

Scale-dependence of Cope's rule in body size evolution of Paleozoic brachiopods

Philip M. Novack-Gottshall* and Michael A. Lanier

Department of Geosciences, University of West Georgia, Carrollton, GA 30118-3100

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The average body size of brachiopods from a single habitat type increased gradually by more than two orders of magnitude during their initial Cambrian–Devonian radiation. This increase occurred nearly in parallel across all major brachiopod clades (classes and orders) and is consistent with Cope's rule: the tendency for size to increase over geological time. The increase is not observed within small, constituent clades (represented here by families), which underwent random, unbiased size changes. This scale-dependence is caused by the preferential origination of new families possessing initially larger body sizes. However, this increased family body size does not confer advantages in terms of greater geological duration or genus richness over families possessing smaller body sizes. We suggest that the combination of size-biased origination of families and parallel size increases among major, more inclusive brachiopod clades from a single habitat type is best explained by long-term, secular environmental changes during the Paleozoic that provided opportunities for body size increases associated with major morphological evolution.

body volume | origin of clades | macroevolutionary trend | species selection | maximum likelihood

Increasing body size is a pervasive predictor of population-level selection (1), and although macroevolutionary trends of increasing size, including Cope's rule (2–7), are known for many fossil groups, the mechanisms by which short-term size advantages are manifested at longer time scales remains poorly understood. Macroevolutionary size increases can occur via two distinct pathways: (i) maximum and mean size can increase within a clade because of passive diffusion from an unchanging lower size (sometimes termed “increasing variance”) or (ii) size increase can be driven and accompanied by increases in minimum size (7–10). Here, we confine Cope's rule to this second, driven pathway because it implies that clades with larger body sizes have greater evolutionary fitness than smaller clades. Such advantages can arise in several ways, including from the biological benefits of larger, optimal sizes (1, 4, 7); from size-linkages with changing environmental conditions (11–13); or from preferential sorting of clades associated with larger body size (14, 15). Analyses of size trends have focused on post-Paleozoic groups, limiting our understanding of size evolution during the otherwise well studied Cambrian and Ordovician radiations of animals and during the Paleozoic in general. Brachiopods offer a natural exemplar for such studies because of their fundamental contribution to these Lower Paleozoic radiations, their ecological dominance in most Paleozoic benthic marine communities, and their unrivaled fossil record (16–19). This study uses the largest and temporally most extensive database of fossil brachiopod sizes assembled to date to evaluate the existence and causes of size increases during the Cambrian through Devonian: the 170-million-year (Myr) interval covering the initial ascent of brachiopods to their zenith of Phanerozoic diversity. Recent cladistically based brachiopod classifications (17–20) allow detailed testing of the mechanisms responsible for these trends.

Results and Discussion

Size Trends Within Large Clades (Phylum, Classes, and Orders). A database of brachiopod body sizes (measured here as shell

volume) for 369 adult genera [see supporting information (SI) Appendix, Tables 1 and 2] from deep-subtidal, soft-substrate habitats demonstrates that brachiopod body size increased substantially and gradually during the Early and Mid-Paleozoic (Fig. 1), from a Cambrian mean of 0.04 ml ($-1.40 \log_{10} \text{ ml} \pm 0.27 \text{ SE}$, $n = 18$ genera) to a Devonian mean of 1.55 ml ($0.19 \log_{10} \text{ ml} \pm 0.06$, $n = 150$). The magnitude of size increase between periods is statistically significant. We evaluated within-phylum dynamics by using maximum-likelihood comparisons among three evolutionary models: directional (driven, biased, general random walk) change (DRW), unbiased (passive) random walk (URW), and stasis (22), with DRW generally resulting in a pattern of Cope's rule when there is a positive directionality parameter (a maximum-likelihood estimate of the magnitude of the rate of size change). The brachiopod phylum-level size trend is overwhelmingly supported by the directional model (SI Appendix, Table 3), with a constant and positive rate of size increase of $0.013 \log_{10} \text{ ml/Myr} \pm 0.005$. This rate of change is small but is sufficient to gradually increase brachiopod size by an order of magnitude every 77 Myr, on average. Sparse sampling during the Cambrian makes it impossible to resolve here whether size increase was continuous throughout the Cambrian–Devonian or was delayed until the Ordovician Radiation. Regardless, the increasing minimum size of brachiopods overall is consistent with Cope's rule, excluding a passive, diffusional trend of increasing variance through time (7–10). These increases are not the result of sampling heterogeneities because they are observed when sampling is standardized by rarefaction (SI Appendix, Fig. 5).

