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Phylogenetic signal in extinction selectivity in Devonian terebratulide brachiopods

Paul G. Harnik, Paul C. Fitzgerald, Jonathan L. Payne, and Sandra J. Carlson

Abstract.—Determining which biological traits affect taxonomic durations is critical for explaining macroevolutionary patterns. Two approaches are commonly used to investigate the associations between traits and durations and/or extinction and origination rates: analyses of taxonomic occurrence patterns in the fossil record and comparative phylogenetic analyses, predominantly of extant taxa. By capitalizing upon the empirical record of past extinctions, paleontological data avoid some of the limitations of existing methods for inferring extinction and origination rates from molecular phylogenies. However, most paleontological studies of extinction selectivity have ignored phylogenetic relationships because there is a dearth of phylogenetic hypotheses for diverse non-vertebrate higher taxa in the fossil record. This omission inflates the degrees of freedom in statistical analyses and leaves open the possibility that observed associations are indirect, reflecting shared evolutionary history rather than the direct influence of particular traits on durations. Here we investigate global patterns of extinction selectivity in Devonian terebratulide brachiopods and compare the results of taxonomic vs. phylogenetic approaches. Regression models that assume independence among taxa provide support for a positive association between geographic range size and genus duration but do not indicate an association between body size and genus duration. Brownian motion models of trait evolution identify significant similarities in body size, range size, and duration among closely related terebratulide genera. We use phylogenetic regression to account for shared evolutionary history and find support for a significant positive association between range size and duration among terebratulides that is also phylogenetically structured. The estimated range size–duration relationship is moderately weaker in the phylogenetic analysis due to the down-weighting of closely related genera that were both broadly distributed and long lived; however, this change in slope is not statistically significant. These results provide evidence for the phylogenetic conservatism of organismal and emergent traits, yet also the general phylogenetic independence of the relationship between range size and duration.

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Introduction

Taxonomic durations vary markedly within and among clades as well as over time. Disentangling the biotic and abiotic factors that cause this variation is critical for explaining macroevolutionary patterns (Stanley 1979; Jablonski 2008b; Benton 2009), and for conserving existing biodiversity (Dietl and Flessa 2011; Harnik et al. 2012a; Condamine et al. 2013). Two general approaches have been used, largely in isolation, to investigate the effects of biological traits on taxon durations and rates of extinction, origination, and net

diversification: (1) analyses of taxon occurrences over space and time and (2) comparative phylogenetic analyses. The former approach has been used extensively in studies of the fossil record (e.g., Liow et al. 2008; Aberhan et al. 2012; Finnegan et al. 2012), whereas the latter approach has been applied predominantly to data for extant taxa by using molecular phylogenies (e.g., Goldberg and Igić 2012; Price et al. 2012; Maliska et al. 2013).

Analyses of the fossil record have shown that variation in taxon durations and probabilities of extinction and survival correlate

with a number of biological traits, including geographic range size (Kiessling and Aberhan 2007; Payne and Finnegan 2007; Jablonski 2008a; Crampton et al. 2010; Harnik 2011; Harnik and Lockwood 2011; Harnik et al. 2012b; Foote and Miller 2013; Nürnberg and Aberhan 2013), habitat breadth (Kammer et al. 1998; Heim and Peters 2011; Harnik et al. 2012b; Nürnberg and Aberhan 2013), abundance (Lockwood and Barbour Wood 2007; Simpson and Harnik 2009; Payne et al. 2011; Zaffos and Holland 2012), and morphological variability (Liow 2007; Kolbe et al. 2011) among others. For example, short taxon durations were associated with small geographic range sizes (e.g., Harnik 2011) and narrow habitat tolerances (e.g., Kammer et al. 1998) at times in the geologic past. Due to the real and/or perceived challenges of using morphological data gathered from fossil specimens to develop explicit phylogenetic hypotheses (e.g., because of limited numbers of morphological characters and homoplasy), most studies of extinction selectivity using the fossil record have ignored phylogenetic relationships (though see Carlson et al. 2004; Smith and Roy 2006; Fitzgerald and Carlson 2007; Carlson and Fitzgerald 2008a; Friedman 2009; Crampton et al. 2010; Green et al. 2011; Hopkins 2011; Kolbe et al. 2011). This omission inflates the degrees of freedom in statistical analyses, because taxa are assumed to be independent despite their shared evolutionary history (Felsenstein 1985; Harvey and Pagel 1991), and leaves open the possibility that observed associations are indirect, reflecting shared evolutionary history rather than the direct influence of particular biological traits on taxon durations and extinction rates. Furthermore, the extent to which different biological traits associated with extinction risk are phylogenetically conserved (i.e., the traits of more closely related taxa are more similar than expected by chance) cannot be determined in the absence of a phylogenetic framework (Purvis 2008).

