



## Phanerozoic trends in brachiopod body size from synoptic data

Zixiang Zhang, Michael Augustin, and Jonathan L. Payne

**Abstract.**—Body size is one of the most studied phenotypic attributes because it is biologically important and easily measured. Despite a long history of study, however, the pattern of body-size change in diverse higher taxa over the Phanerozoic remains largely unknown because few relevant data sets span more than a single geological period or provide comprehensive, global coverage. In this study, we measured representative specimens of 3414 brachiopod genera illustrated in the *Treatise on Invertebrate Paleontology*. We applied these size data to stage-resolved stratigraphic ranges from the *Treatise* and the Paleobiology Database to develop a Phanerozoic record of trends in brachiopod size. Using a model comparison approach, we find that temporal variation in brachiopod size exhibits two distinct modes—a Paleozoic mode of size increase and a post-Paleozoic mode indistinguishable from a random walk. This transition reflects a change in the identities of the most diverse brachiopod orders rather than a shift in mode within any given order. Paleozoic size increase reflects a small, persistent bias toward the origination of new genera larger than those surviving from the previous stage and is identifiable as a statistically supported trend in three orders representing both Class Strophomenata (Order Productida) and Class Rhynchonellata (orders Atrypida and Spiriferida). Extinction exhibits no consistent bias with respect to size. The shift in evolutionary mode across the end-Permian mass extinction adds to long-standing evidence from studies of diversity and abundance that this biotic catastrophe suddenly and permanently altered the evolutionary history of what was, until that time, the most diverse animal phylum on Earth.

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### Introduction

Body size correlates with physiological, behavioral, and population-level traits that influence survival prospects over time (Peters 1983; Schmidt-Nielsen 1984; Calder 1984; Brown 1995), making it an ideal variable for examining controls on macroevolution across geological time. Despite longstanding interest in the topic (e.g., Newell 1949; Nicol 1966; Stanley 1973a; Jablonski 1996, 1997; Trammer and Kaim 1997; Alroy 1998; Dommergues et al. 2002; Trammer 2005; Twitchett 2007; Bell and Braddy 2012), however, the pattern of body-size change remains incompletely documented. Whereas synoptic data on the stratigraphic ranges of marine animal genera are nearly two decades old (Sepkoski 1996, 2002), there exists no comparable data set regarding the body sizes of marine animals even for a single class or phylum. The largest published data sets

comprise only a few hundred genera each of bivalves, brachiopods, and gastropods (Payne 2005; Novack-Gottshall 2006; Novack-Gottshall and Lanier 2008; Kosnik et al. 2011) and only one of these studies (Kosnik et al. 2011) spans the Phanerozoic. Consequently, it remains unclear whether documented examples of size increase over tens to hundreds of millions of years (e.g., Newell 1949; Hunt and Roy 2006; Novack-Gottshall 2006; Novack-Gottshall and Lanier 2008; Hunt et al. 2010) and decrease across mass extinction events (e.g., Arnold et al. 1995; Smith and Jefferey 1998; Fraiser and Bottjer 2004; Payne 2005; Twitchett and Oji 2005) reflect general rules or, alternatively, a bias toward publication of the most readily recognizable patterns.

Brachiopods present an ideal test case for examining Phanerozoic trends in organism size. They are diverse and abundant in the

fossil record and their systematics have been studied in depth for more than a century. Their predominantly calcite shells make them comparatively resistant to diagenetic loss from the fossil record (Cherns and Wright 2000, 2009; Wright et al. 2003). Moreover, studies of representative brachiopod genera suggest an early Paleozoic interval of substantial body-size increase (Stanley 1973a; Novack-Gottshall 2006; Novack-Gottshall and Lanier 2008; Kosnik et al. 2011), perhaps as part of an ecosystem-wide trend (Novack-Gottshall 2006). However, the largest brachiopods, such as the Carboniferous giant *Gigantoproductus giganteus*, lived during Paleozoic time (Payne et al. 2009) and visual inspection of the representative data compiled by Kosnik et al. (2011: Fig. 5D) suggests that size increase did not persist to the present day. The cause, timing, and even the existence of this possible shift in the trend of brachiopod size have yet to be tested quantitatively.

In this study, we present a synoptic, genus-level size database for the phylum Brachiopoda and use it to test whether the mean size across all brachiopod genera increased during the Paleozoic, whether this size increase is distinguishable from a random walk, and whether the statistical mode of size change differs between Paleozoic and post-Paleozoic time. The revised edition of the *Treatise on Invertebrate Paleontology* (Williams et al. 1997, 2000a,b,c, 2006, 2007) illustrates representative specimens for more than 3400 brachiopod genera and provides stage-resolved stratigraphic range information for most of these genera. Brachiopods are also well represented in the Paleobiology Database ([www.paleobiodb.org](http://www.paleobiodb.org); PaleoDB), enabling a sensitivity test of the pattern of size change implied by stratigraphic range information in the *Treatise* versus the PaleoDB.