Such a phylum-wide increase can result from the accumulation of within-clade processes where constituent clades are all tending toward larger size or from among-clade processes where constituent clades remain at a constant size throughout each of their histories but clades with small body-sized genera are replaced over time by clades with larger-sized genera (14, 15). Because recent brachiopod classifications use cladistically informed standards and recognize many monophyletic groups (17–20), we treated classes, orders, and families as representative clades of varying levels of hierarchical nestedness. Although many of these clades, especially families, are likely paraphyletic, our results remain adequate summaries of the evolutionary relationship between morphological and body size evolution in Paleozoic brachiopods because these taxonomic groups are defined by morphological similarity.

We evaluated the underlying mechanism for this trend by using two distinct tests. The first test applies the maximum-likelihood approach used above to differentiate DRW, URW,

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*To whom correspondence should be addressed. E-mail: pnovackg@westga.edu.

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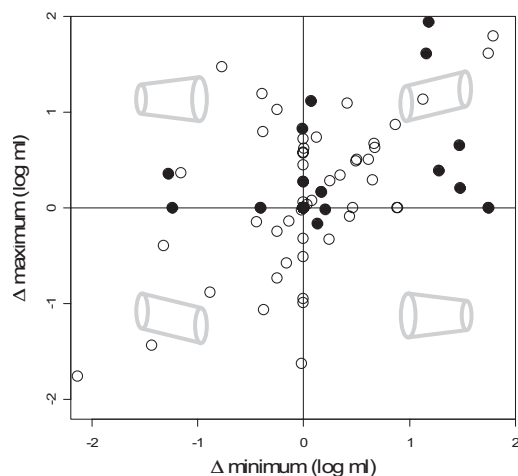


Fig. 4. Net behavior of minimum and maximum size transitions within individual brachiopod orders (filled circles, $n = 17$) and families (open circles, $n = 86$). Axes note the change in the minimum (on abscissa) and maximum sizes, measured in \log_{10} ml, from oldest to youngest occurrences in each taxon (10); this overall behavior is portrayed by gray images, with time progressing to the right. For example, the upper right quadrant (quadrant 1) represents increases in the minimum and maximum (i.e., Cope's rule), while the upper left quadrant (quadrant 2) represents an increase in the overall size range (i.e., increased variance) caused by increasing maximum and decreasing minimum sizes. Several points overlap on origin (values provided in *SI Appendix, Table 4*).

This parallelism for increases in size among independent clades reduces the likelihood that the trends are an artifact of methodological or taphonomical biases. There is no reason to suspect that changes occurred in the field practices used to collect fossils from these periods, making it unlikely that small brachiopods were overlooked by systematists in Mid-Paleozoic collections. Indeed, the brachiopod order with the consistently smallest sizes, Acrotredida, also displays simultaneously increasing minimum and maximum size trends (*SI Appendix, Fig. 6B and Tables 3 and 4*). The increases also transcend differences in shell structure and mineralogy, decreasing the likelihood that the trends are simple artifacts of taphonomical biases. Classes Lingulata and Paterinata have organophosphatic shells, and the remaining classes share calcitic shells that have a variety of structural fabrics (17–20). Finally, the trends are also unlikely to be an artifact of taxonomic practice because of the cladistic basis for high-level brachiopod classification (20) and standardized taxonomic practices for families and lower levels (17–19). Improbably large degrees of bias—not simply error—would have to exist to eliminate these broadly congruent trends.

