve the average inclusion of prey species in fossil assemblages because of morphologic and behavioral responses that favor their preservation, but it might also decrease the average quality of the prey fossil record because most forms of durophagous predation result in the fragmentation and destruction of shells.

It is extremely unlikely that any of these potential biases—either individually or in their combined effect—have remained constant over any large temporal or spatial extent. Here we ignore possible variation in the completeness of the rock record and focus instead on variation in the traits of fossils that are preserved in the global rock record, particularly among the genera that occur most frequently. To evaluate whether changes in the number of shell genera or occurrences are products of taphonomic bias rather than the evolutionary history of individual groups, we compare the timing of changes in intrinsic shell durability (including infaunal versus epifaunal life habit) among three shelled groups that dominate the fossil record—brachiopods, bivalves, and gastropods. Changes in preservation potential—e.g., fluctuations in ocean saturation state, secular increases in bioturbation, durophagous predation and lithification, cumulative elapsed time in general—should create synchronous changes or similar long-term trends in the relative abundance of intrinsic traits across taxonomic groups because the same external circumstance is imposed on all taxa (e.g., Fig. 1A). For example, an increase in predation on the benthos would be expected to drive synchronous increases in durability across groups. In contrast, the evolutionary history of a morphological trait is by definition specific to a particular taxonomic group, and thus synchronous changes across groups are not expected. For example, the development of siphons by bivalves and gastropods were evolutionarily independent events that occurred at different times (e.g., Fig 1B).

Here we use information on the intrinsic durability of the most common brachiopod, bivalve, and gastropod genera in the marine

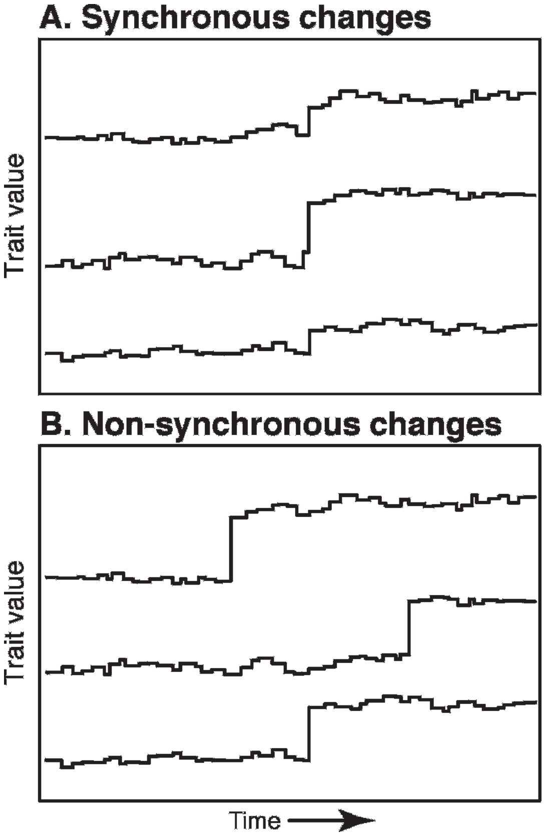

FIGURE 1. Examples of synchronous (A) and non-synchronous (B) changes through time in three different groups (e.g., brachiopods, bivalves, and gastropods over the Phanerozoic). Synchronous changes over time in the average durability of different groups suggests that they responded to the same extrinsic driver, which might be biological or taphonomic (e.g., a shared response to increased predation as a result of the Mesozoic Marine Revolution, to increased bioturbation and its cascading effects on dissolution, or to decreasing lithification and associated sieve effects). Non-synchronous changes in durability, denoting a different history for each group, indicate intrinsic causes (caused by macroevolution within each group).

record to assess the relative importance of evolutionary and taphonomic drivers of Phanerozoic-scale patterns in the numbers of genera and occurrences. These three shelly macrobenthic groups arguably include the most common and best-preserved higher taxa in the marine fossil record (Sepkoski 1981; Alroy et al. 2001, 2008; Miller et al. 2009; Alroy 2010). Building on our earlier analysis (Behrensmeyer et al. 2005), we recognize durable taxa as having shells that are relatively large and/or reinforced by ribs, folds, spines (Table 1). We also consider three other variables thought to affect shell preservation, namely life habit (epifaunal versus infaunal), shell mineralogy, and, for bivalves, shell organic content (Table 1). We find that these variables do not show synchronous patterns of change in the three groups through the Phanerozoic record indicative of taphonomic megabias but instead provide evidence for biologically interesting trends relating to shell durability.

Methods

Our analyses are based on two data sets: (1) *occurrence data set*, a download of brachiopod, bivalve, and gastropod genera in the Paleobiology Database (PaleoDB, http://paleodb.org/); and (2) *durability data set*, consisting of data on the durability characteristics for the most frequently occurring genera in the occurrence data set, based on examination of specimens in museums, other academic collections, and monographs (following Behrensmeyer et al. 2005, where this was referred to as the ''taphonomic data set'').

Occurrence Data Set

Data on the number of genera and the frequency of their occurrence were derived from the PaleoDB as of 17 December 2009. The PaleoDB recorded 39426 brachiopod, 58640 bivalve, and 42170 gastropod occurrences, representing 2610, 2460, and 3595 unique genus names respectively. Occurrence frequency does not reflect the abundance of *specimens* of a genus in individual collections, but rather the number of *collections* in which the genus is present, where a collection is the fauna reported from a particular stratigraphic unit at a particular locality. An individual occurrence in our data set may thus be based on the recovery of thousands of complete specimens or a single fragment. For each taxonomic group, occurrences were tabulated independently. Most taxa are numerically rare, both in modern communities and in the PaleoDB (e.g., Plotnick and Wagner 2006). We thus focus here on the most common genera within each of three major groups. The most common genera should be least prone to bias associated with incomplete knowledge of the fossil record in that additional sampling

TABLE 1. Metrics of durability and component variables used to calculate those metrics. No. genera and No. specimens indicate the number of genera and specimens were measured or scored. *na* variables were compiled at the supergeneric level. Organic content was scored for bivalves only.

Durability metric	No. of genera	No. of specimens	Description	Units
Size	933		$\sqrt{X * Y}$	mm
Shell reinforcement	929		(ribs + folds + spines) / 3	
Life-habit score	1002		life habit score	
Mineralogy score	981		mineralogy score	
Organic content score	277		organic content score	
Component variables				
X	933	2525	maximum dimension	mm
Y	933	2525	maximum dimension perpendicular to X	mm
Ribs, folds, spines	929	2326	0 = absent, 1 = present, 2 = prominent	rank
Life-habit score	1002	*na*	0 = epifaunal, 0.5 = semi-infaunal, 1.0 = infaunal	rank
Mineralogy score	981	*na*	0 = phosphatic, 0.5 = aragonitic 1.0 = bimineralic, 1.5 = calcitic	rank
Organic content score	277	*na*	0 = high, 0.25 dom-high, 0.5 = hetero 0.75 = dom low, 1.0 = low	rank

often uncovers additional rare taxa, whereas significant effort is generally required for an uncommon taxon to become common. Our approach should yield robust estimates of the most commonly occurring taxa at the expense of ignoring less frequently occurring genera.

Each group's occurrence data set was created by identifying the most frequently occurring genera in each time bin, with the Phanerozoic divided into 48 ~11-Myr-long time bins (see Appendix 1 in the online supplemental material at http://dx.doi.org/10.1666/10022.s1). From this, we selected for analysis the most frequently occurring genera that cumulatively represented 40% of that group's total occurrences in each bin, with a minimum of five genera per time bin. This selection criterion yields a reasonable number of genera (median = 37) and occurrences (median = 668) per bin throughout the Phanerozoic for all three groups combined but allows the relative proportions of the three groups to vary from bin to bin, mirroring patterns seen in the total PaleoDB for these groups (black versus light gray lines in Fig. 2A–C). Our occurrence data set includes 328 brachiopod, 283 bivalve, and 391 gastropod genera and 15827, 23821, and 16910 occurrences respectively (see Appendix 2, online).

This occurrence data set encompasses about 12% of the brachiopod, bivalve, and gastropod genera recorded in the PaleoDB. It includes genera that commonly occur, for example, in more than 600 collections (i.e., *Turritella, Ostrea,* and *Chlamys*) as well as genera occurring in only one or two collections (22 genera). Subgenera are treated as genera for consistency with previous analyses (e.g., Sepkoski 1993; Alroy et al. 2001; Behrensmeyer et al. 2005). All occurrences of the same (sub)genus in a collection were considered to be a single occurrence regardless of multiple species. Multiple collections from identical geographic coordinates and formation were treated as a single collection to minimize the effect of multiple records within single well-studied localities or stratigraphic units, and to maximize consistency with previous analyses (e.g., Alroy et al. 2001; Behrensmeyer et al. 2005).

Focusing on these most common genera, the numbers of genera and occurrences in the three groups vary through time, with brachiopods dominating Paleozoic assemblages and molluscs the post-Paleozoic (Fig. 2). The data set spans the Phanerozoic except the first Cambrian bin, which is largely devoid of macrobenthic fossils. Taxonomic diversity and turnover among higher groups seen in this data set resemble the well-established patterns documented by previous studies (e.g., Sepkoski 1981; Alroy 2010). The numbers of brachiopod genera and occurrences per time bin peak in the early to mid-