## Data and Methods

**Body-size Data.**—We collected size data from the revised brachiopod volumes of the *Treatise on Invertebrate Paleontology* (Williams et al. 1997, 2000a,b,c, 2006, 2007), which contains scaled photographs illustrating 4802 brachiopod

species across 3414 genera. Of these, 3377 genera were reported with stage-resolved stratigraphic ranges. We measured holotype specimens when they were available. If there was no illustration of a holotype specimen for a given species, we moved to a paratype, neotype, or best-resolution illustration, in that order. Barring significant differences in the quality of image for the ventral and dorsal shell, we measured the ventral shell. If neither the ventral nor the dorsal shell was depicted or both were depicted at low resolution, we measured other available illustrations, such as the posterior and lateral profiles of the dorsal or ventral shells. In total, we measured non-dorsal or non-ventral profiles for 1.7% of the specimens. We made all measurements using digital calipers with resolution to the nearest tenth of a millimeter (prior to correction for image magnification).

**Stratigraphic Range Data.**—We collected stratigraphic range data from two sources: (1) the *Treatise* and (2) the PaleoDB (accessed 1 August 2011). To reflect the time scheme for stage assignments used in both sources, we correlated brachiopod occurrences to the stages listed in the Gradstein et al. (2008) geologic timescale. Resolution for the Cambrian stages was enhanced by using Russian stage boundaries from the GeoWhen Database (<http://www.stratigraphy.org/bak/geowhen/index.html>). For ranges from the *Treatise*, the Hirnantian stage was merged with the Llandovery stage because according to the *Treatise*, no genera originated during Hirnantian time, and only one genus went extinct within that stage.

**Data Treatment.**—For all analyses, we used log-transformed shell area (i.e., the product of width and length) as a measure of body size. For 3068 genera with stage-resolved stratigraphic ranges, only one specimen was illustrated such that area could be determined and so the size of this specimen was used to represent the genus. For 309 genera (9.1%), more than one species was illustrated (up to a maximum of five species). In these cases, we took the mean of the log-transformed shell area across illustrated species as the representative size for the genus. We did not use shell volume because nearly half of all brachiopod genera were not illustrated in a view illustrating

specimen height. However, the use of shell area rather than shell volume is unlikely to influence our results because variation in log-transformed area explains 98% of the variation in log-transformed volume (ordinary least-squares linear regression: slope =  $1.50 \pm 0.008$ , intercept =  $-0.21 \pm 0.02$ , adjusted  $R^2 = 0.98$ ,  $p < 2 \times 10^{-16}$ ) for specimens of known volume in our data set and the form of this relationship does not change meaningfully across geological time (Fig. 1). This finding is consistent with previous studies showing that shell length or area typically captures most of the variation in volume within and among higher taxa (Novack-Gottshall 2008). Moreover, the volume of type specimens and specimens illustrated in monographs generally correlate with the median size of a typical adult individual of the species for marine invertebrate fossils, including brachiopods (Kosnik et al. 2006; Krause et al. 2007). Thus, although there is often a positive bias in the sizes of illustrated specimens and type specimens relative to specimens from bulk collections, representative specimens should still be sufficient to capture trends in the distribution of sizes across species and genera. In addition, the

existence of these biases does not necessarily affect the interpretation of the trend in the mean. Such biases would only affect analyses of trends in mean size if the nature of the bias varied substantially and systematically as a function of geological time. We are not aware of any evidence that the size bias in the illustration of specimens or the selection of representative species for the *Treatise* does in fact vary systematically with respect to the stratigraphic ranges of brachiopod genera. Data used in analyses are archived within the Stanford Digital Repository (<http://purl.stanford.edu/sw967vm0154>) as Supplementary Tables 1 and 2.

*Analysis of Evolutionary Mode.*—We used the “joint” parameterization of the “paleoTS” package (v. 0.4-1; Hunt 2011) in R (v. 2.13.1; R Development Core Team 2011) to examine support across three statistical models of body-size change: unbiased random walk, directional trend, and stasis. An unbiased random walk is the null mode in the absence of any selective pressure on body size (McShea 1994). A directional trend is the expected mode when selective pressures favor size increase or decrease to a constant extent over time, whether due to species sorting or within-lineage trends. Stasis is expected when size is optimized to invariant biological, ecological, and environmental factors (Kingsolver and Pfennig 2004). We compared support across these three models using the small-sample corrected version of Akaike’s information criterion (AICc) and the associated Akaike model weight (Akaike 1974; Hunt 2006).

Based on visual evidence for an increasing trend in size that ended late in Paleozoic time, we examined statistical support for a case in which the evolutionary mode was allowed to shift at some point during the Phanerozoic, either from one mode to another or from one set of parameter values to another within a given mode. The optimal breakpoint in the Phanerozoic for the two-phase model was identified by comparing the AICc value of aggregate models for every possible breakpoint. The best evolutionary mode for each subset was identified using the AICc. We required each interval within a given mode to be at least six geologic stages long in order to constitute a true, long-term evolutionary mode.