Here we investigate global patterns of extinction selectivity in terebratulide brachiopods over the Devonian, and compare the results of taxonomic vs. comparative phylogenetic approaches to identifying correlates of

extinction risk. We focus specifically on the associations between geographic range size, body size, and taxon duration. Small range size is one of the primary factors associated with elevated extinction risk today and in the geologic past (Jones et al. 2003; Kiessling and Aberhan 2007; Payne and Finnegan 2007; Powell 2007; Jablonski 2008a; Davidson et al. 2009; Crampton et al. 2010; Lee and Jetz 2010; Harnik 2011; Harnik et al. 2012b, though see Stanley 1986 and Myers et al. 2012). Geographic range size can also be phylogenetically structured, with more closely related lineages exhibiting ranges that are more similar in size than expected by chance. This pattern of phylogenetic conservatism occurs in sister species (Taylor and Gotelli 1994) and putative ancestor-descendant pairs (Jablonski 1987; Hunt et al. 2005) and larger clades (Jones et al. 2005; Hopkins 2011), as well as across a diversity of distantly related groups including trilobites (Hopkins 2011), fish (Taylor and Gotelli 1994), mollusks (Jablonski 1987; Hunt et al. 2005), and mammals (Jones et al. 2005). Presumably the phylogenetic pattern of range size conservatism reflects heritable aspects of life history (e.g., dispersal mode) and physiology (e.g., thermal tolerance) that give rise to the realized geographic distributions of taxa.

Body size has also been hypothesized to affect extinction risk, with larger-bodied taxa at greater risk due to lower fecundities and smaller populations among other factors. These expectations were developed primarily with vertebrates in mind (e.g., Cardillo et al. 2005; Davidson et al. 2009), however, and may not hold for marine invertebrates in which fecundity may scale positively, rather than negatively, with body size (Jablonski et al. 2003). The greatest empirical support for a link between body size and extinction risk exists in groups such as marine fishes and marine and terrestrial mammals in which direct exploitation by humans is the primary driver of extinction risk (Lyons et al. 2004; Anderson et al. 2011). In contrast, analyses of marine invertebrates over geologic time tend to show either no association between body size and extinction risk (Lockwood 2005; Finnegan et al. 2009) or pronounced differences among clades in the direction and strength of the

association between body size and risk (Jablonski 1996; Harnik 2011). As with geographic range size, the body sizes of closely related lineages are often more similar than expected by chance (Smith et al. 2004; Purvis et al. 2005; Rego et al. 2012; Safi et al. 2013), although strong selection can obviously result in pronounced differences in body size among congeneric species (e.g., McClain et al. 2006). Because of the phylogenetic correlation of body sizes, geographic range sizes, and the clade-dependence of patterns of body size selectivity, it is worth revisiting the associations between these biological traits and taxon duration in a comparative phylogenetic framework to ensure that the strengths of these associations have not been overestimated.

Brachiopods were abundant and taxonomically diverse in shallow marine ecosystems throughout the Paleozoic and, as a result, have been the focus of most analyses of extinction selectivity before the Triassic. Brachiopods exhibit a positive association between geographic range size and genus duration in the late Paleozoic (Powell 2007) and between range size and survivorship in the latest Ordovician through earliest Silurian (Finnegan et al. 2012) and in the Late Devonian (Rode and Lieberman 2004). Across the Phanerozoic as a whole, the association between geographic range and extinction risk in brachiopods is indistinguishable from associations present in the fossil records of other well-skeletonized macrobenthic invertebrate groups (Harnik et al. 2012b). Terebratulide brachiopods are the most diverse group of brachiopods alive today (approximately 100 extant genera), and have a rich fossil record extending back over 400 million years to their first occurrence in the Lochkovian stage of the Lower Devonian (Carlson and Fitzgerald 2008b) (Fig. 1). Previous work has established a phylogenetic hypothesis for all of the earliest members of the clade (Carlson and Fitzgerald 2008b). A large set of geographic occurrence data for Paleozoic terebratulides exists because of previous work focused on latitudinal diversity gradients (Fitzgerald and Carlson 2006), which, in combination with body size measurements (Fitzgerald 2006; this study), offers a rich data set for investigating phylo-