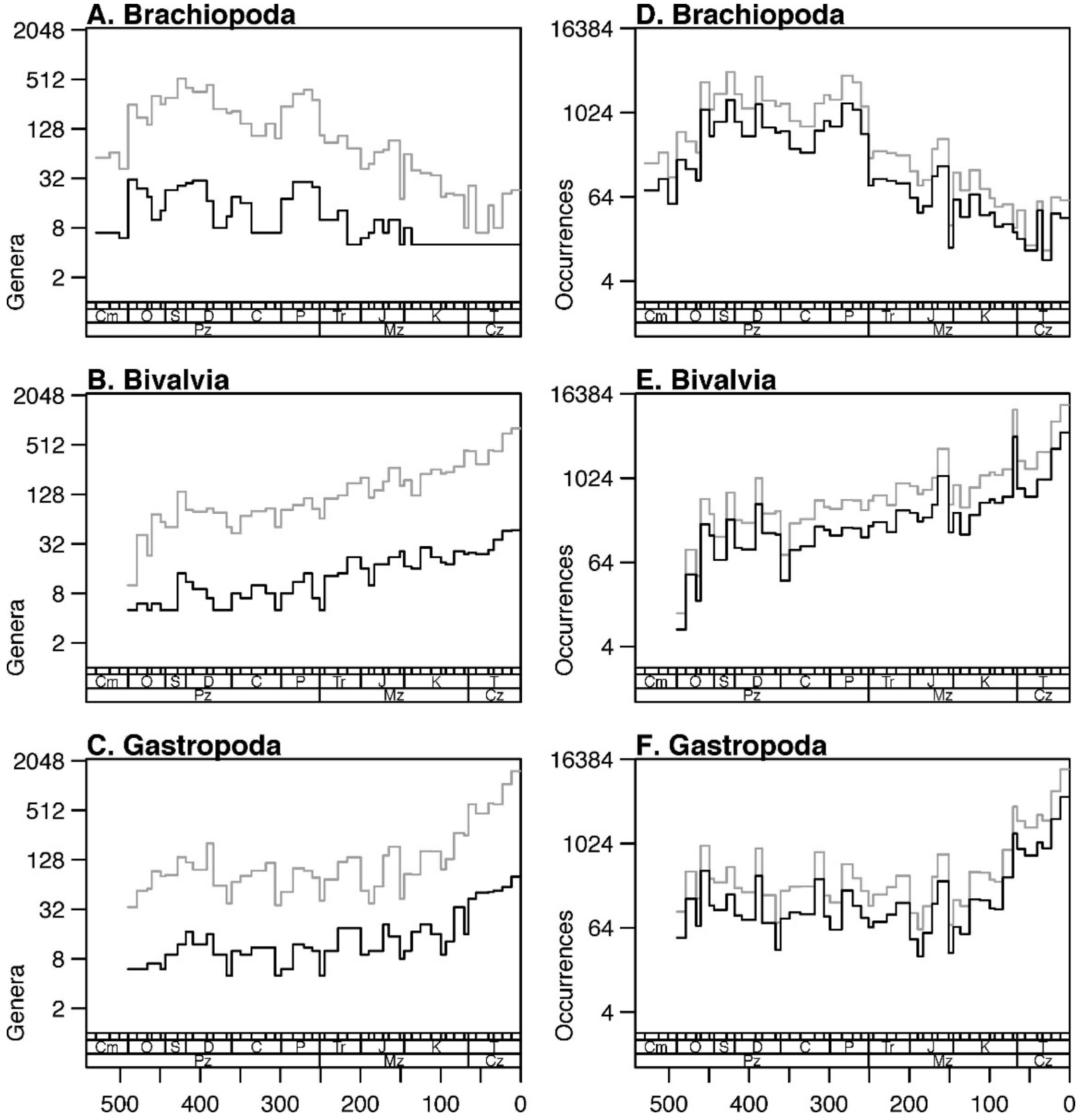

FIGURE 2. Change over the Phanerozoic in the number of genera (A–C, left column; $\log_2$) and number of occurrences (D–F, right column; $\log_2$) of the major taxonomic groups analyzed here, based on data from the PaleoDB. Phanerozoic timescale on the x-axis with geologic age (Ma), eras, periods, and analytic time bins (~11 Myr each). Gray lines indicate the total numbers recorded in the PaleoDB, and black lines indicate numbers for the most common 1002 genera analyzed here (occurrence data set).

Paleozoic and decline through the Meso-Cenozoic (Fig. 2A,D), the number of bivalve genera and occurrences per bin increase through the Meso-Cenozoic (Fig. 2B,E), and the number of gastropod genera and occurrences per bin increase strongly in the late Mesozoic and Cenozoic (Fig. 2C,F).

In some bins, certain taxonomic groups have low numbers of occurrences, notably post-Permian brachiopods (Fig. 2D), and molluscs before the Middle Ordovician (Fig. 2E,F), but we have retained these intervals because these patterns appear to reflect actual biological conditions (e.g., Yochelson 1981; Qian and Bengtson 1989; Xu and Grant 1994; Wagner 1999; Pojeta 2000). Brachiopod analyses include all 48 time bins from the Middle Lower Cambrian (Cambrian 2) through the Holocene. Bivalve and gastropod analyses include all 45 time bins from the Ordovician through the Holocene. Two Early Cambrian bivalves (*Pojetaia* and *Fordilla*) are included in the figures for reference but are not included in the quantitative analyses because of the low number of genera in the bin, the 20-Myr gap between those occurrences and all other bivalve occurrences, and the debate over their systematic placement (Yochelson 1981; Pojeta 2000; Elicki and Gürsu 2009). Our coverage of the most frequently occurring 40% of the genera in each higher taxonomic group is fairly consistent through the Phanerozoic, but in a few bins it reaches as much as 90% of occurrences where the total number of taxa and occurrences are low (e.g., Cenozoic brachiopods).

Durability Data Set

A wealth of evidence from manipulative and observational experiments over the last several decades indicates that shell preservation potential in modern environments generally increases with durability, which includes shell size, presence of prominent shell reinforcements (ribs, folds, spines), inclusion of calcite and/or low-organic microstructures, and infaunal life habit (for reviews, see Parsons and Brett 1991; Kidwell and Bosence 1991; Briggs 1995; Martin 1999; Harper 2000; Sanders 2003, and Zuschin et al. 2003). In addition, larger shells are probably more likely to be seen and recovered (especially if specimens are collected from outcrop surfaces rather than processed from bulk samples) and more likely to be identified to the species or at least genus level (see Cooper et al. 2006). Shells with more and/or stronger ribs, folds, and spines will leave more taxonomically identifiable fragments than unornamented or unreinforced shells (e.g., Kowalewski et al. 2003). Both of these durability-related traits should increase the probability that genera possessing them will be mentioned in geological as well as specialist paleontological publications and thus will be incorporated into compendia of fossil taxa such as the PaleoDB. For simplicity, in the discussion below we use ''durability'' to refer to all intrinsic traits, both morphological and ecological, that increase preservation potential.

Information on intrinsic traits relevant to postmortem durability (e.g., preservation potential) was gathered for each genus in the occurrence data set (see Appendix 3, online). Specimens were scored by one or more of the authors using the durability metrics listed in Table 1 (described in more detail in Behrensmeyer et al. 2005). Shell size and reinforcement data were based on examination of individual specimens from museum and teaching/research collections and from published illustrations (monographs, treatises). When possible we included a range of species for each genus. The majority of the material measured originated from Northern Hemisphere museum collections.

Shell Size.—We measured the X, Y, and Z linear dimensions of specimens (mm), with X the longest dimension, Y the longest dimension perpendicular to X, and Z the dimension perpendicular to X and Y. Given the difficulty of obtaining all three measurements for some genera, we used the geometric mean of X and Y as our measure of shell size. This is a standard method of measuring shell size (Krause et al. 2007) and has been shown to be a good proxy for more complex measures of shell size (Kosnik et al. 2006). The mean size was used when size measurements were available for multiple specimens or congeneric species. Shell sizes were $\log_2$ transformed to normalize distributions and to reduce the effect of outliers. We measured specimens representing 933 of 1002 target genera (93%) and the mean number of specimens measured per genus was 2.7 (Table 1, Fig. 3A).

Shell Reinforcement.—Individual specimens were scored for each of three characters (ribs, folds, spines) using ordinal ranks, from lowest to highest preservation potential: 0 = absent, 1 = present, 2 = prominent. Commarginal banding or irregularities in shells caused by growth lines were not considered reinforcement. However, concentrically ridged ornament (including axial sculpture on gastropods due to apertural thickening during shell growth) was included, along with radial or spiral ridges, as ribs. Folds are relatively large invaginations of the commissure (bivalves, brachiopods) or aperture (gastropods) that deflect the interior as well as exterior surface

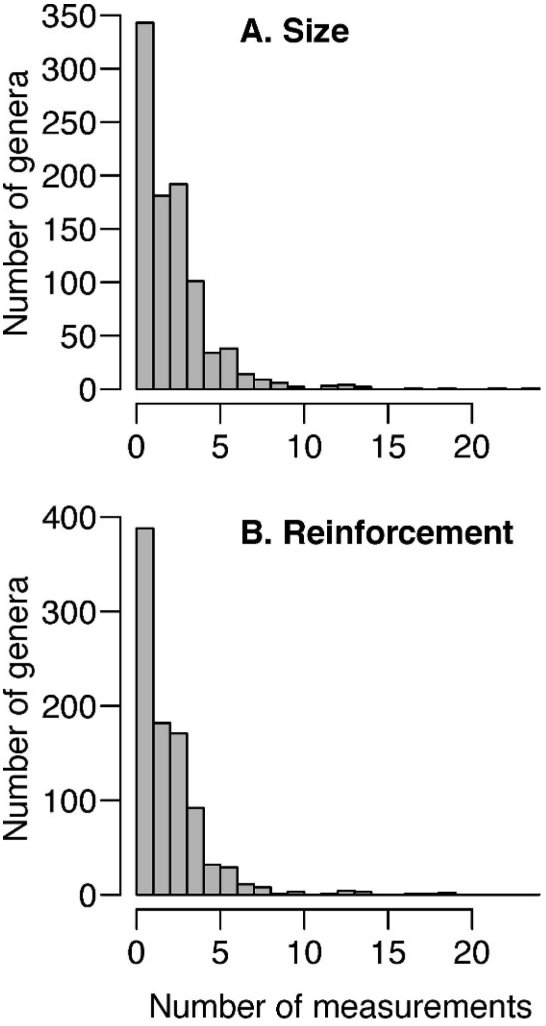

FIGURE 3. Histograms of the number of genera (y-axis) with a given number of specimens (x-axis) measured for shell size (A) and shell reinforcement (B). Approximately half of the genera in our durability data set are based on examination of two or more specimens.

of the shell (if such deflections are filled, they were considered ribs). The mean score was used when scores were available for multiple specimens or congeneric species. Scores for ribs, folds, and spines were combined into a single shell-reinforcement score by taking the mean of the three characters. We scored 929 of 1002 target genera (93%) and the mean number of specimens scored per genus was 2.5 (Table 1, Fig. 3B).

Life Habit.—Life habit was scored in ordinal ranks, from lowest to highest preservation potential: 0 = epifaunal, 0.5 = semi-infaunal, and 1.0 = infaunal taxa. Data for our 1002 genera were derived from existing life-habit assignments in the PaleoDB, which relied on taxonomic assignment to higher taxa (family, order) and analogy to living forms. The only boring bivalve (*Lithophaga*) in our data set was classified as infaunal.

Shell Mineralogy.—Shell mineralogy was scored in ordinal ranks, from lowest to highest preservation potential: 0 = organophosphatic, 0.5 = aragonite, 1.0 = bimineralic (both aragonite and low-Mg calcite shell layers present), and 1.5 = low-Mg calcite. To classify shell mineralogy we used published data for major shell layers (volumetrically minor myostracal shells layers were ignored) and the assignment of genera to families and orders, which tend to be conservative in mineralogy. Mineralogy was based largely on order-level information for brachiopods (Williams et al. 2000), and largely genus-level information for bivalves following Kidwell (2005), which drew upon many original sources but especially Taylor et al. (1969, 1973), Carter (1990), Harper et al. (2000), and Schneider and Carter (2001). See detailed supplementary information of Kidwell (2005). Gastropod mineralogy was based on a few compendia (e.g., MacClintock 1967; Batten 1984; Bandel 1990; Hickman and McLean 1990), widely scattered sources on individual genera, and consultation with taxonomic specialists. We classified the mineralogy of 981 of the 1002 target genera (98%). Genera without mineralogy data were all gastropods.

Bivalve Shell Organic Content.—Published information on shell microstructures was used to assign bivalve genera to five ordinal ranks, where high-organic microstructures such as nacreous and prismatic are thought to convey low preservation potential and low-organic microstructures such as crossed-lamellar and foliated have the highest preservational potential (following Kidwell 2005): 0 = exclusively high organic, 0.25 = heterogeneous but dominantly high, 0.5 = heterogeneous but equal mix, 0.75 = heterogeneous but dominantly low, and 1.0 = exclusively low organic. We were able to score 277 of the 283 bivalve genera (98%). Knowledge of brachiopod and gastropod shell microstructures and organic content is too incomplete for analysis here.