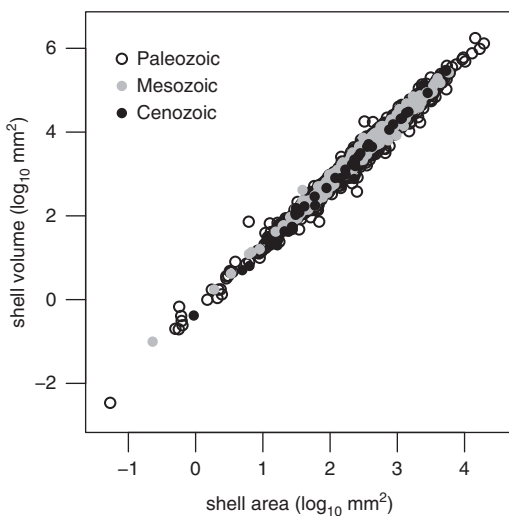


FIGURE 1. Scatter plot of brachiopod shell volume versus shell surface area, illustrating the strong linear correlation between area and volume in logarithmic space. The tight correlation between these measures of size demonstrates that shell area is a reliable proxy for shell volume. Variation in log-transformed area explains 98% of the variation in log-transformed volume (slope =  $1.50$  (SE =  $0.008$ ), intercept =  $-0.21$  (SE =  $0.02$ ), adjusted  $R^2 = 0.98$ ,  $p < 2 \times 10^{-16}$ ).

*Analysis of Size Selectivity in Extinction and Origination.*—To test for size bias in the extinction and origination processes, within each stage we compared the mean shell area of originating genera with that of genera surviving from the previous stage, and the mean of extinction victims with the mean of genera surviving into the subsequent stage using two-tailed, two-sample *t*-tests assuming unequal variances. We also calculated the effects of extinction and origination on the overall size distribution following the methodology of Rego et al. (2012). This approach accounts for the fact that the effect of extinction and origination on the overall size distribution depends both on the differences in mean values between victims and survivors (or between originators and survivors from the previous stage) and on the number of genera in each category. For example, extinction may be strongly size biased but have only a small effect on the overall mean size if extinction intensity is low.

## Results

*Pattern of Body-size Evolution.*—Figure 2 illustrates the sizes of all brachiopod genera and stage-level mean values across the Phanerozoic using stratigraphic range constraints from the *Treatise* (Fig. 2A) and the Paleodb (Fig. 2B). The two treatments agree closely in trend and absolute value across Paleozoic and Mesozoic time (Pearson's  $r=0.89$ ,  $p<0.0001$ ), despite dissimilar diversity trends during the late Paleozoic (Fig. 3). Mean body size increased steadily from the Late Cambrian to the Early Carboniferous (Mississippian) before stabilizing during the Late Carboniferous (Pennsylvanian) and Permian. This trend toward larger size persists across large increases and decreases in total genus diversity. Both data sets show decreases in mean and maximum size across the Permian–Triassic transition, although the decrease appears gradual during Late Permian time when using stratigraphic ranges from the *Treatise* versus abrupt when using ranges from the Paleodb (Fig. 3A). Both data sets show an increase in mean size from the Early Triassic to the Middle Jurassic. The *Treatise* data indicate a

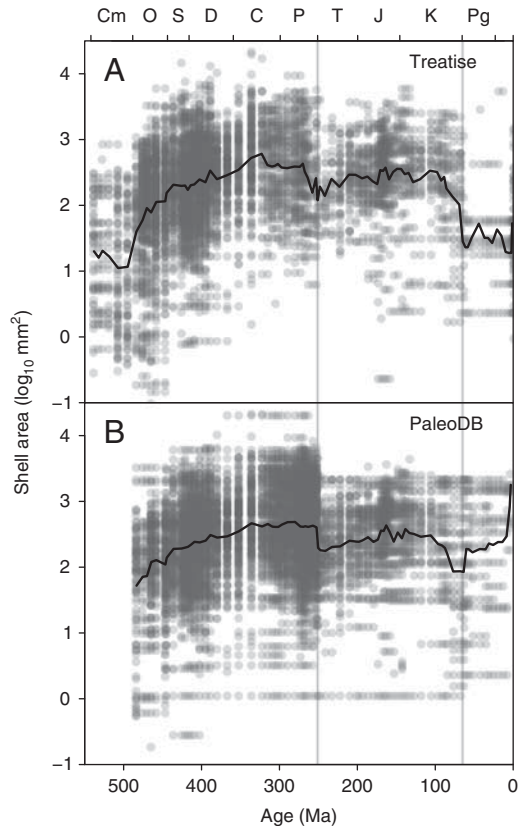


FIGURE 2. Plot of brachiopod body sizes across the Phanerozoic illustrating the range of sizes as well as trends in the mean. A, Shell area applied to stratigraphic ranges from the *Treatise*. B, Shell area applied to stratigraphic ranges from the Paleodb. Each dot represents the size of a genus within a geological stage. The black lines illustrate the trend in the mean for each data treatment.