genetic signal in macroecological traits and patterns of extinction selectivity in the clade. More broadly, this clade offers a test case for exploring how comparative phylogenetic approaches can contribute to our understanding of extinction selectivity in the geologic past.

Data and Methods

Phylogenetic Framework

For this study, we use the strict consensus of 71 phylogenetic trees reported by Carlson and Fitzgerald (2008b) for our phylogenetic hypothesis (Fig. 2). Carlson and Fitzgerald's analysis included all 71 named Devonian terebratulide genera and seven outgroup taxa, and involved the analysis of 29 binary and 38 multistate morphological characters using parsimony. In their study, Carlson and Fitzgerald recovered terebratulides as a monophyletic clade and demonstrated that inferred phylogenetic relationships were robust to a variety of data treatments; readers are referred to Carlson and Fitzgerald (2008b) for additional details regarding their phylogenetic analysis and sensitivity tests.

Comparative phylogenetic methods require estimates of branch lengths. For phylogenies generated from molecular sequences, branch lengths are estimated assuming a molecular clock (e.g., Erwin et al. 2011; Jetz et al. 2012). For analyses of morphological character data, branch lengths must be estimated in other ways. Some have proposed the use of a morphological clock (e.g., Ronquist et al. 2012; Lee et al. 2014). Although such an approach makes explicit the tacit assumption of many studies that morphological divergence is proportional to the amount of time elapsed since a last common ancestor, one can envision many instances in which morphological evolution is unlikely to evolve in a clock-like fashion. Additional work is needed to investigate the effects of violating, and/or the opportunities for relaxing, model assumptions under a morphological clock.

An alternative approach for estimating branch lengths in morphological phylogenies that are composed of fossil taxa is to use the ages of taxon first occurrence (Norell 1992; Smith 1994). With this approach, node age is