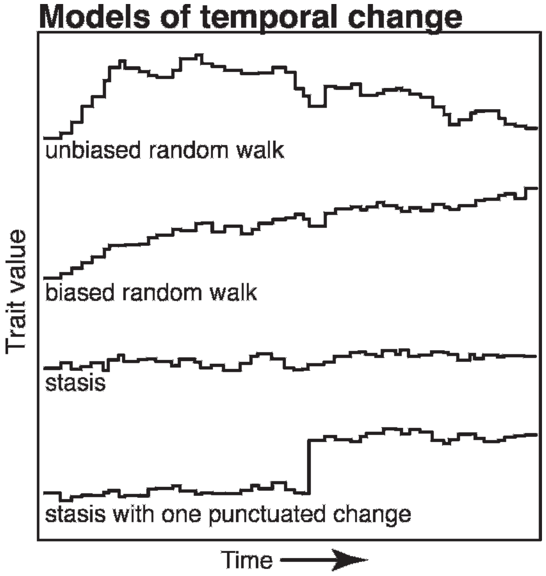

FIGURE 4. Examples of four alternative models of character change through time, with a hypothetical character (y-axis) plotted against time (x-axis). An unbiased random walk is equally likely to increase or decrease. A biased random walk tends to move in one direction over the alternative (illustrated here as a secular increase). Stasis tends to maintain a single mean value. Stasis with punctuated change is a model of stasis with two different mean values separated by a distinct transition. See Hunt (2006, 2008a,b) for more detailed explanations of the four models.

Analyses

We calculated the durability of each major group within each bin using occurrence-weighting, so that the average durability preferentially reflects the most common genera occurring in that time bin. These results should be robust to additional occurrence data and should reflect the durability of a typical bin-scale assemblage. Both measuring the most frequently occurring genera in each time bin and weighting genera relative to their occurrence frequency cause these analyses to emphasize the durability patterns among the most frequently occurring genera through the Phanerozoic.

Temporal Trends.—Our goal here is to test for secular trends through the Phanerozoic in occurrence-weighted traits thought to confer postmortem durability (e.g., increased preservation potential) and to discriminate among alternative numerical models for these time series (Fig. 4). Our data are thus analogous to morphological data used to examine evolutionary changes in fossil lineages (e.g., Hunt 2006, 2008a), and our analyses also are similar except that we examine changes in the occurrence of durability traits of genera within higher taxonomic groups rather than changes in the morphology of individuals within species. We thus evaluate our data using recent advances in fitting and comparing models of evolutionary change based on four models: the Biased Random Walk, the Unbiased Random Walk, Stasis, and Punctuated (2–4 periods of stasis with a minimum stasis period of ten time bins), as implemented by *PaleoTS*, version 0.3-1 (Hunt 2008b). In each case we are quantifying patterns of change through time and not suggesting the underlying evolutionary theories apply to our data set. All analyses reported here were implemented in the R statistical programming language, version 2.10 (R Developmental Core Team 2009), and we made extensive use of the functions from the package *PaleoTS*, version 0.3-1 (Hunt 2008b). The R software and *PaleoTS* package are freely available (http://r-project.org/).

The model-fitting procedures implemented in *PaleoTS* require four types of data (Hunt 2006). The time interval between data points (t), in our case PaleoDB time bins, was calculated using the midpoint of each time bin. The mean (x) and variance (V_p) of shell size or other durability score were determined using the R functions mean() and var() while excluding genera without data. The number of scored genera (not the number of occurrences) was used as the sample size (n) for each bin to avoid overestimating the precision of our means. The results presented here are not overly sensitive to different measures of variance or sample size. *PaleoTS* performs two types of model fits: (1) ancestor-descendant fitting, which in this case examines individual transitions for a given durability metric (e.g., shell size) between bins; and (2) joint fitting, which examines the entire time series at once for significant ''breaks'' in the trajectories through time. We present the results using the joint fitting functions. We found that the joint fitting functions were less likely to support models of stasis using our data than were the ancestor-descendant fitting functions. Models of punctuated change were fit using the puncGfit() function because no joint fitting function is available for punctuated models.

Model selection (i.e., goodness of fit) was performed using Akaike weights based on the AICc values provided by *PaleoTS.* Akaike weights can be considered the weight of evidence in favor of a model being the best of the models compared (Burnham and Anderson 2002). They are a convenient metric for the evidence favoring each model and can be used to indicate which model or models are most consistent with the observed data. These weights evaluate only the models being compared and do not preclude an untested model (such as U- or hump-shaped functions) providing a better fit to the data. We evaluate the four models illustrated schematically in Figure 4, and we discriminate non-synchronous step-functions (such as in Figure 1) by comparing the best-supported models.

In studies of morphological evolution, both the mean and the variance of a trait are often examined. While the model selection methods proposed by Hunt (2006, 2008a) explicitly include the variance around the mean, they do not measure changes in trait variance through time. Here, however, we use the same model-selection methods to examine changes in the range of durability through time. For shell size we examined changes in the 95th and 5th quantiles as proxies for larger and smaller shells. For shell reinforcement we examined changes in the 95th quantile as a proxy for the most-reinforced shells. We use type 2 quantiles calculated using the quantile() function in R. These quantiles do not assume any underlying value distribution, but instead report the unmodified value at the indicated position or the average value of the two adjacent positions if the specified quantile falls between two positions. For life habit, mineralogy, and organic content, we examined only the mean score, because of the variance structure imposed by discrete scoring at the genus level for these characters. The results presented here are not overly sensitive to different measures of variance or sample size. The overall results are consistent using other quantiles, but specific outcomes are affected.

Predicting the Number of Genera in a Time Bin Using Durability.—In addition to temporal trends these data can also be used to examine the relation between durability characteristics and the number of genera in a time bin. We make use of the stepAIC() function in R to perform a stepwise selection of durability metrics using AIC (Venables and Ripley 2002). For these analyses each durability measure is evaluated independently and the measures significantly contributing to the best multivariate model predicting the $\log_2$ number of genera in each time bin for each of the three taxonomic groups are identified. This comparison is potentially complicated by correlations among shell durability, shell production rates, and the size of geographic and stratigraphic ranges (see ''Caveats'' section below).

Predicting Genus Occurrences Using Durability.—Similar analyses also can be used to examine the relative importance of the various taphonomic characteristics in predicting the number of occurrences of each genus. As above, we make use of the stepAIC() function to perform a stepwise selection of durability metrics using AIC (Venables and Ripley 2002). For these analyses each durability measure is evaluated independently, and the measures that contribute significantly to the multivariate model that best predicts the $\log_2$ number of occurrences are identified. These analyses allow us to evaluate the relative importance of the different durability measures for each taxonomic group.

Results

Durability: Temporal Trends

Shell Size.—Each taxonomic group shows distinct, independent changes in shell size through the Phanerozoic (Fig. 5), using the mean, 5th, and 95th quantile shell sizes used as proxies for the average, smallest and largest occurring shells. Model supports are summarized in Table 2.

Brachiopod mean shell size is best represented by an unbiased random walk, although a biased random walk has some

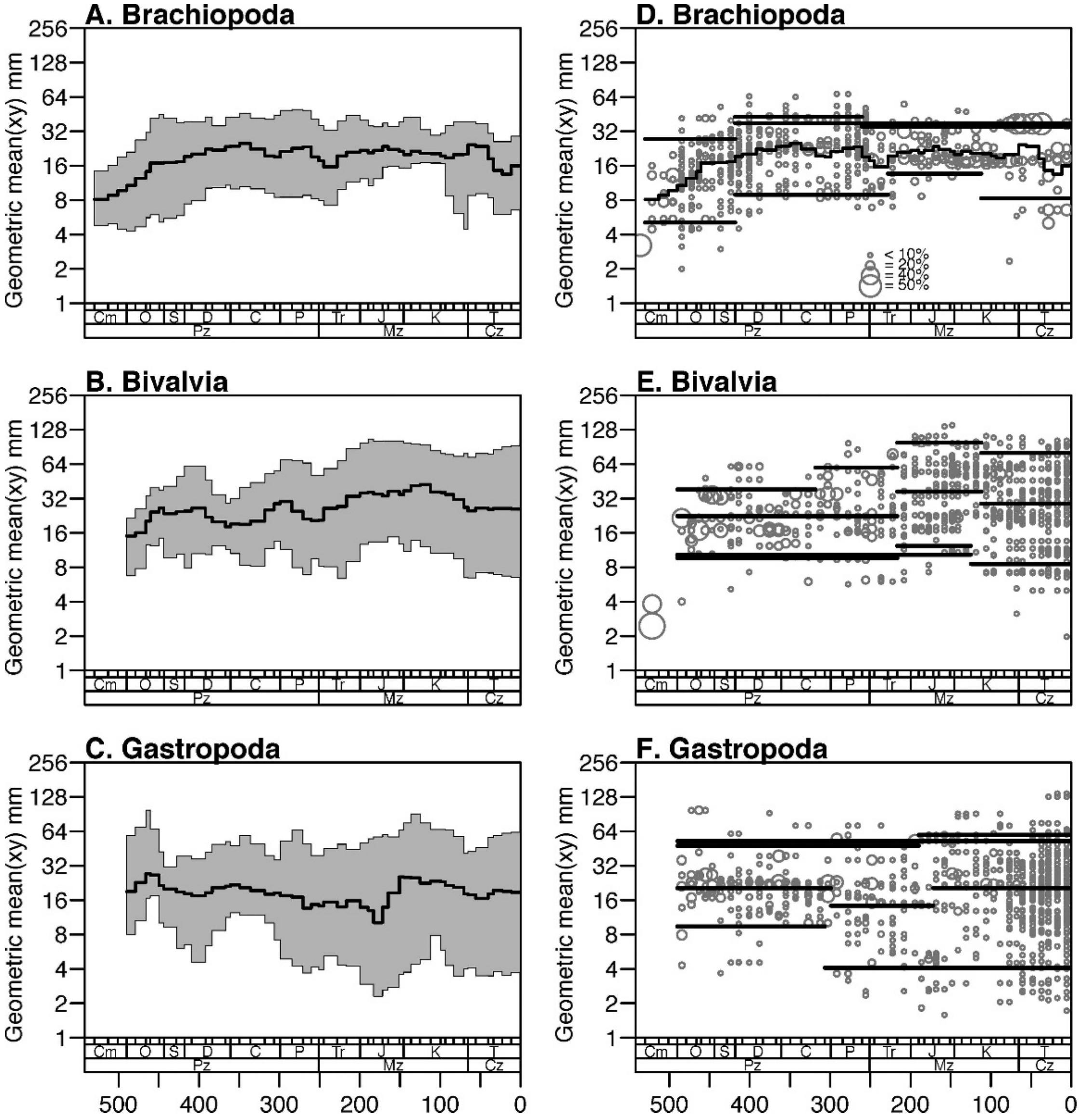

FIGURE 5. Occurrence-weighted shell size by taxonomic group. Phanerozoic timescale on the x-axis as in Figure 2. Geometric mean of x and y on the y-axis in millimeters with a $\log_2$ scale. In the left column (A–C), the solid black line is a three-point (three-bin) moving average of the mean occurrence-weighted shell size. The gray area is bounded by the 5th and 95th quantiles, which are used as proxies of the smallest and largest occurring shell sizes. In the right column (D–F) are the mean, 5th, and 95th quantiles as fit by *PaleoTS* (heavy black lines); each genus is plotted with a circle the size of which is proportional to its relative occurrence in the time bin. The three groups show distinct and independent histories of change in shell size.

support (Table 2). The support for a directional trend is found entirely within the Cambrian–Ordovician when brachiopods more than double in size from ~8 mm to >16 mm (Fig. 5A,D). Once the Silurian shell size is achieved it remains essentially unchanged through the remainder of the Phanerozoic, and if the Cambro-Ordovician time bins are removed a model of stasis is overwhelmingly favored. The increase in shell size through the Cambrian–Ordovician is also seen in largest occurring shells (the 95th quantile). Maximum size remains high (~45 mm) through the remainder of the Paleozoic, but decreases slightly to ~35 mm in the Meso-Cenozoic coincident with the

TABLE 2. Model support summary for mean, 5th and 95th shell size trends. GRW = general (biased) random walk. URW = unbiased random walk. P(X) = punctuated model where X is the number of periods of stasis. AICc = the Akaike Information Criterion for small samples, Δ AICc = the AICc relative to the lowest AICc. Weight = the Akaike weight for a particular model. Akaike weights are in bold font if they received ≥0.20 weight and they are in italic font if they received <0.05.