decrease in mean size across the Cretaceous–Paleogene transition and stable small body sizes during the Cenozoic. The Paleodb data suggest, instead, a slight size decrease during the Late Cretaceous followed by a return to typical Mesozoic sizes during Cenozoic time. The small number of genera present within Cenozoic stages (<25 in the Paleodb and <10 in the *Treatise*) and the limited reporting of Cenozoic brachiopod occurrences from Cenozoic strata make it difficult to interpret the differing trajectories of mean size between the *Treatise* and Paleodb data treatments over the past 66 Myr but suggest that they result from effects related to small sample size.

*Analysis of Evolutionary Mode.*—In the analysis assuming a single mode of body-size variation

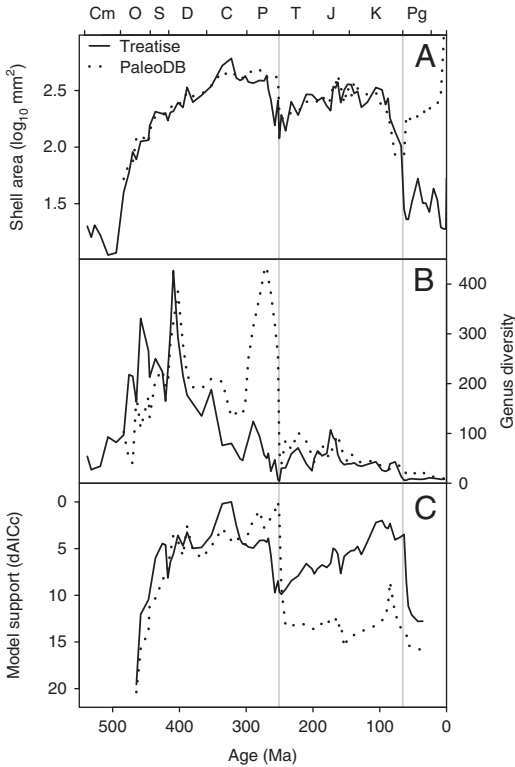


FIGURE 3. Histories of stage-level mean body size (A) and sampled biodiversity throughout the Phanerozoic (B). C, Plot of relative AICc values generated from the breakpoint analysis quantify the fit of all two-phase models based on the location of the breakpoint. For each analysis, the model with the minimum AICc value (i.e., the best-supported model) was set to zero and all other breakpoints are presented in terms of relative support, where larger positive numbers indicate weaker model fit. The best-supported breakpoint for the *Treatise* data is in the Serpukhovian (Mississippian) and in the Changhsingian for the PaleoDB data.

across the entire Phanerozoic, unbiased random walk modestly outperforms the directional trend model when stratigraphic ranges from either the PaleoDB or the *Treatise* are used (Table 1). Neither data set provides meaningful statistical support for stasis (Table 1).

In the analysis allowing for two intervals with potentially different modes, the optimal breakpoint occurs in the terminal Mississippian (Serpukhovian stage) for stratigraphic ranges determined from the *Treatise*, and in the terminal Permian (Changhsingian stage) for stratigraphic ranges determined from the PaleoDB. Using ranges from the *Treatise*, both pre- and post-Serpukhovian body-size change are best

described by directional trends. Directionality is positive throughout the Paleozoic ( $\mu_{\text{step}} = 0.0069$ ;  $\sigma_{\text{step}}^2 = 0.0004$ ), and negative thereafter ( $\mu_{\text{step}} = -0.0043$ ;  $\sigma_{\text{step}}^2 = 0.0011$ ). Using ranges from the PaleoDB, pre-Changhsingian body-size evolution is best described by a directional trend ( $\mu_{\text{step}} = 0.0035$ ;  $\sigma_{\text{step}}^2 = 0.0002$ ), whereas post-Changhsingian body-size evolution is best described by an unbiased random walk ( $\sigma_{\text{step}}^2 = 0.0013$ ). The two-phase model is overwhelmingly supported relative to the one-phase model in both data treatments (Table 1). In aggregate, there is clear evidence for a driven trend toward larger body size in brachiopods during most of Paleozoic time but substantial uncertainty in the dynamics thereafter, due to both greater differences between data treatments and smaller evidence ratios among models within data treatments (Table 1).