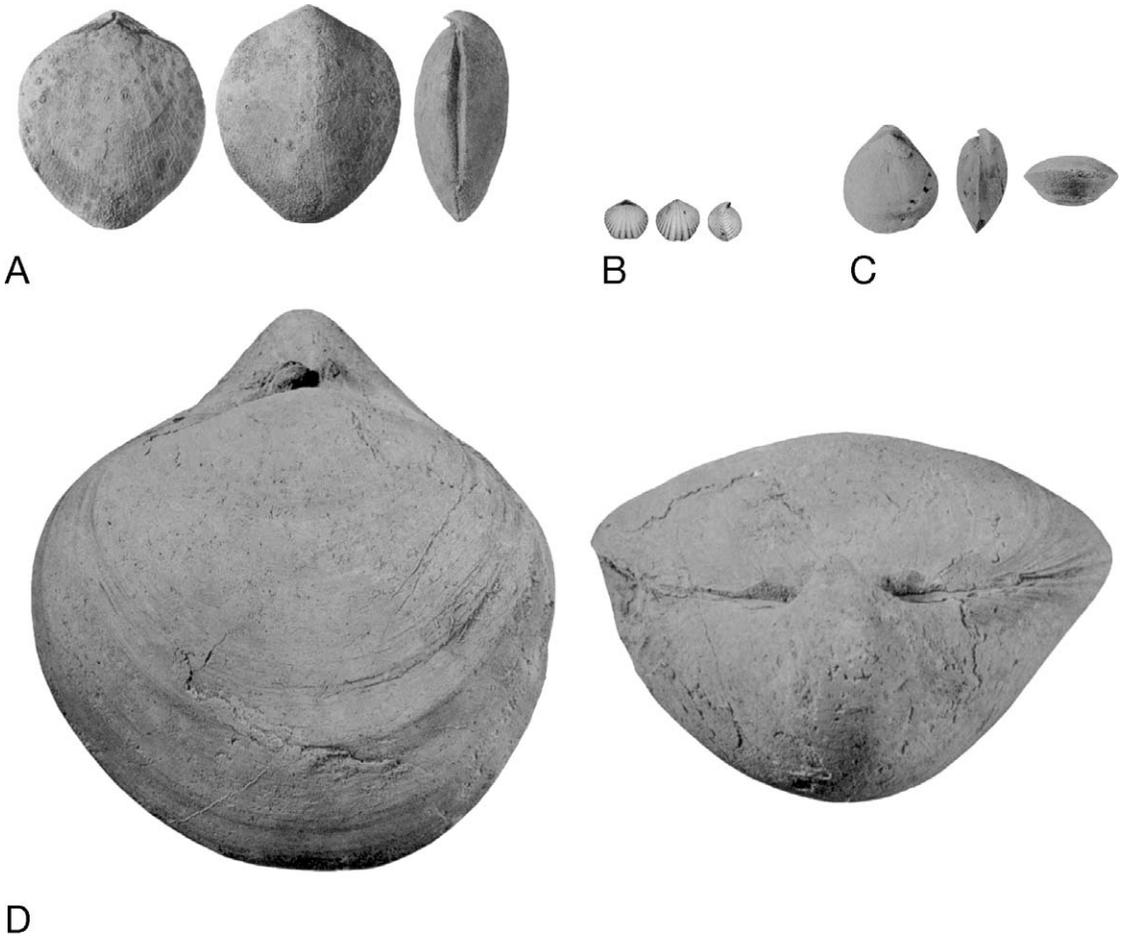


FIGURE 1. Selected genera of Devonian terebratulide brachiopods illustrating a range of adult body size and shape. All images are illustrated at actual specimen size, $\times 1$. A, *Beuchia suessana* (Hall); dorsal, ventral, and lateral views (from Cloud 1942). B, *Adrenia expansa* (Chatterton); dorsal, ventral, and lateral views (from Chatterton 1973). C, *Hamburgia typa* (Weller); dorsal, lateral, anterior views (from Cloud 1942). D, *Stringocephalus burtini* (Defrance); dorsal and posterior views (from Cloud 1942).

estimated as the age of first occurrence of the earliest descendant from that node (e.g., Hunt and Roy 2006). Here we temporally calibrate, or “time-scale,” the Carlson and Fitzgerald (2008b) phylogeny for Devonian terebratulides, using this latter approach of assigning node ages in the tree based on the observed first occurrence of the earliest descendant from that node. Geological stages of first occurrence were compiled from the revised brachiopod volume of the *Treatise on Invertebrate Paleontology* (Curry and Brunton 2007), with genera assumed to originate at the base of the stage in which they first occurred. This approach to time-scaling the phylogeny results in many zero-length internal branches (Bapst 2013). As

has been commonly done in other molecular and morphological studies (e.g., Laurin et al. 2009; Hopkins 2011), we add a small, arbitrary amount of time (0.01 Myr) to all zero-length branches in the terebratulide tree. We obtained radiometric ages of stage boundaries from the revised Devonian timescale of Ogg et al. (2009). Temporal calibration of the terebratulide cladogram was conducted in R using the timePaleoPhy function in the *paleotree* package (Bapst 2012). Note that tips in the time-scaled tree correspond to the first occurrences of terebratulide genera, not last occurrences, so as to reduce any circularity when we use the tree for comparative analyses that include genus duration (see *Analyses* below).

Genus Duration

Genus durations were calculated from the observed first and last occurrence data from the revised brachiopod *Treatise on Invertebrate Paleontology* (Curry and Brunton 2007), with genera assumed to range from the base of the stage in which they first occurred to the top of the stage in which they last occurred. First and last occurrences reported in the *Treatise on Invertebrate Paleontology* are congruent with occurrences compiled from the published literature for biogeographic analyses (see *Geographic Range Size* below). As has been noted previously (Fitzgerald and Carlson 2006), many Devonian terebratulide genera are known from only a single geological stage (singletons) (Fig. 2), although some occur at many different localities within the stage. Although some of these singletons may have truly been short lived, others may appear so simply because lower probabilities of sampling or preservation artificially truncate their observed stratigraphic durations (Signor and Lipps 1982; Meldahl 1990; Holland and Patzkowsky 2002). To assess what effect, if any, singletons have on the associations between body size, geographic range size, and genus duration, we conducted analyses both including and excluding singletons.