	Brachiopoda			Bivalvia			Gastropoda		
Model	AICc	Δ AICc	Weight	AICc	Δ AICc	Weight	AICc	Δ AICc	Weight
Mean									
GRW	30.38	0.45	**0.28**	39.89	0.02	*0.01*	44.82	0.00	*0.00*
URW	28.80	1.00	**0.61**	37.87	0.05	*0.03*	42.52	0.00	*0.00*
Stasis	59.34	0.00	*0.00*	55.13	0.00	*0.00*	46.89	0.00	*0.00*
P(2)	32.96	0.13	0.08	36.99	0.07	0.05	44.86	0.00	*0.00*
P(3)	34.73	0.05	*0.03*	31.73	1.00	**0.74**	30.36	1.00	**0.95**
P(4)	40.16	0.00	*0.00*	34.87	0.21	0.15	36.39	0.05	*0.05*
5th									
GRW	88.30	0.01	*0.01*	110.72	0.00	*0.00*	127.51	0.00	*0.00*
URW	86.04	0.02	*0.02*	108.42	0.00	*0.00*	125.21	0.00	*0.00*
Stasis	104.01	0.00	*0.00*	87.71	0.09	0.05	123.36	0.00	*0.00*
P(2)	87.11	0.01	*0.01*	84.75	0.39	**0.23**	100.89	1.00	**0.85**
P(3)	87.22	0.01	*0.01*	82.88	1.00	**0.59**	104.41	0.17	0.15
P(4)	78.65	1.00	**0.94**	86.05	0.21	0.12	111.70	0.00	*0.00*
95th									
GRW	63.29	0.13	0.06	41.83	0.11	0.07	95.94	0.00	*0.00*
URW	61.08	0.41	0.19	41.52	0.13	0.08	93.64	0.00	*0.00*
Stasis	67.88	0.01	*0.01*	88.25	0.00	*0.00*	80.86	0.94	**0.44**
P(2)	60.72	0.49	**0.23**	42.64	0.08	*0.05*	80.73	1.00	**0.47**
P(3)	59.28	1.00	**0.46**	40.17	0.26	0.16	84.15	0.18	0.08
P(4)	63.63	0.11	0.05	37.46	1.00	**0.63**	89.14	0.01	*0.01*

decline in brachiopod occurrence frequency. The best-fit models support an increase in the smallest occurring brachiopods in the Triassic–early Cretaceous (~15 mm) followed by a decrease to Paleozoic sizes (~9 mm) in the Late Cretaceous through Holocene (~8 mm), but Meso-Cenozoic changes are confounded by a dramatically decreasing number of occurrences and relatively few genera.

All measures of bivalve shell size are best fit by punctuated models (Table 2). Mean bivalve size is stable through the Paleozoic (~22 mm), increases in the Late Triassic (~37 mm) and then decreases in the mid-Cretaceous (~29 mm) (Fig. 5B,E). The largest occurring shell size is stable at ~38 mm through most of the Paleozoic, increases towards the end of the Carboniferous to ~60 mm, increases again in the Late Triassic to ~99 mm, and then decreases in the mid-Cretaceous to the size it maintains to the present (~80 mm). The smallest occurring bivalve shells size is best supported by a three-punctuation model (Table 2), where small bivalves are ~9 mm except for the latest Triassic through Early Cretaceous where small bivalves are ~12 mm in size. This temporary size increase is minor relative to the coarseness of our data and analyses.

All of the gastropod shell size metrics are best fit by punctuated models of change (Table 2). Mean gastropod size is consistent at ~20 mm through the Phanerozoic except for a decrease during the Permian–middle Jurassic when mean gastropod size is ~14 mm (Fig. 5C,F). That decrease coincides with a period with relatively few gastropod occurrences and genera (Fig. 2C,F). The largest occurring gastropods are ~47 mm through the Paleozoic and increase in the late Triassic to ~59 mm (Fig. 5F). The smallest occurring gastropods become dramatically smaller (~9 mm to ~4 mm) at the end of the Carboniferous and then are steady to the present (Fig. 5F).

Shell Reinforcement.—Each taxonomic group shows distinct changes in shell reinforcement as measured using ribs, folds, and spines (Fig. 6). In all groups ''least reinforced'' forms (those without ribs, folds or spines) are present in every time interval, and so the 5th quantile

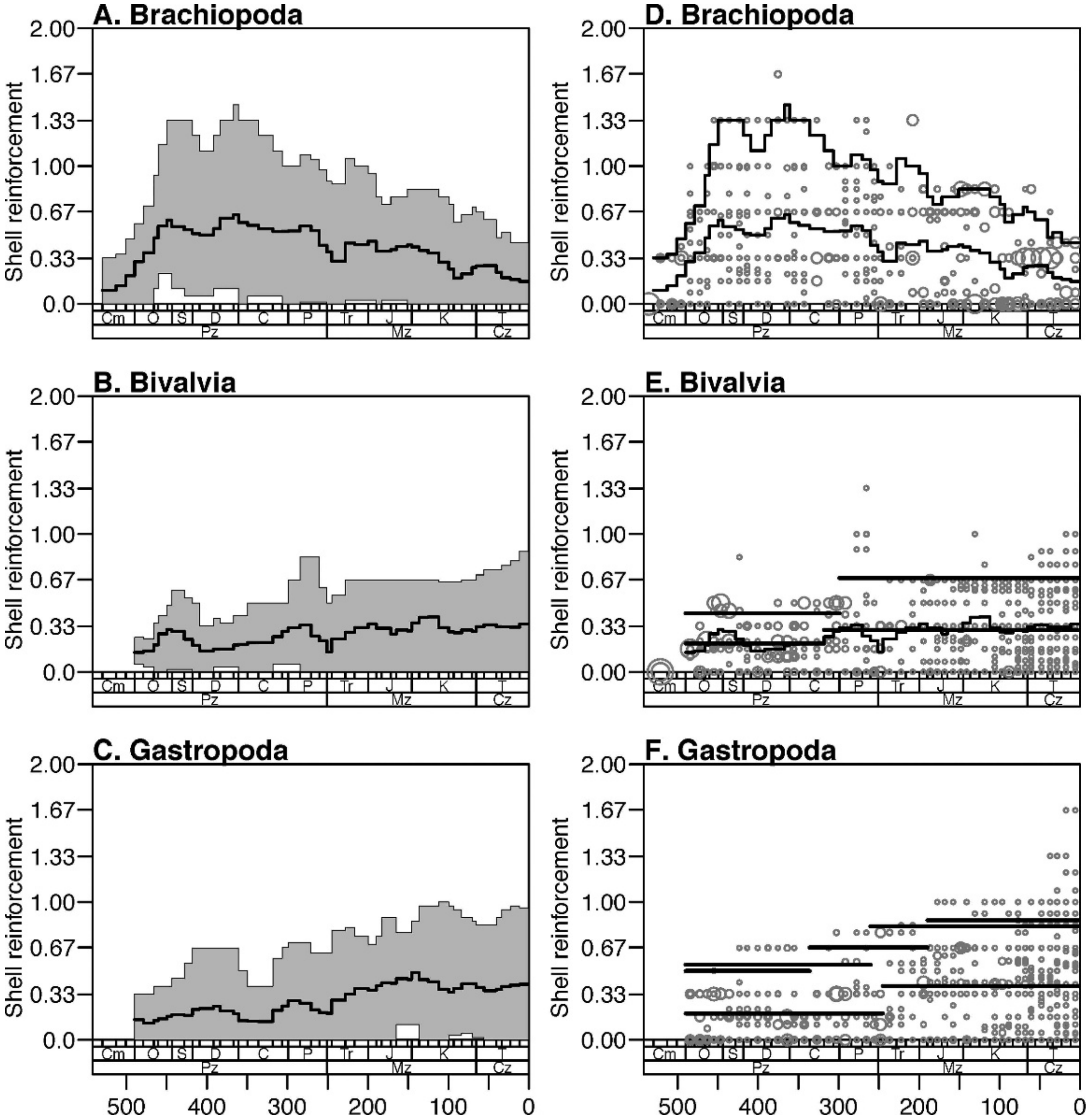

FIGURE 6. Occurrence-weighted shell reinforcement by taxonomic group. Shell reinforcement on the y-axis with an arithmetic scale; format otherwise as in Figure 5. Groups show distinct patterns of change, providing support for both random walk and punctuated models.

does not vary notably and is not discussed further. We focus on the mean and 95th quantiles (average and most durable); model support summaries are provided in Table 3.

Brachiopod shell reinforcement overwhelmingly supports random walk models (Table 3). Reinforcement mostly increases from the Cambrian through Silurian and then decreases from the Carboniferous to the present (Fig. 6A,D). Subdividing the reinforcement into pre- and post- maximum number of genera (at the end of the Silurian, Fig. 2A,D) results in >98% support for two biased random walks.

Mean bivalve shell reinforcement best supports a biased random walk model with continual incremental increases in reinforcement through the Phanerozoic, although a single-punctuation model (step increase at the base of the Permian) also receives substantial support (Table 3, Fig. 6B,E). Post-Permian reinforcement scores are higher than pre-Permian

TABLE 3. Model support summary for mean and 95th reinforcement score trends. Format and abbreviations are the same as in Table 2.

	Brachiopoda			Bivalvia			Gastropoda		
Model	AICc	Δ AICc	Weight	AICc	Δ AICc	Weight	AICc	Δ AICc	Weight
Mean									
GRW	−61.29	0.32	**0.23**	−93.05	1.00	**0.49**	−98.56	0.01	*0.01*
URW	−63.57	1.00	**0.73**	−88.80	0.12	0.06	−97.91	0.01	*0.01*
Stasis	−36.13	0.00	*0.00*	−83.81	0.01	*0.00*	−59.03	0.00	*0.00*
P(2)	−52.40	0.00	*0.00*	−92.49	0.75	**0.37**	−108.17	1.00	**0.87**
P(3)	−54.71	0.01	*0.01*	−89.48	0.17	0.08	−104.09	0.13	0.11
P(4)	−56.43	0.03	*0.02*	−83.30	0.01	*0.00*	−98.84	0.01	*0.01*
95th									
GRW	−2.84	0.32	**0.24**	−29.61	0.00	*0.00*	−22.34	0.01	*0.00*
URW	−5.11	1.00	**0.76**	−31.24	0.00	*0.00*	−23.97	0.02	*0.01*
Stasis	31.54	0.00	*0.00*	−20.33	0.00	*0.00*	−4.59	0.00	*0.00*
P(2)	16.66	0.00	*0.00*	−45.88	1.00	**0.92**	−31.13	0.69	**0.40**
P(3)	17.82	0.00	*0.00*	−40.97	0.09	0.08	−31.86	1.00	**0.57**
P(4)	18.15	0.00	*0.00*	−33.48	0.00	*0.00*	−24.41	0.02	*0.01*

scores, but bin-to-bin variation in both intervals is too high to strongly support a punctuated model. Temporal patterns in the most reinforced (95th quantile) bivalves are best described by stasis with a single punctuation occurring in the latest Carboniferous (Table 3, Fig. 6B,E).

Mean gastropod shell reinforcement strongly supports a model of punctuated change near the Permo-Triassic boundary, when mean reinforcement nearly doubles (Tri1/Tri2, Fig. 6C,F). The most reinforced (95th quantile) gastropods support both a model of punctuated change in the latest Permian and a model with two punctuations (Table 3, Fig. 6F).