Analysis of evolutionary mode by class and order using the more complete set of stratigraphic ranges from the *Treatise* suggests that the shift in evolutionary mode between the Paleozoic, especially the early Paleozoic, and the post-Paleozoic results from a change in evolutionary mode within Class Rhynchonellata due to a shift in the identities of the most diverse constituent orders. Classes Strophomenata and Rhynchonellata exhibit similar mean sizes and trajectories in mean size across Paleozoic time (Fig. 4A). A driven trend toward larger size is strongly favored in Class Strophomenata (AICc weight = 0.998) and modestly favored in Class Rhynchonellata (AICc weight = 0.809) for the interval prior to the overall transition in evolutionary mode across the entire data set ca. 325 Mya (Table 2). In contrast, an unbiased random walk is modestly favored for Rhynchonellata in post-Paleozoic time (AICc weight = 0.713) and Strophomenata became extinct. At the order level, two rhynchonellate orders (Atrypida and Spiriferida) and one strophomenate order (Productida) receive strong support for a driven trend toward larger size and all of the orders for which the driven trend is the best-supported model exhibit increasing trends (Table 2, Fig. 4B). No order exhibits strong support for any other model of size change. The one order that is sufficiently abundant for analysis both during the early Paleozoic and

TABLE 1. Comparison of model support between best one- and two-phase treatments and among unbiased random walk (URW), directional random walk (DRW), and stasis (STA) for each phase.

Model	<i>Treatise</i>			PaleoDB		
	Akaike wt.: 0.002			Akaike wt.: 0.001		
One-phase	<i>n</i> = 75			<i>n</i> = 76		
Model	LogL	AICc	Akaike wt	LogL	AICc	Akaike wt
URW	40.39	-76.62	0.74	60.24	-116.31	0.59
DRW	40.44	-74.53	0.26	60.98	-115.63	0.42
STA	-32.10	68.37	0	6.84	-9.51	0
Two-phase	Akaike wt.: 0.998			Akaike wt.: 0.999		
1 <sup>st</sup> phase	(483.5 – 322.25 Ma; <i>n</i> = 20)			(483.5 – 252.4 Ma; <i>n</i> = 34)		
URW	15.72	-26.74	0.04	42.27	-80.16	0.05
DRW	20.43	-33.35	0.97	46.43	-86.06	0.95
STA	-3.67	12.04	0	-2.33	9.05	0
2 <sup>nd</sup> phase	(322.25 – 4.47 Ma; <i>n</i> = 56)			(252.4 – 35.6 Ma; <i>n</i> = 43)		
URW	27.28	-50.33	0.25	23.06	-41.83	0.76
DRW	29.51	-52.55	0.75	23.06	-39.52	0.24
STA	-29.33	62.88	0	14.02	-23.74	0

during the post-Paleozoic, Rhynchonellida, receives modest support for an unbiased random walk during both intervals (Table 2); and the other abundant and diverse post-Paleozoic order, Terebratulida, also receives modest support for an unbiased random walk (Table 2). The differences in size trajectories are apparent when comparing mean values between the Paleozoic orders for which a driven trend is favored and the rhynchonellids and terebratulids, for which an unbiased random walk is better supported (Fig. 4B). Because the unbiased random walk is a special case of the driven trend model, in which the mean step size is exactly zero, it is impossible for the unbiased random walk to receive more than 0.75 AICc weight (Hunt 2006). Consequently, the support for the unbiased random walk in these cases is nearly as high as is possible given the nature of the model comparison, indicating that nearly all support is for a random walk with a mean step size indistinguishable from zero.

*Effects of Extinction and Origination on Size Evolution.*—Changes in the distribution of brachiopod sizes across stages in our data set are necessarily caused by the differential effects of extinction and origination. Figure 5 illustrates the differences in mean body size between newly originating genera and those that survived into the stage from the previous

stage (Fig. 5A) and the differences in mean body size between extinction victims and survivors for each stage (Fig. 5B), using the more complete stratigraphic range information from the *Treatise*. The direction of the size difference varies from stage to stage for both origination and extinction (Fig. 5), and two-sample *t*-tests indicate that few of these differences are statistically distinguishable from zero (Supplementary Tables 3, 4). Similarly, the effects of origination and extinction on the size distribution (integrating effects from the differences in mean size with the number of originators versus survivors from the previous stage and with the number of extinction victims versus the number of survivors to the subsequent stage) are variable in direction from stage to stage (Fig. 5C,D). A *t*-test of the distribution of size differences between originators and survivors shows that there is a significant bias toward the preferential origination of larger genera during the Paleozoic (Table 3), which appears to be the primary control on the overall increase in mean size across this era. In contrast, there is no significant overall bias in the size difference between extinction victims versus survivors (Table 3). The origination effect is also significantly different from zero (Table 3). There is also a significant bias toward size decrease from the extinction effect in the