Geographic Range Size

A database containing the occurrences of terebratulide genera was used to estimate genus latitudinal range sizes. These occurrence data were compiled previously in an exhaustive search of the published literature for a study of Paleozoic terebratulide latitudinal diversity gradients (Fitzgerald and Carlson 2006). The data set consists of 476 occurrences, resolved to 5° paleolatitudinal bins, ranging from 85°S to 45°N. Geographic occurrence data exist for approximately 90% of named Devonian terebratulide genera (63 out of 71). Only two of these genera (*Cranaena* and *Hamburgia*) are known to have survived into the Mississippian (Fig. 2); the geographic ranges for these two genera were calculated from their Devonian and Mississippian occurrences.

Because paleolongitude is poorly constrained for occurrences older than approxi-

mately 100 Ma (Scotese et al. 1979; Schmachtenberg 2011), we estimate the geographic range size of each genus using its paleolatitudinal range and do not consider other range measures, such as occupancy or total area. Different geographic range measures often covary (e.g., occupancy and maximum extent among Paleogene bivalves [Harnik 2011] and Neogene mollusks [Crampton et al. 2010]). Thus, although the results presented below apply specifically to paleolatitudinal range size, they may also hold for other measures of geographic range size.

The latitudinal extent of rocks containing terebratulide genera with Devonian first occurrences varies considerably over time (e.g., the minimum absolute latitudinal range in the Tournasian equals 45°, whereas the maximum latitudinal range in the Emsian equals 115°). Variation in outcrop extent and/or sampling effort over geologic time may artificially strengthen the observed association between geographic range size and duration when analyses include taxa from different time intervals (Harnik 2011). This is because measures of range size and duration are expected to covary positively with the completeness of geological and paleontological records. To account for this variation, we scale the latitudinal range size of each genus to the maximum latitudinal range possible over the interval of interest (Foote et al. 2008; Crampton et al. 2010; Harnik 2011; Heim and Peters 2011). This transformation does not produce more accurate estimates of the true geographic ranges of fossil taxa but instead is intended to conservatively bias against detecting a strong signal of extinction selectivity (i.e., bias against Type I errors) in instances in which variation in the quality of the record challenges our abilities to distinguish biological pattern from sampling artifact.

In our analyses we considered two range-size measures: (1) the maximum range size of a genus in a given stage and (2) the aggregate (or cumulative) range size of a genus throughout its duration. Each of these range-size measures was scaled accordingly to the maximum range size possible at that time. To assess the association between these measures, we calculated the partial correlation