Life Habit.—Each taxonomic group shows distinct changes in life-habit through the Phanerozoic (Fig. 7). Owing to the variance structure of the life-habit score data apparent in Figure 7D–F, only the mean life-habit score is examined. Model support summaries are provided in Table 4.

Brachiopods are almost exclusively epifaunal (Fig. 7A), and thus their life-habit scores remain close to zero through the Phanerozoic (Fig. 7D). Brachiopod life-habit score data provide nearly equal support to both a single-punctuation model of increasing infaunality in the early Cretaceous and a two-punctuation model with increased infaunality during the Cambrian through mid-Silurian and again in the mid-Cretaceous (Table 4, Fig. 7D). After the Ordovician radiation, infaunal brachiopods are a significant portion of occurrences only in intervals when the numbers of brachiopod genera and occurrences are especially low (Figs. 2A,D, 7A).

Bivalve life-habit scores support random walk models (Table 4). Epifaunal genera constitute ~40% of bivalve occurrences over most of the Phanerozoic, reaching a maximum of ~60% of occurrences in the Permian–Cretaceous (Fig. 7B). Cenozoic life-habit scores for this group (~0.6) are similar to the life-habit scores seen in the Devonian–Carboniferous, with fluctuating but mostly lower values (smaller numbers of infaunal genera) in other intervals (Fig. 7E).

Gastropods in our data set are nearly exclusively epifaunal (Fig. 7C), and so their scores are always close to zero (Fig. 7F). They expand into infaunal habits first in the Carboniferous and again in the Cretaceous, but even in the Cenozoic infaunal gastropods represent <20% of the fauna (Fig. 7C). Gastropod life-habit scores support a single-punctuation model with increased infaunality in the latest Jurassic (Table 4).

Shell Mineralogy.—Each taxonomic group shows distinct changes in mineralogy through the Phanerozoic, and all three groups strongly support random walks (Fig. 8); no punctuated model receives significant support (Table 5). Brachiopods are dominantly calcitic (Fig. 8A) but the oldest and youngest

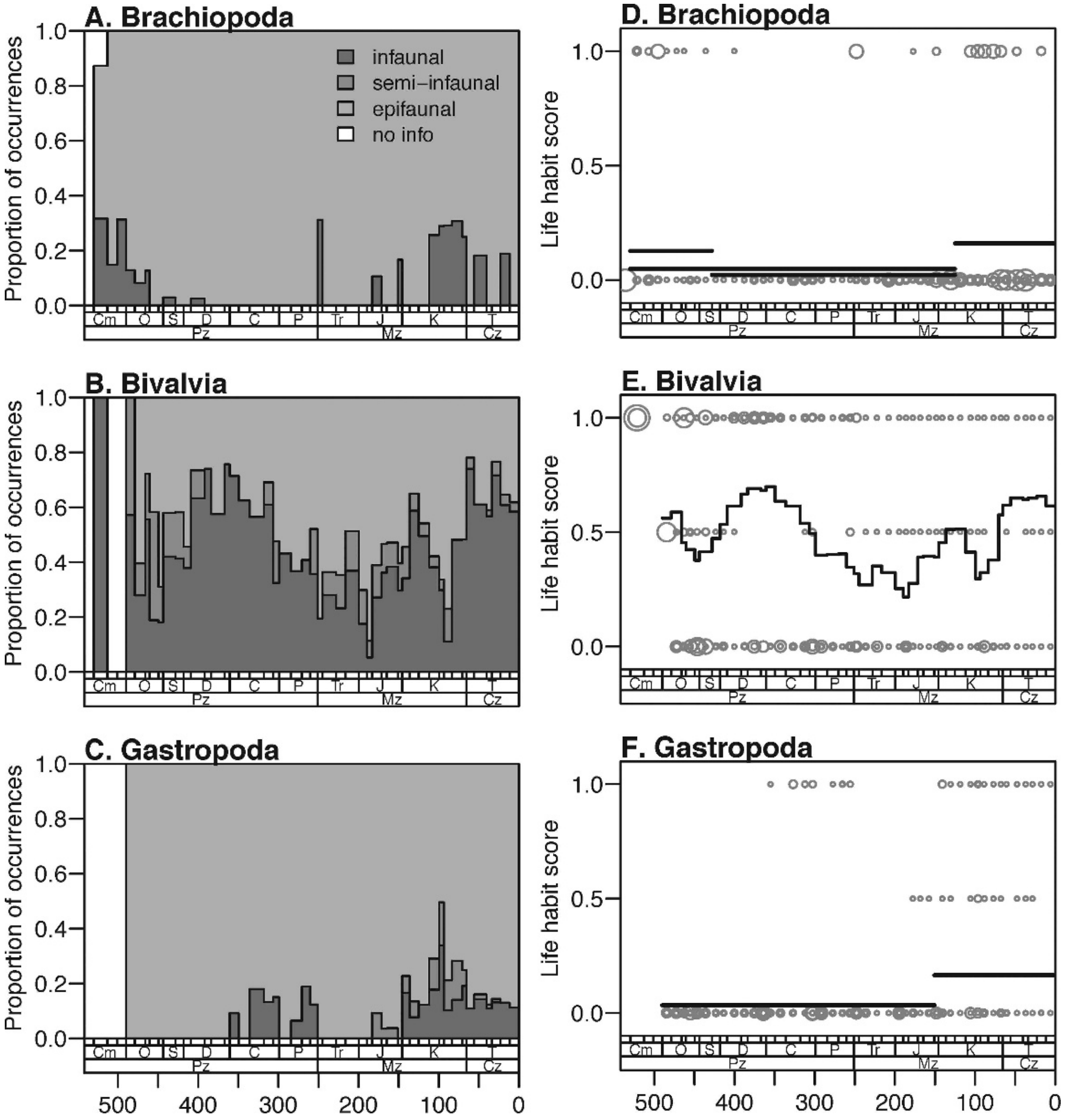

FIGURE 7. Occurrence-weighted life habit by taxonomic group. The left column (A–C) depicts the proportion of each bin's occurrences represented by each life habit on the y-axis. The right column (D–F) shows the mean life-habit score as fit by *PaleoTS* (black line), with each genus plotted as a circle proportional to its relative occurrence in the time bin. Life-habit scores: 0 = epifaunal, 0.5 = semi-infaunal, 1 = infaunal. Each group exhibits a different pattern of change in intrinsic durability, and peak durability (maximum infaunality) occurs at different times.

TABLE 4. Model fit summary for mean life-habit score trends. Format and abbreviations are the same as in Table 2.

	Brachiopoda			Bivalvia			Gastropoda		
Model	AICc	Δ AICc	Weight	AICc	Δ AICc	Weight	AICc	Δ AICc	Weight
GRW	−83.58	0.16	0.06	−34.73	0.33	**0.23**	−98.12	0.08	0.05
URW	−85.66	0.46	0.17	−36.93	1.00	**0.69**	−97.59	0.06	*0.04*
Stasis	−72.90	0.00	*0.00*	−26.23	0.00	*0.00*	−80.23	0.00	*0.00*
P(2)	−86.98	0.88	**0.32**	−26.55	0.01	*0.00*	−103.07	1.00	**0.61**
P(3)	−87.23	1.00	**0.36**	−32.50	0.11	0.07	−99.96	0.21	0.13
P(4)	−84.55	0.26	0.09	−25.18	0.00	*0.00*	−100.52	0.28	0.17

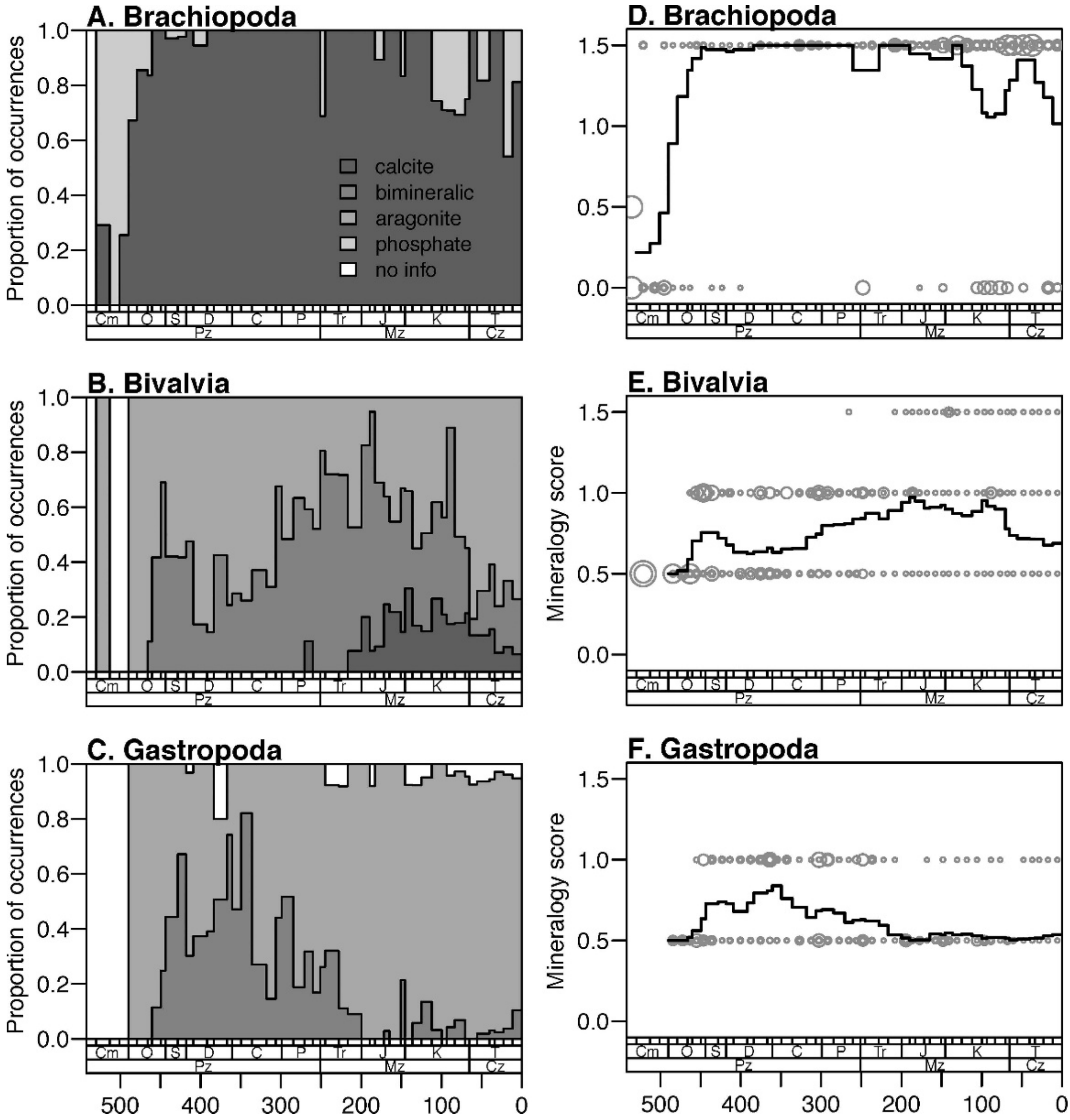

FIGURE 8. Occurrence-weighted shell mineralogy by taxonomic group. Format as in Figure 7. Mineralogy scores from least to most durable are 0 = organophosphatic, 0.5 = entirely aragonitic, 1.0 = bimineralic, 1.5 = entirely calcitic. Each group exhibits a different pattern of change in intrinsic durability, and peak durability (maximum calcitic genera) occurs at different times.