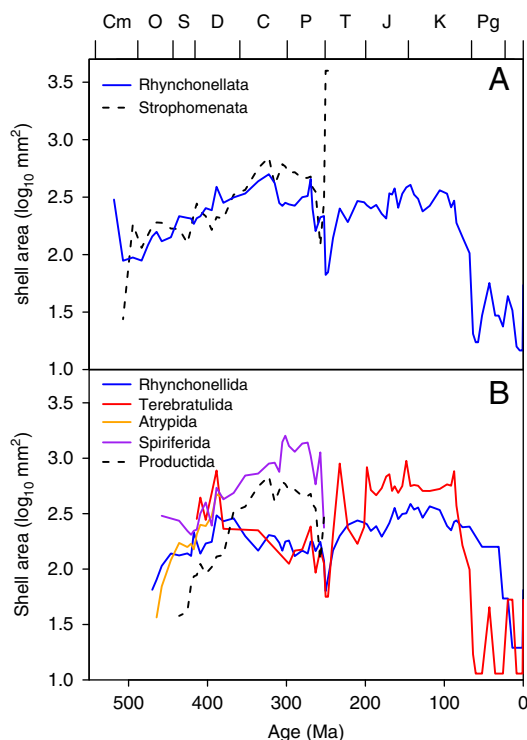


FIGURE 4. Line graph illustrating close similarity of mean size and trends in mean size for brachiopod classes and orders. A, Classes. A driven trend is the favored model for the interval prior to 325 Ma in both classes, whereas a random walk is the best-supported model for Rhynchonellata during post-Paleozoic time (Table 2). B, Trends in mean size for representative orders (full results presented in Table 2). An unbiased random walk is favored for the two most diverse post-Paleozoic orders (Terebratulida and Rhynchonellida) during post-Paleozoic time and for Rhynchonellida during Paleozoic time. In contrast, three Paleozoic orders (Spiriferida, Atrypida, and Productida) exhibit strong driven trends toward larger size during Paleozoic time. The differing trajectories between the former and latter groups, even during Paleozoic time, suggest that the overall transition in body-size trend may result from clade replacement rather than a change in pattern within any order.

post-Paleozoic but no significant bias in the extinction effect during the Paleozoic (Table 3). Thus, Paleozoic size increase in brachiopods occurred more through size bias in origination than in extinction.

## Discussion

Synoptic data on brachiopod body sizes indicate that this phylum experienced two distinct phases of body-size change: a Paleozoic trend toward larger size followed by a post-

Paleozoic interval that cannot be clearly distinguished from an unbiased random walk. The evidence for a driven trend toward larger size during Paleozoic time corroborates findings from previous studies of more limited scope. Novack-Gottshall and Lanier (2008; see also Novack-Gottshall 2008) found evidence for a driven trend toward larger size from the Cambrian through the Devonian in a data set of 369 genera known from deep-subtidal, soft-bottom fossil assemblages. Kosnik et al. (2011) used a data set of the 328 most commonly occurring genera in the Paleobiology Database and found that the Phanerozoic pattern of size evolution was best characterized by an unbiased random walk, but that there was support for a driven trend toward larger size in the early Paleozoic component of their data set. The consistency between these previous findings and our synoptic results demonstrates that the Paleozoic trend toward larger size is not confined to the most common or abundant ~10% of genera; rather, it characterizes the evolution of the entire phylum.

The difference in the timing of the shift in mode of size change implied by the *Treatise* versus PaleoDB stratigraphic ranges reflects emerging data from south China that most dramatically affect the stratigraphic ranges of Permian genera as well as a distinct Carboniferous peak in mean size in the *Treatise* data that is not expressed in the PaleoDB treatment (Figs. 2, 3). Many genera that have last occurrences in the Middle Permian rock record of North America have recently documented Upper Permian occurrences in south China (Clapham et al. 2009), which have recently been incorporated into the PaleoDB but were likely not available to be incorporated into the *Treatise* at its time of publication. These occurrences have prompted a substantial downward revision in the magnitude of the end-Guadalupian (latest Middle Permian) mass extinction (Clapham et al. 2009) and, based on the results presented here, appear also to impact the apparent dynamics of body-size evolution. Based on the general agreement between the *Treatise* and PaleoDB records and the identifiable cause for the latest Paleozoic discrepancy, we ascribe more weight to the results from the PaleoDB regarding the precise timing of the shift in evolutionary mode.

TABLE 2. Comparison of model support among unbiased random walk (URW), directional random walk (DRW) and stasis (STA) for brachiopod classes and orders during the early Paleozoic (>325 Ma) and the post-Paleozoic (<251 Ma), illustrating that the only model that receives strong support (AICc weight >0.90) is the directional random walk during the Paleozoic.