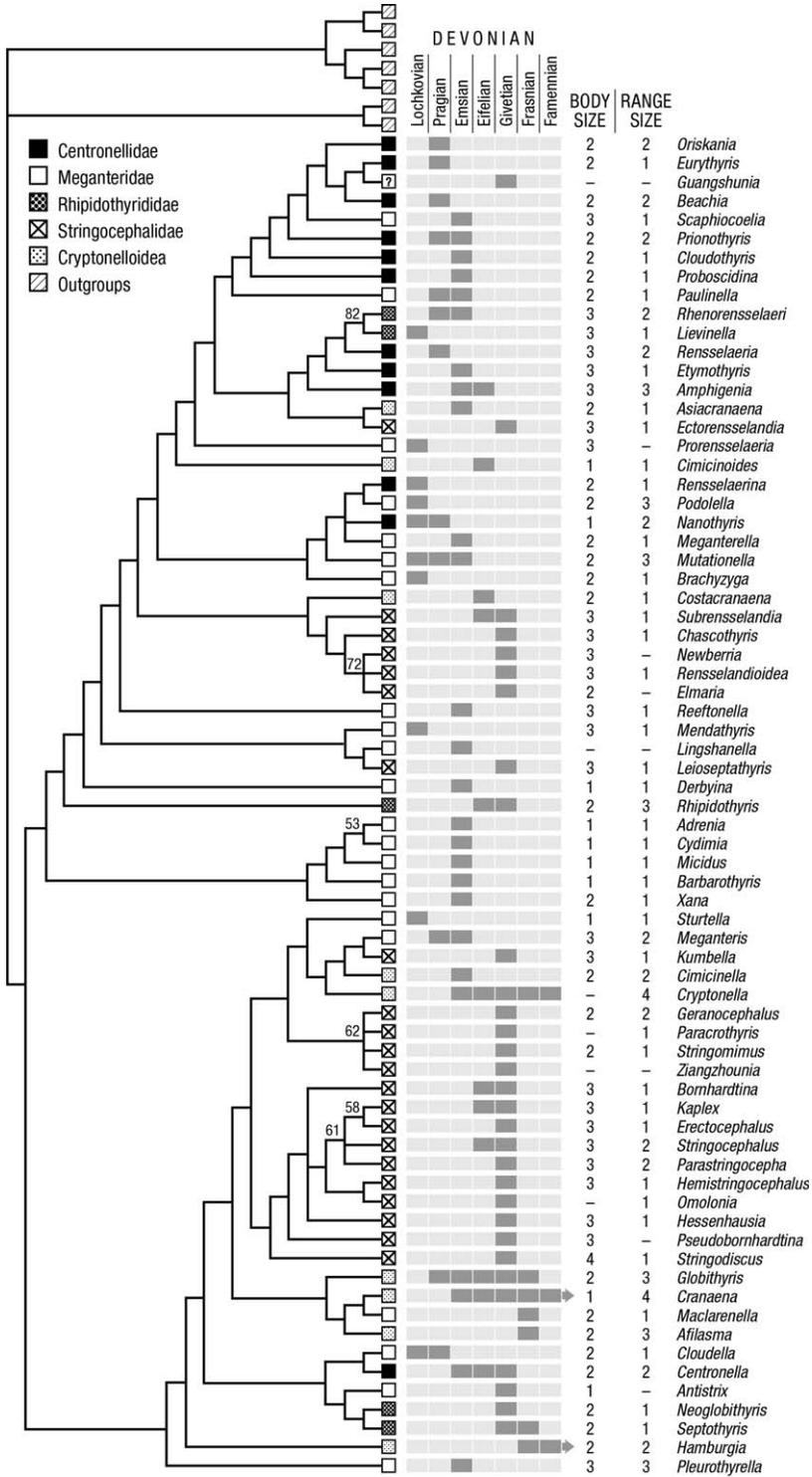


FIGURE 2. Strict consensus of 71 trees obtained from a parsimony analysis (PAUP 4.0b10) of all 71 named Devonian terebratulide genera. Numbers above certain nodes indicate "fast bootstrap" values supporting those nodes. For further details on the analysis performed, see Carlson and Fitzgerald (2008b). Stratigraphic ranges by stage are plotted for each genus, to the right of the terminals in the tree. A categorical designation of body size is listed in the column to the right of the stratigraphic ranges; these numbers represent a range of valve areas (log of length × width), where 1 = 1.00 to 2.00;

between the maximum range in a stage and the aggregate range, holding duration fixed, for all genera as well as for genera found in two or more intervals (Crampton et al. 2010; Harnik 2011); too few genera occur in three or more intervals (3+ timers) to calculate this partial correlation for that subset.

Body Size

Data on the maximum body size of terebratulide genera were collected from two sources: measurements of (1) museum specimens (Fitzgerald 2006) and (2) figured specimens in the *Treatise on Invertebrate Paleontology* (Kaesler 2000). More than 2000 intact specimens of Paleozoic terebratulides were measured in the collections at the Natural History Museum (London), the National Museum of Natural History (Washington, D.C.), and the Yale Peabody Museum (New Haven, CT). Each specimen was aligned and photographed from two orthogonal angles, one angle representing the commissure margin and the other representing the “profile,” or the side view. We sampled 101 equally spaced coordinates around the commissure margin, using the software program tpsDig v. 1.4 written by James Rohlf and then scaled to millimeters. We then calculated centroid size for each individual, using the coordinates sampled from the commissure view. Each genus is represented by the individual specimen with the largest measured centroid size. Centroid sizes were gathered for 28 Devonian genera, with the median number of specimens measured per genus equal to 5.5 (interquartile range was 2 to 18.25 specimens). For the taxa figured in the *Treatise on Invertebrate Paleontology*, linear measurements of shell width and length were gathered, as well as shell height wherever possible. For genera comprising two or more species, genus body size was calculated as the geometric mean of the holotype