TABLE 5. Model fit summary for mean mineral score trends. Format and abbreviations are the same as in Table 2.

	Brachiopoda			Bivalvia			Gastropoda		
Model	AICc	Δ AICc	Weight	AICc	Δ AICc	Weight	AICc	Δ AICc	Weight
GRW	−4.96	0.39	**0.28**	−72.43	0.34	**0.25**	−99.26	0.32	**0.24**
URW	−6.82	1.00	**0.72**	−74.57	1.00	**0.71**	−101.57	1.00	**0.75**
Stasis	32.19	0.00	*0.00*	−49.06	0.00	*0.00*	−64.64	0.00	*0.00*
P(2)	21.92	0.00	*0.00*	−64.52	0.01	*0.00*	−91.53	0.01	*0.00*
P(3)	20.05	0.00	*0.00*	−67.92	0.04	*0.03*	−90.42	0.00	*0.00*
P(4)	25.37	0.00	*0.00*	−66.03	0.01	*0.01*	−84.95	0.00	*0.00*

intervals include abundant phosphatic genera, closely mirroring life-habits (Fig. 7A,D). Organophosphatic genera from infaunal inarticulate families that dominate the Cambrian appear subsequently only in bins having very low numbers of genera and occurrences (Figs. 2A,D, 8A,D). The earliest bivalves are entirely aragonitic, but bimineralic genera appear by the mid-Ordovician, and entirely calcitic genera appear by the Late Permian (Fig. 8B). Despite heterogeneity in composition among bivalves and a peak abundance of calcite-bearing shells in the Mesozoic, the average mineralogy score in the Cenozoic is similar to that through most of the Paleozoic (Fig. 8E). Gastropods are also entirely aragonitic initially and first become bimineralic by the mid-Ordovician, but never evolve entirely calcitic shells (Fig. 8C). The gastropod mineralogy score peaks in the mid-Paleozoic, and it is largely invariant from the Jurassic through the Holocene (Fig. 8F). Genera having unknown mineralogical composition are too rare to substantially change these patterns (Fig. 8C).

Bivalve Organic Content.—Bivalves show a strong directional trend of decreasing organic content through the Phanerozoic (Table 6, Fig. 9). The post-Paleozoic portion of this trend is an especially clear directional trend, with genera from the Cenozoic having the highest scores and preservation potential of any bins in the entire history (Fig. 9B). Genera having unknown organic content are too rare to substantially change this pattern (Fig. 9A).

Predicting the Number of Genera in a Time Bin Using Shell Durability

Larger size, greater reinforcement, infaunal life habit, calcite-rich shell mineralogy, and low-organic shell structure are thought to increase the probability that a genus will occur in the published fossil record, whether through biased taphonomic processes or a bias in collection or identification. If so, then time bins where genera have high average durability should also have high numbers of documented genera and occurrences. Because the number of genera and the number of occurrences are highly correlated, either of those two variables can be used to evaluate the relation between shell durability and the quality of the fossil record. Here, we evaluate the predictive value of mean durability of common genera in a time bin by using the number of genera recorded for a given higher taxon in that time bin. The number of brachiopod genera in a bin is best predicted by shell size and reinforcement ($r^2 = 0.61$, $p < 0.001$). The number of bivalve genera in a bin is best predicted by shell mineralogy and organic content ($r^2 = 0.64$, $p < 0.001$). The number of gastropod genera in a bin is best (but not very well) predicted by reinforcement and life-habit score ($r^2 = 0.17$, $p = 0.007$). The results predicting occurrence frequency are substantively similar because the number of occurrences and the number of taxa are highly correlated.

Causality cannot be tested with this data set, but these relations are not temporal patterns: the number of brachiopod genera and the brachiopod reinforcement score both peak in the Paleozoic whereas the number of bivalve genera and organic score both peak in the Cenozoic. It is not surprising that different durability characteristics are useful in predicting different taxonomic groups. Although it is intuitive that increased brachiopod reinforcement and/or size might increase the number taxa differentiated by taxonomists, it is much less clear how decreased bivalve shell organic content would lead to that bias. Our data indicate a strong relation for both brachiopods and bivalves between the numbers of genera and a taxon-specific subset of our durability metrics, within a given time interval, for the Phanerozoic fossil record as documented by the PaleoDB.

Predicting Genus Occurrence Frequency Using Shell Durability

Each intrinsic durability character shows largely distinct patterns in each group, which is contrary to the expectation that taphonomic durability should be a combined function of all of these metrics. Using a multiple-parameter regression model to evaluate the relative importance of durability metrics, we find that brachiopod size, ribs, and life-habit score were all meaningful predictors of occurrence frequency although the predictive power of

TABLE 6. Model fit summary for mean bivalve organic content trends. Format and abbreviations are the same as in Table 2.

	Organic content		
Model	AICc	Δ AICc	Weight
GRW	−55.00	1.00	**0.59**
URW	−54.09	0.63	**0.38**
Stasis	−4.96	0.00	*0.00*
P(2)	−46.17	0.01	*0.01*
P(3)	−48.52	0.04	*0.02*
P(4)	−43.26	0.00	*0.00*

the best-fit model was low (r^2 = 0.14, $p <$ 0.001). For bivalves, mineralogy, organic content, and life-habit scores were useful predictors of variation in genus occurrences although the predictive power of the best-fit model was low (r^2 = 0.12, $p <$ 0.001). Gastropod size, spines and life-habit were meaningful predictors of occurrence frequency but the predictive power of the best-fit model was low (r^2 = 0.11, $p <$ 0.001).

Our finding that genus occurrence frequency cannot be predicted confidently by any of the shell durability traits is an important negative result for first-order preservational controls on the fossil record of common shelly benthos, and suggests that genus occurrences behave differently than numerical abundance of taxa in any given collection (sample). Although these traits (variables) may predict per capita preservation probabilities related to numerical abundance at smaller scales, they do not predict occurrence frequency at the Phanerozoic scale. The most obvious explanation is that occurrence frequencies are the combined result of a taxon's per capita preservation potential, its shell production rate, and its geographic and stratigraphic ranges within the bin in question. This is demonstrated in several studies that have found general agreement in preserved abundances despite differences in durability (Tomašových 2004; Tomašových and Rothfus 2005). This result is distinct from the bin average durability values, which can be used to predict the number of occurrences in a bin.

Caveats

On Preservation Potentials and Scales.—Taphonomic studies examine different aspects of preservation potential and it is easy to confuse them. The fundamental preservation potential is the probability of a single shell's being preserved. This per capita preservation potential is typically the focus of actualistic or experimental studies. In a fossil collection this scales smoothly to discussions of taxon abundance, because that is a joint function of per capita preservation potential and shell production rate, which, in turn, controls the probability of at least a single representative of a taxon being sampled in a collection (e.g.,

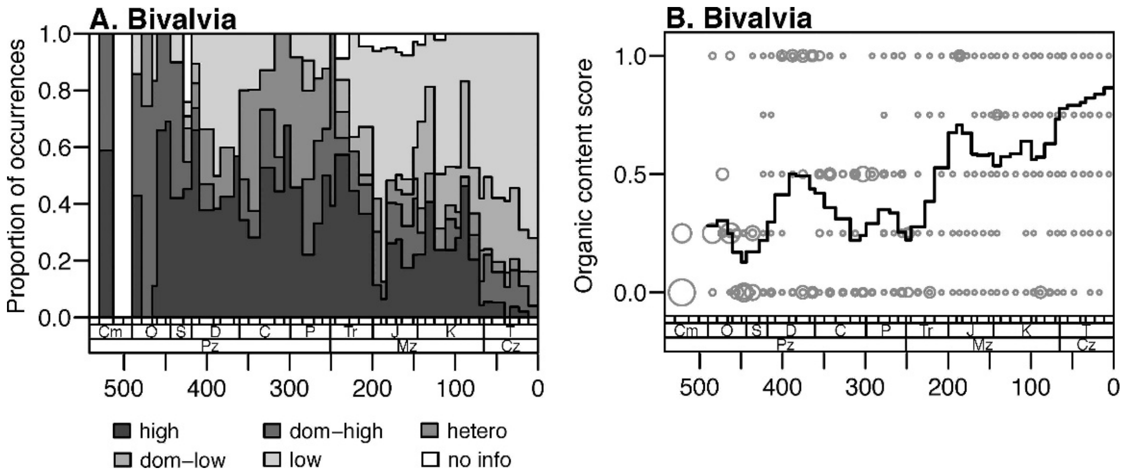

FIGURE 9. Occurrence-weighted shell organic content for bivalves. Format as in Figure 7. Organic content scores from least to most durable are 0 = high organic, 0.25 = dominantly high hetero-organic, 0.5 = hetero-organic, 0.75 = dominantly low hetero-organic, 1.0 = low organic. Genera having the most durable shells (composed entirely of low-organic-content microstructures) become increasingly abundant over time.

occurrence preservation potential). Scaling up again to this study, the number of occurrences per time bin is a further function of the taxon's geographic and stratigraphic ranges within the time bin. Taxa with relatively large ranges are more likely to be sampled than taxa with small ranges in the same way that numerous taxa are more likely to be sampled relative to less numerous taxa. The final complication is that a taxon's absolute preservation potential is less important than its preservation potential relative to the other taxa in the time bin. When comparing taxonomic studies and expectations it is critical to take into consideration the scale of the investigation.

Investigations of genus occurrences at the ~11-Myr-bin scale are potentially least likely to show a durability effect, owing to the many other influences on the preservation potentials outlined above, and we recognize that this is an inefficient scale for investigations of taphonomic processes operating at the scale of individual assemblages, environments, and communities. However, there is a substantive literature that uses genus occurrences from the PaleoDB tabulated using ~11-Myr time bins. To the extent that the diversity curves of Alroy et al. (2001, 2008) are used by paleontologists to inform our understanding of diversity trends through time, it is important to examine the potential taphonomic biases at the same scale. Finer-scale studies are likely to uncover interesting details in taphonomic processes and elucidate their effects on paleobiological understanding, but we have intentionally framed our investigation at the same scale as the large diversity curves that have so often driven paleobiological research (e.g., Sepkoski 1981).

Commonly Occurring Genera.—Our results need to be viewed in the context of our target sample set—the most common genera in the PaleoDB. We evaluated only the most frequently occurring 40% of genera in ~11-Myr time bins through the Phanerozoic and found that these most common forms show remarkable consistency (absence of long-term trends) in shell size, reinforcement, and other shell traits. We did not attempt to measure changes among the less commonly occurring 60% of genera recorded in the PaleoDB, which is itself an incomplete sample of the known fossil record biased toward common taxa. Our focus on the most commonly occurring genera is not because we think rare taxa are unimportant, but because collecting data on rare genera is significantly more difficult. The most commonly occurring genera are arguably best known and least likely to shift out of this category with increasing sampling effort, although expansion or intensification of effort to understudied areas and time intervals may well add new genera to the ''common'' list in future.

We encourage our results to be seen as a ''fossil collector's view'' of benthic communities. The genera examined here constitute 47% of the total occurrences of brachiopod, bivalve, and gastropod genera, and so a collector is likely to find a shell of similar size and reinforcement, regardless of taxonomic group or time period. Important changes may have taken place in the unsampled (rare) tail of the occurrence distribution, but that does not invalidate the general conclusion about the dominant genera, which lack a dramatic change in durability (e.g., preservation potential). Examining changes in the intrinsic durability across all occurrences is not practical, and a more productive approach to this problem might be via functional analysis of predators in relation to the evolution of durability-related traits over time.