Class	Order	Interval	DRW	URW	Stasis
<b>Rhynchonellata</b>		<b>&gt; 325 Ma</b>	<b>0.998</b>	<b>0.002</b>	<b>0.000</b>
Strophomenata		> 325 Ma	0.809	0.191	0.000
Rhynchonellata		< 251 Ma	0.287	0.713	0.000
Lingulata	Lingulida	> 325 Ma	0.229	0.769	0.002
<b>Rhynchonellata</b>	<b>Atrypida</b>	<b>&gt; 325 Ma</b>	<b>0.994</b>	<b>0.006</b>	<b>0.000</b>
<b>Rhynchonellata</b>	<b>Spiriferida</b>	<b>&gt; 325 Ma</b>	<b>0.955</b>	<b>0.044</b>	<b>0.002</b>
Rhynchonellata	Athyridida	> 325 Ma	0.869	0.126	0.005
Rhynchonellata	Pentamerida	> 325 Ma	0.535	0.465	0.000
Rhynchonellata	Orthida	> 325 Ma	0.349	0.616	0.035
Rhynchonellata	Rhynchonellida	> 325 Ma	0.282	0.714	0.005
<b>Strophomenata</b>	<b>Productida</b>	<b>&gt; 325 Ma</b>	<b>0.997</b>	<b>0.003</b>	<b>0.000</b>
Strophomenata	Strophomenida	> 325 Ma	0.569	0.430	0.001
Rhynchonellata	Rhynchonellida	< 251 Ma	0.346	0.654	0.000
Rhynchonellata	Terebratulida	< 251 Ma	0.255	0.745	0.000

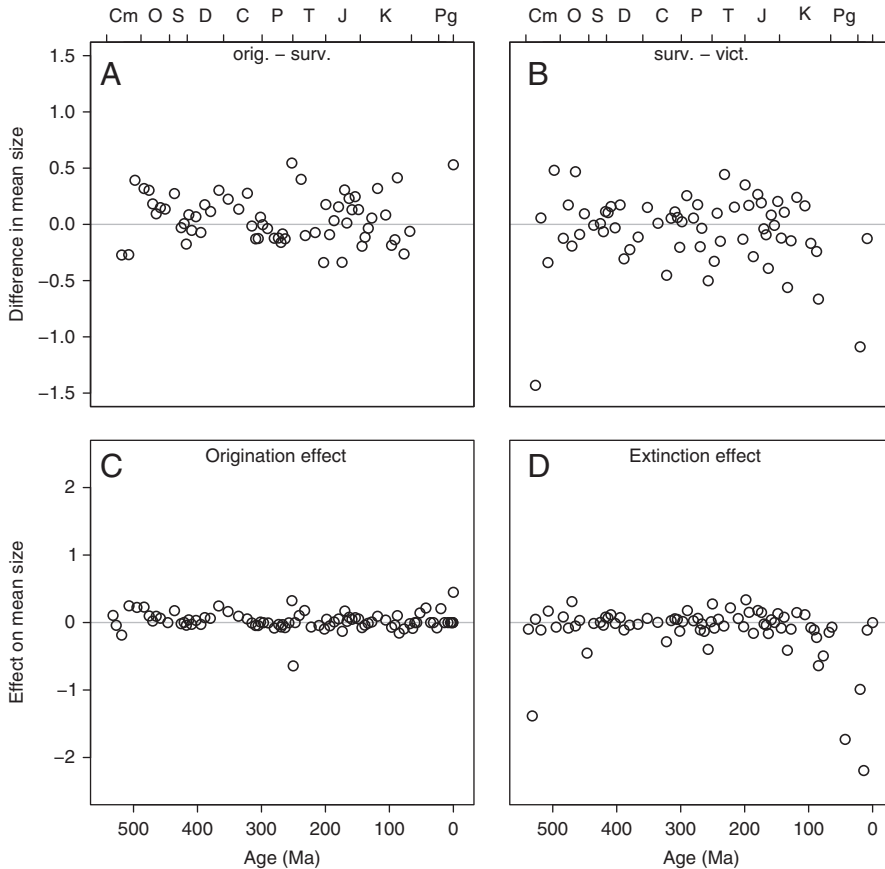


FIGURE 5. Scatter plots of the difference in mean body size between newly originating genera and those that survived into the stage from the previous stage (A), and between extinction victims and survivors into the next stage (B) for stages in which there were at least five victim and survivor genera. Positive values indicate that originating genera (or victims) were larger than survivors. Analysis is based upon the more comprehensive *Treatise* data set. Panels C and D are scatter plots illustrating the change in mean size attributable to origination (C) and extinction (D) across each stage boundary. The bias toward origination of larger genera and the significantly positive effect of origination on overall mean size during Paleozoic time are confirmed by *t*-tests (Table 3).



TABLE 3. Comparison of model support among unbiased random walk (URW), directional random walk (DRW) and stasis (STA) for brachiopod classes and orders during the early Paleozoic (>325 Ma) and the post-Paleozoic (<251 Ma), illustrating that the only model that receives strong support (AICc weight >0.90) is the directional random walk during the Paleozoic. For origination the size difference is calculated as originators minus survivors and for extinction as survivors minus victims.