Size Trends Within Smaller Constituent Clades (Families). The same tendency toward size increase is not observed within smaller constituent clades, represented here by families. Trends at this level are more variable (Fig. 2), and individual clades are best fit by the URW model (*SI Appendix, Table 3*), with much less support for the DRW and stasis models compared with their more-inclusive clades (classes and orders). This random, unbiased behavior across families is most clearly visible in the distribution of directionality parameters (Fig. 3), which is indistinguishable from zero tendency (*SI Appendix, Table 5*) and displays greater variation compared with their more-inclusive clades (orders and classes). This lack of an overall tendency is also evident in the behavior of maximum and minimum sizes in these families (Fig. 4 and *SI Appendix, Table 4*). Substantial numbers of families plot in all four quadrants, with most displaying either mutual increases in minimum and maximum size (i.e., Cope's rule) or mutual decreases. The rarity of changes

in variance (quadrants 2 and 4) might be expected here because these smallest clades have short durations and few genera per interval. However, maximum size increases are neither significantly more frequent than decreases (12 vs. 8) nor of greater magnitude when analyses are restricted to the 20 best-sampled families. There is also no statistical support for Cope's rule in the families displaying increasing maximum size, with only eight of these plotting in quadrant 1.

It might be argued that the decreasing tendency for size increases within smaller clades is an artifact of diminishing sample sizes (25, 26). This is unlikely here for two reasons. In the second test (Fig. 4), those families not demonstrating size trends were the ones with the most occurrences and longest durations; poorly sampled families were removed to preclude such biases. Also, although sampling can decrease the precision of parameter estimates and the power of model discrimination in the maximum-likelihood tests (Fig. 3), it does not affect the accuracy of these parameters (22). It is notable, in this light, that the joint directionality parameter calculated across all families (a measure less prone to sample-size effects because it estimates a shared size tendency across all clades simultaneously) remains negligibly positive ($4.7 \times 10^{-7} \log_{10} \text{ ml/Myr} \pm 9.6 \times 10^{-6}$) and substantially below that for classes ($0.007 \log_{10} \text{ ml/Myr} \pm 0.004$) and orders ($0.007 \log_{10} \text{ ml/Myr} \pm 0.003$). Thus, the dynamics in clades of varying hierarchical nestedness are distinct and consistent within each level of nestedness, with dynamics within the smallest constituent clades insufficient to ratchet up to those observed within larger, more inclusive clades.

Macroevolutionary Selection Among Families. One way to reconcile such discrepancies would be if size-related macroevolutionary processes within constituent clades (e.g., those represented here by families) are different from those within their more inclusive clades (14, 15, 27, 28). Three possibilities—none mutually exclusive but each capable of creating the observed trends (27)—include (i) positive bias in the mean size of originating families, (ii) positive correlation between family mean body size and geological duration, and (iii) positive correlation between family mean body size and genus richness (a proxy for speciation rate). The first hypothesis implies that size-biased selection acts only during speciation events, coincident with major morphological changes of an extent that a systematist would define a new family. The latter two hypotheses imply that larger size preferentially connotes greater family-level fitness. Because family-level brachiopod phylogenies are not available, we tested these three hypotheses for the 87 best-sampled families by computationally resampling candidate ancestor–descendent pairs at random on the basis of order of stratigraphic occurrence and evaluating how frequently each hypothesis was demonstrated as statistically significant. This technique essentially evaluates the sensitivity of each hypothesis to changing phylogenetic structure (29) and has been used in other analyses of Cope's rule in fossil taxa where phylogenies were unavailable (4). Such stratigraphically based phylogenies are also reasonable given the exceptionally complete fossil record of brachiopods (16, 20, 30, 31).

Newly originating brachiopod families here have significantly larger body sizes—on average $0.238 \log_{10} \text{ ml} (\pm 0.072 \text{ SD})$, more so per origination event—than their ancestors in $\approx 75\%$ of candidate phylogenies (*SI Appendix, Fig. 7 and Tables 6 and 7*). These few increases alone are nearly sufficient to account for the magnitude of the overall phylum-level size trend (Fig. 2). This result is unlikely to be caused by taxonomic practice because body size is not a basis for brachiopod classification (17). In contrast, significant size-biased relationships for family duration or genus richness occur in fewer than 17% and 3% of phylogenies, respectively. These results are upheld when restricted to families whose last occurrences here predate the final D5 bin, where artificial truncation might bias results. Taken together, these results suggest that major morphological changes resulting

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