Genus Values As Averages.—Ideally, the value of a genus's shell trait would be determined on the basis of multiple specimens and species that constitute the occurrences in a given time bin (e.g., Finnegan et al. 2011 [this volume]). This was not a realistic goal here, although it should become feasible in the future as the quantity of species-level data increases with accelerating professional effort and more digitally accessible specimen-level information. We instead have applied a single genus mean value to all occurrences of that genus, regardless of time bin, with the majority of these values based on more than one specimen (59% of genus size determinations and 58% of genus reinforcement values; mean number of specimens scored per genus was 2.7 and 2.5, respectively). The ~30 genera with more than six size- and reinforcement-scored specimens reflect the work of multiple investigators as part of the consistency analysis discussed by Behrensmeyer et al. (2005). All other genera and all other traits (life habit, mineralogy) were scored by a single investigator, albeit using multiple primary data sources (see Methods).

Trashcan Genera.—Most genera appear in the top 40% of occurrences in only one time bin (60% of genera) and most have only a few occurrences total (median 24). However, a few genera occur in many time bins (i.e., *Chlamys, Ostrea, Terebratula, Lingula* each occur in >13 bins) and have many total occurrences (i.e., *Chlamys, Ostrea,* and *Turritella* each have >600 occurrences). These extremely common genera tend to be widely recognized as overly broadly defined, mostly outdated Linnean genera that either need revision or persist in the (mostly non-specialist, geological) literature despite revision. We have used subgenera to minimize such taxonomic artifacts, but the remaining "trashcan" genera still tend to have overly high occurrences. Nonetheless, this lumping should not unduly reduce the accuracy of our durability data set because closely related genera often have similar shell sizes and levels of reinforcement (Plotnick and Wagner 2006). It would not affect life-habit or mineralogy scores because these traits tend to be conservative at the family or even ordinal level.

Discussion

The goal of this study was to test the extent to which changes in durability over time, rather than individual macroevolutionary histories, among three major shelly macrobenthic groups might reflect a Phanerozoic-scale taphonomic megabias in preservation. Strong external taphonomic filtering of shell traits should result in shared patterns of temporal change among groups as well as strong correlations between intrinsic durability and the number of genera and/or occurrences. Although we did find an overall correlation between the number of genera in a time bin and shell durability, each group's temporal changes in shell reinforcement are largely distinct, as are changes in life habit and shell mineralogy. All three groups tend to converge on a shell size between 16 and 32 mm, but the timing and magnitudes of changes in the smallest and largest occurring shells are disjunct and thus unrelated to any broad-scale taphonomic filter favoring the preservation of shells of this particular size (e.g., Fig. 1B). Trends in shell reinforcement tend to support models of gradual change, and when models of punctuated change are supported, this change tends to occur within the Carboniferous–Triassic time periods. Except for a tendency for the earliest members of each group to be small and unreinforced, the timing and mode of evolutionary change do not appear to be temporally linked. In fact, the correlate of increased durability is more genera, not more recent time, but our data do not allow us to determine a causal relationship.

Our analyses illustrate the value of a multi-taxon approach in distinguishing passive and actively driven trends. Mean shell size is essentially static and very similar across groups for nearly 450 Myr. In contrast, the pattern of change in shell reinforcement of brachiopods (with peak reinforcement in the early Paleozoic) is quite distinct from that of bivalves or gastropods, whose reinforcement scores are fairly stable (mean values) or increase steadily toward the present (maximum values; Fig. 6). These two durability metrics thus act independently within each group and changes are non-synchronous across the taxonomic groups. The trend in maximum reinforcement among the mollusks is contrary to a taphonomic expectation that durable forms should be more common in older rocks (the forms with the lowest preservation potential are most abundant in the oldest record), as is the peaking of brachiopod reinforcement midway through their history. The finding that brachiopods become less reinforced at the same time that they become less common (Figs. 2C, 6D) is evidence against a model of purely passive diffusion from the initial boundary conditions. Although brachiopods were constrained to become larger and more reinforced than the small, unreinforced ancestral brachiopod, there clearly was no similar requirement for them to become less robust as they became less diverse. Note, for example, that the size of the smallest occurring brachiopods did not become notably smaller as the number of brachiopod genera dwindled (Figs. 2D, 5D).

Trends in Shell Size.—Our results build upon the earlier finding (Behrensmeyer et al. 2005) that shell size is not correlated with formation-occurrence frequency and show that, through time and for all three groups, shell size has had a consistent mean value falling between 16 and 32 mm since the Ordovician. It is difficult to argue for an optimal preservation size (i.e., a taphonomic limit) to explain this consistency given (1) the distinct trajectories through time of this and other durability measures for each of the three groups, and (2) the apparent unresponsiveness of mean size to major extrinsic events in the history of Phanerozoic marine life (e.g., the Permo-Triassic and Cretaceous/Tertiary extinction events, global icehouse intervals of the late Ordovician, Carboniferous, and Neogene). Our focus, however, on the most common genera may cause the timing of our punctuation events to be offset from patterns based on the entire clade. For example, within our data set of the most common fossil genera, the smallest occurring gastropods become smaller in the Permian whereas the size of the smallest occurring bivalves remain largely unchanged through the Phanerozoic (Fig. 5). The size of the largest occurring gastropods remains largely unchanged through the Phanerozoic but the size of the largest occurring bivalves increases in the late Carboniferous and again in the early Mesozoic. These differences suggest that evolutionary factors specific to higher taxonomic groups may determine the shape of shell-size distributions despite the consistency in mean size through the Phanerozoic across all three groups.

Gastropods are the only target group whose earliest representatives are large shelled, and the largest occurring gastropods do not become appreciably larger through the Phanerozoic (Fig. 5F). In contrast, the smallest occurring gastropods become smaller toward the end of the Carboniferous. One possible explanation for this decrease in size is the evolutionary change to a single-gilled condition, which happens in many different gastropod clades during the late Paleozoic (Erwin 1990). Although many monopectinate gastropods are large bodied, this state may enable smaller body sizes. Erwin (1990) also showed that the end-Permian mass extinction and the subsequent rebound had a dramatic impact on gastropod morphologies, with many changes foreshadowing the Mesozoic Marine Revolution (MMR).

Although we cannot rule out that consistency in mean shell size across groups and time is a preservational artifact, our finding that all groups show distinct changes in minimum and maximum size through the Phanerozoic indicates that the fossil record preserves a wide range of shell sizes in all time bins, even with our focus on only the most common genera. Presumably there are physiological limits to body size at both ends of the spectrum given certain levels of developmental complexity, and perhaps these are demonstrated empirically in our results. We have documented the pattern, but determining its cause is beyond the scope of this paper. Also notable is a general lack of correspondence between the timing of hypothesized drivers of size changes (e.g., the MMR, increasing lithification) and the timing of the observed changes in the groups.

Life Habit and Shell Composition.—Changes in both life habit and mineralogy through the Phanerozoic mainly approximate random walks for each group and neither trait shows any coordinated pattern of change that would imply extrinsic taphonomic controls on preservation. Very few brachiopod and gastropod genera are infaunal; thus the lack of any substantial trend in occurrence data for these groups is perhaps not surprising. The relatively minor increase in infaunality seen in brachiopods and gastropods does occur during the time typically associated with the MMR. Among bivalves, which exhibit a wide range of life habits, the relative occurrence of infaunal to epifaunal forms varies but within a remarkably small range, from ~30:70 to ~60:40, and depending on the measure has either multiple peaks or a U-shaped pattern with infauna being most common in the early

Mesozoic (Fig. 7), which is also inconsistent with a megabias linked to life habit.

Infaunality protects organisms from some modes of predation and probably conveys higher preservation potential by isolating shells from the taphonomically destructive agents operating largely at the sediment-water interface (e.g., bioerosion). Only bivalves have suitable numbers of both infaunal and epifaunal taxa to compare their intrinsic durability (135 infaunal and 130 epifaunal genera). Epifaunal bivalves are significantly more reinforced ($p < 0.001$) and significantly larger ($p = 0.001$) than infaunal bivalves, although the magnitude of these differences is small relative to the coarseness of our data (mean epifaunal reinforcement = 0.35 versus mean infaunal reinforcement = 0.23; mean epifaunal size = 5.0 mm versus mean infaunal size = 4.6 mm). Infaunal genera do not occur with greater frequency than epifaunal genera ($p = 0.18$). These results are consistent with either different durabilities and sizes between infauna and epifauna in the original communities or, if there are no such community-based differences, the taphonomic loss of less durable and smaller epifaunal taxa in the preserved assemblage.

Mineralogy is less variable among brachiopods and gastropods than among bivalves, but again the patterns are inconsistent with a preservational megabias. All three groups exhibit a broad, hump-shaped pattern, with the most durable shell types (composed partly or entirely of low-Mg calcite) showing the highest occurrence midway rather than early in the group's history. Proportionally, the least durable genera occur most frequently both very early and late in the Phanerozoic, contrary to the taphonomic prediction of the highest frequency in the youngest part of the record. The pattern in gastropods is most consistent with taphonomic megabias—the more easily dissolved aragonitic genera do become proportionally more important toward the present—but the appearance of this trend in only one of three groups argues that this is an evolutionary trajectory particular to gastropods rather than a general taphonomic megabias. Like Kiessling et al. (2008), we find little evidence to link the prevalence of different shell mineralogies to periods of high or low Mg/Ca ocean chemistry despite using very different approaches to the question. Our occurrence-based trends in bivalve mineralogy are very similar to those generated from range-through data for all ~3000 known bivalve genera (Kidwell 2005), where the peak of calcite-bearing genera was found to coincide with major clade turnovers at the Permo-Triassic boundary (rather than later in the Mesozoic as found here). This offset in the timing of this event may be due to our focus on the most common genera: the rare genera included in exhaustive data sets can detect changes associated with trait innovation early in clade history, whereas common genera reflect later ecological expansion of the clade.

Bivalves exhibit a strong directional trend away from high-organic microstructures: the youngest fossil record contains a greater proportion of the more readily preserved low-organic shell types, contrary to the expectation of a taphonomic bias toward increased survival of organic content toward the Recent. The same significant trend was found among bivalves when all known fossil bivalve genera and range-through rather than occurrence-based data are used (Kidwell 2005). This implies an evolutionary (selection) control on decreased organic content in shells through the later Phanerozoic.

The Mesozoic Marine Revolution (MMR).—Contrary to expectation, the MMR is a minor event among the most frequently occurring genera captured by our data set. Support for the MMR requires increased reinforcement in the late Mesozoic and early Cenozoic coinciding with the evolution of major marine predatory groups such as teleost and batoid fish, asteroid echinoderms, decapod crustaceans, and neogastropods (see recent review by Vermeij [2008]). The well-documented decline in brachiopod taxa in this interval (e.g., Fig. 2) could be linked to the evolution of predatory groups, but in our data set the decline in brachiopod genera, occurrences, and reinforcement began well before the Mesozoic (Figs. 2, 6). In addition, bivalve reinforcement increases at the end of the Carboniferous, not in the Meso-Cenozoic, although infaunality increases through this latter interval (Fig. 7). It is possible that by supplementing our data set with additional less common genera and focusing on the number of genera rather than occurrence frequency we might find an increase in reinforced bivalves in the Cenozoic, but this possibility—that the revolution is expressed most strongly among rare genera—remains untested (but see Madin et al. 2006). The decline in bivalve shell size in the Cretaceous is consistent with experimental studies suggesting that large epifaunal bivalves from the Mesozoic were not sufficiently durable and/or mobile to survive modern marine predators (LaBarbera 1981), but these declines are relatively minor. Bivalve size patterns are more consistent with an unusually large bodied Jurassic and early Cretaceous fauna following the main increase in bivalve size in the late Triassic.