Process	Variable	Interval	Mean	<i>p</i> -value	df	lower 95% CI	upper 95% CI
Origination	Size difference	Phanerozoic	0.07	0.13	71	-0.02	0.17
<b>Origination</b>	<b>Size difference</b>	<b>Paleozoic</b>	<b>0.08</b>	<b>0.05</b>	<b>36</b>	<b>0.00002</b>	<b>0.17</b>
Origination	Size difference	post-Paleozoic	0.06	0.48	34	-0.12	0.24
Extinction	Size difference	Phanerozoic	-0.13	0.07	72	-0.24	0.02
Extinction	Size difference	Paleozoic	-0.05	0.37	37	-0.15	0.06
<b>Extinction</b>	<b>Size difference</b>	<b>post-Paleozoic</b>	<b>-0.21</b>	<b>0.04</b>	<b>34</b>	<b>-0.42</b>	<b>-0.01</b>
Origination	Effect on mean size	Phanerozoic	0.03	0.08	71	-0.004	0.06
<b>Origination</b>	<b>Effect on mean size</b>	<b>Paleozoic</b>	<b>0.05</b>	<b>0.02</b>	<b>36</b>	<b>0.01</b>	<b>0.08</b>
Origination	Effect on mean size	post-Paleozoic	0.01	0.66	34	-0.04	0.07
<b>Extinction</b>	<b>Effect on mean size</b>	<b>Phanerozoic</b>	<b>-0.11</b>	<b>0.02</b>	<b>73</b>	<b>-0.20</b>	<b>-0.01</b>
Extinction	Effect on mean size	Paleozoic	-0.05	0.21	38	-0.14	0.03
Extinction	Effect on mean size	post-Paleozoic	-0.17	0.06	34	-0.35	0.01

The coincidence of the shift in mode for brachiopod body size with the end-Permian mass extinction adds to an already voluminous body of evidence testifying to the lasting effects of this biotic catastrophe on macroevolutionary dynamics. Response to the end-Permian extinction is the most important feature distinguishing the Paleozoic versus Modern faunas in Sepkoski's (1981) factor analysis of diversity dynamics in the fossil record. At the same time, the abundance distributions of marine animal communities changed in ways that suggest an increase in ecological complexity (Wagner et al. 2006). The terminal Permian event was also an important event in the rise of bivalves as the most diverse, abundant, and ecologically important benthic suspension feeders in the oceans (Gould and Calloway 1980; Fraiser and Bottjer 2007; Payne et al. 2014) within a longer-term trend from brachiopod to bivalve dominance at the community level (Sepkoski and Miller 1985; Kidwell and Brenchley 1994; Clapham and Bottjer 2007). Foraminifera also exhibit a shift in the dynamics of size evolution across the Permian-Triassic transition, from environmental control to stasis (Payne et al. 2012), suggesting that the effects of the Permian extinction on body-size evolution may have been as pervasive as those on the taxonomic and ecological structure of marine communities. As with brachiopods, the post-Paleozoic shift in foraminiferan body-size dynamics reflects a shift in the dominant

orders rather than a change in mode within any order (Payne et al. 2012).

In contrast to the end-Permian shift in the mode of body-size change, the causes of the Paleozoic trend toward larger body size remain difficult to pinpoint. The coincidence of size increase across several phyla and classes during the early Paleozoic (Novack-Gottshall 2008) suggests that size increase was controlled by factors affecting the entire biosphere, rather than processes influencing brachiopods alone. Molybdenum isotope evidence indicates a gradual increase in oxygen availability in Paleozoic seawater, which could potentially explain ecosystem-wide increases in animal size through progressive removal of oxygen limitation on respiration and growth (Dahl et al. 2010). Alternatively, increases in the quantity and nutritional quality of primary production could account for the trend if food resources were limited during early Paleozoic time (e.g., Vermeij 1995, 2004; Martin 1996; Bambach 1999; Martin and Quigg 2012). A further possibility is that the advent of predation not only enabled the diversification of macroscopic marine animals (Stanley 1973b; Marshall 2006; Sperling et al. 2013), but also promoted evolution toward larger size as a refuge from predation pressure. Because these factors are not mutually exclusive, determining their relative contributions to the observed trend in size will require improved quantification of both the redox history of seawater and the structural evolution of marine ecosystems.

## Conclusions

Brachiopod body-size evolution has been characterized by two distinct phases: an interval of size increase spanning the Paleozoic, and an interval indistinguishable from a random walk characterizing the post-Paleozoic. Synoptic data thus confirm previous findings of a driven trend toward larger size during Paleozoic time from data sets of more limited temporal and taxonomic coverage (e.g., Novack-Gottshall 2006; Novack-Gottshall and Lanier 2008; Kosnik et al. 2011). The coincidence of the shift in dynamics with the end-Permian mass extinction adds yet another line of evidence for the rapid and permanent effects of this biotic crisis on the long-term evolution of the marine biosphere (Sepkoski 1981; Erwin 1993; Wagner et al. 2006; Payne and Clapham 2012; Payne et al. 2012). Although the cause of the 200-Myr-long trend toward larger size in Paleozoic brachiopods remains difficult to fingerprint, these data greatly strengthen the evidence for a global trend toward larger body sizes across the first half of animal life.

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