Gastropod reinforcement increases notably at the Carboniferous/Permian and Permo-Triassic boundaries (depending on metric; Fig. 6F), clearly preceding the MMR. Although it is possible that by focusing our data set on the most common genera we missed an increase in reinforcement in the *late* Mesozoic, our omission of rare genera does not explain the distinct increases that we do observe among common genera in the late Paleozoic and earliest Mesozoic. Those changes coincide with other evidence suggesting an increase in the trophic complexity of marine communities at this time (Wagner et al. 2006) and important shifts in gastropod morphology and diversity associated with the Permo-Triassic mass extinction event (Erwin 1990). Erwin (1990) also found significant morphological changes consistent with those predicted by the escalation hypothesis occurring in the late Paleozoic and Triassic, well before the MMR. Although we did not score a number of gastropod characters identified by Vermeij (1977) as important defensive adaptations, such as the closure or filling of the umbilicus and development of columellar folds in gastropods, the morphological changes we do see precede the hypothesized drivers. The increase in gastropod infaunality documented in the latest Jurassic is consistent with an MMR mechanism.

Combined, these findings suggest an earlier, under-documented ecological expansion of durophagous predators. Molecular data argue for a late Paleozoic origin of ray-finned fishes (Inoue et al. 2005; Hurley et al. 2007), and although this could be consistent with some of the late Paleozoic changes we see among shelly prey, there is no evidence for morphologically capable fish in ecologically relevant abundance from this time interval. Although fish are likely to have been nocturnal feeders since the Triassic, evidence for the visual capabilities required by nocturnal and high-precision feeding by teleost fish first appears in the Eocene (Goatley et al. 2010). There is increasingly strong evidence that marine reptiles capable of durophagy occurred in reasonable abundance in the earliest Triassic (Motani 1999; Maisch and Matzke 2000; Benson et al. 2010), and a Late Triassic radiation of skates and rays represents a substantial change to the durophagous predator community (Underwood 2006; Kriwet et al. 2009). Decapods have had adaptations for durophagous predation on mollusks since the early Triassic (Schweitzer and Feldmann 2010). The effectiveness of these Mesozoic predators is not universally accepted. For example, investigations of the frequency of broken shell material suggest that durophagous predation was not significant until the Cenozoic (Oji et al. 2003), whereas recent work on crinoids indicates that they experienced high levels of predation pressure in the earliest Triassic (Baumiller et al. 2010). The history of reinforcement among both bivalves and gastropods in our analyses (Fig. 6) is consistent with an earlier onset of predatory marine groups and thus a prolonged series of evolutionary events rather than a revolution. This suggests the need for greater functional analysis of early teleosts and perhaps marine reptiles for durophagous adaptations.

Ordovician Radiation.—One of the most dramatic events—and the only synchronous change across groups that was identified in our analyses—is the Cambro-Ordovician increase in body size and reinforcement observed among all groups. This occurs over a very short period of time relative to our analyses (five to eight bins depending on the taxonomic group, out of a total of 48 bins). These increases are gradual over the time period, but in brachiopods the increase is the largest in the Phanerozoic. Studies at finer temporal resolution could determine whether this increase is related to changes in taphonomic environment involving increased bioturbation (e.g., Droser and Bottjer 1989) or a more general consequence of the greatest radiation in the history of metazoan life (e.g., Miller 2004). Our findings are consistent with the body-volume increase documented among brachiopods by Novack-Gottshall and Lanier (2008), and support the conclusion that the Ordovician radiation is one of the key periods in establishing marine diversity, including attaining maximum body sizes and levels of reinforcement that persist to the present day. Trace fossil evidence of predation (drill holes and repair scars) also suggests that marine predation may have first intensified in the Ordovician (Huntley and Kowalewski 2007).

Taphonomic Filtering.—Major environmentally or biologically driven changes in the taphonomic environment (e.g., shift in ocean chemistry, increased bioturbation) or sampling-related shifts in the documented fossil record (e.g., due to differing degrees of lithification) should affect all three shelly groups similarly and be synchronous across them (e.g., Fig. 1A). Our analyses find neither shared trends among groups—a single durability trait may show a random walk in one group and a punctuated model in another—nor any synchronicity in punctuated changes.

Phanerozoic trends in diagenesis and in particular lithification exemplify the strengths and weaknesses of our study. More pervasive lithification in older rocks has been shown to influence Cenozoic sampled diversity by decreasing the frequency with which smaller specimens are sampled (Hendy 2009; Sessa et al. 2009; and see Cooper et al. 2006 and Kowalewski et al. 2006). Although both of these studies examined sample abundance, we are constrained by the scale of our analysis to use occurrence data within relatively coarse (~11 Myr) time bins. We examined the Phanerozoic rather than just the Cenozoic, and our punctuated models were constrained to find periods of stasis longer than ten time bins (i.e., encompassing more than just the Cenozoic rise in unlithified units). In our data, gastropods show a decrease in minimum shell size that could be attributed to sampling from unlithified units. The same best model of stasis with a single punctuation (in the Paleozoic) is found when models are fit to minimum stasis periods of five bins instead of ten bins. Fitting the punctuated models with shorter minimum periods of stasis leads to additional periods of stasis and punctuations in the Paleozoic, but not the Cenozoic (unpublished analyses). Limiting the analysis to only the latest Carboniferous through Holocene (requiring minimum stasis periods of three time bins, and permitting two to five periods of stasis) still does not return a best-fit model with a punctuated shift in the Cenozoic.

The results of our study can be reconciled with Hendy (2009) and Sessa et al. (2009) if the small taxa affected by the size bias in those studies are rare (occur infrequently). Alternatively, results could be reconciled through biases acting in the opposite direction, for example if widespread silicification in the Paleozoic (Schubert et al. 2007) is as effective in increasing the preservation of smaller taxa as is incomplete lithification in the Cenozoic, or if the relatively rare unlithified and friable samples from the Paleozoic are preferentially targeted. In this case, two extrinsic factors each create a documented megabias in the fossil record when examined alone, but because they favor preservation in different segments of the Phanerozoic record, their net effect is no strong temporal bias, permitting largely evolutionary patterns to emerge. Similarly, increased preservation of original molluscan aragonite toward the present has been thought to bias diversity records significantly (especially at the alpha level of single-bed assemblages; e.g., see discussions in Bush and Bambach 2004; Kowalewski et al. 2006; Cherns et al. 2008, and Cherns and Wright 2009). However, Phanerozoic-scale studies in addition to ours here find no directional trend in the proportional richness or occurrence of aragonitic genera or in their average duration relative to calcite-bearing genera, even when all taxa are considered (e.g., all ~3000 bivalve genera; Kidwell 2005; Kowalewski et al. 2006; Kiessling et al. 2008). Nor do our results or those of most others (e.g., Kidwell and Brenchley 1994, 1996; Kidwell 2005; Kiessling et al. 2008) find strong correlations between shell mineralogy and hypothesized changes in ocean saturation, which should affect preservation during early diagenesis (i.e., favoring aragonite precipitation and preservation during the mid-Carboniferous through mid-Jurassic, and mid-Paleogene through Holocene (Farkaš et al. 2007).

The simple formulation of increased lithification in older strata thus does not explain the patterns observed here within either the post-Paleozoic or the entire Phanerozoic. Therefore, more complex taphonomic explanations are required to account for differences in patterns among the three groups. For example, although the observed Late Cretaceous decrease in minimum brachiopod size might be attributed to increasingly unlithified strata, why do gastropods not show a similar decrease in shell size at approximately the same time? The simplest explanation is that macroevolutionary factors are the main driving force behind the preservation potential of common genera, given the largely independent dynamics of intrinsic traits in our groups.

Using Durability to Predict the Number of Occurrences or Genera.—The apparent link between the number of genera in a bin and shell durability characters is a compelling result that deserves closer examination. Such a correlation could be driven by evolutionary trends in either the number of genera or durability, or it could be an artifact. For example, morphologically reinforced taxa may be more readily identified than unreinforced forms, resulting in more reported occurrences, and shell reinforcements may make it easier for taxonomists to recognize more taxa. A systematic relation between shell durability and production rates could also create this pattern. Several alternative models are also possible for evolutionary trends. Early representatives of each group are unreinforced, and the groups diversify over time. Because the groups cannot become less reinforced as they diversify, a correlation between the number of taxa and reinforcement may signify only passive diffusion from the starting conditions rather than an actively driven evolutionary trend (sensu McShea 1994). Alternatively, some models of predator behavior predict that as prey become more abundant they may become disproportionately more sought after. Increased predation pressure would then select for the survival of individuals with defensive adaptations such as shell reinforcement, thus driving diversification.

Conclusions

Common genera in each of the three higher taxonomic groups—Brachiopoda, Bivalvia, Gastropoda—show distinct patterns in both mode and timing of changes in intrinsic durability (e.g., preservation potential), making it difficult to argue for extrinsic taphonomic drivers of these changes that act at large (global) spatial scales. Over the Phanerozoic, the largest occurring bivalves get larger, but the largest occurring gastropods do not. The smallest occurring gastropods get smaller, but the smallest occurring bivalves do not. Mean brachiopod size is essentially static and similar to the mean size of bivalves and gastropods. Distinct steps in size and reinforcement are generally not synchronous among groups. The proportional occurrence of calcite-bearing shells thought to convey higher preservation potential show no secular trend, but rather unbiased random walks and low-organic microstructures in bivalves are actually less abundant in the older record than in the younger record, contrary to the expected taphonomic megabias. Moreover, the observed increase in molluscan reinforcement does not coincide with the (late) Mesozoic Marine Revolution, but rather precedes this proposed driver, suggesting either that the MMR relates more to rare taxa than common taxa or that it began earlier because of currently under-documented predation pressure. The one pattern that does align with the timing of the MMR is the slight increases in brachiopod and gastropod infaunality near the Jurassic/Cretaceous boundary.

Our finding that mean shell reinforcement correlates with number of brachiopod and gastropod genera in a time bin suggests a bias in preservation and probably also in identifiability (i.e., more durable, diagnostic parts to preserve from each individual; Kidwell [2005] used genus durations to make the same argument for calcitic shells). Moreover, shell mineralogy is correlated with the number of genera and occurrences in bivalves, suggesting a possible preservational bias that does not exist for brachiopods or gastropods. In spite of these few correlations, however, our analyses show no indication of pervasive secular taphonomic bias at the Phanerozoic scale in any of the groups. Instead, the temporal patterns suggest biological explanations, including some that are contrary to existing hypotheses. For example, common taxa in all three groups appear to have a similar mean size, and size changes little through the Phanerozoic. Trends in shell reinforcement suggest that common taxa were responding to increased predation pressure well before the generally postulated onset of the Mesozoic Marine Revolution. Other preservability-related variables, namely infaunality, shell mineralogy, and microstructure, also show trends that are consistent with biological rather than taphonomic drivers.

In this taphonomic study aimed at the scale of Phanerozoic diversity curves (e.g., Sepkoski 1981, 1993; Alroy et al. 2001, 2008), we find no compelling evidence to suggest a secular trend in the durability of the most commonly sampled brachiopods, bivalves, and gastropods that might be explained by taphonomic megabias, or at least any single megabias. Despite a wealth of data indicating that these taphonomic variables are factors in shell preservation over experimental time scales, and well-documented large-scale changes in the taxonomic composition of marine ecosystems over evolutionary time, we find a remarkable lack of similar trends or synchronous shifts in shell durability in the Phanerozoic fossil record that can be attributed to taphonomic drivers. This finding does not mean an absence of taphonomic bias related to shell durability in the fossil record, but rather that multiple smaller-scale biases have had little *net* effect on the relative occurrences of key shell traits over the scale of the Phanerozoic.

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