specimen for each species (Kosnik et al. 2006; Novack-Gottshall 2008). If the holotype was not figured for a species, the paratype, neotype, or best-resolution illustration was used, in that order. Shell volume (the product of shell width, length and height) and shell area (the product of shell width and length) were both calculated. Shell area is a proxy for body volume and correlates with soft-tissue mass (e.g., Shumway 1982; Peck and Holmes 1990; Peck 1993). Shell volume and area data were collected for 50 and 67 Devonian terebratulide genera respectively. We then assessed the agreement between centroid sizes measured from museum specimens and shell areas and volumes measured from figured specimens, using Spearman rank-order correlation. Because all of these measures are highly correlated (see *Results* below), we use shell area in all analyses because of the greater sample size of taxa with available data ($n = 67$). All body size and occurrence data and the time-scaled strict consensus phylogeny are archived in the Supplementary Material at Dryad.

Analyses

For our taxonomic analyses, in which genera are assumed to be independent despite shared evolutionary history, we use two approaches to assess the associations between body size, geographic range size, and genus duration. First, we calculate the Spearman rank-order correlation between genus duration and body size and between genus duration and geographic range size. Second, we use a multiple linear regression model to estimate simultaneously the unique additive effects of body size and geographic range size on duration. These two analyses are similar to the analytical approaches used in many previous studies of extinction selectivity in the fossil record (e.g., Jablonski and Hunt

←
2 = 2.01 to 3.00; 3 = 3.01 to 4.00; 4 = 4.01 to 5.00. Body size analyses were performed on unique values for each genus; categories listed here are simply intended to provide a qualitative illustration of size. Geographic range size is similarly categorized in the column to the right of body size; this number represents a range of values for geographic range size for each genus over its entire history standardized to the maximum potential range during that interval: 1 = 0.00 to 0.25; 2 = 0.26 to 0.50; 3 = 0.51 to 0.75; 4 = 0.76 to 1.00. Geographic range size analyses were performed on unique values for each genus. Genus names are listed in the column on the far right; family assignments are indicated by symbols in the boxes at the tree terminals, and by the legend near the base of the tree.

TABLE 1. Rank-order correlations between body size, geographic range size, and taxonomic duration, including and excluding genera restricted to a single geologic stage. Statistically significant values are in bold.

	Spearman rho	
	Including singletons	Excluding singletons
Body size and duration	-0.13	-0.21
Aggregate geographic range and duration	0.40***	0.55*
Maximum geographic range and duration	0.39**	0.57**

* $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$.

2006; Kiessling and Aberhan 2007; Payne and Finnegan 2007; Harnik 2011). To satisfy assumptions of normality, geographic range size was transformed using an arcsine square root transformation (commonly applied to proportional data) and body size was logarithmically transformed. In addition, geographic range size and body size were each scaled to zero mean and unit variance to allow their relative effects on duration to be assessed on a comparable scale.

For our phylogenetic analyses, we used a Brownian motion model of trait evolution to assess the degree of phylogenetic correlation or signal (these terms are used here interchangeably) in body size, geographic range size, and duration. Under this model, the observed variation in trait values among lineages is proportional to the time elapsed since their divergence from a common ancestor. We use Pagel's λ (Pagel 1999; Freckleton et al. 2002) to summarize the degree of phylogenetic signal in each trait; λ values closer to unity indicate that the trait is evolving under Brownian motion over a given tree, with more closely related lineages exhibiting greater similarity in trait values, and λ values closer to zero indicate that the trait is evolving more independently of the phylogeny (i.e., little phylogenetic signal). Brownian motion models of trait evolution were fit to trait data in R using the `fitContinuous` function in the `geiger` package (Harmon et al. 2008). We use a model-selection approach (Burnham and Anderson 2002) to assess the support for estimated λ values, comparing the Akaike weight for the model in which λ is estimated with two

alternative models, one in which λ is set equal to 1 and one in which λ is set equal to 0.

We use phylogenetic regression (phylogenetic generalized least squares, PGLS) to estimate the associations between body size, geographic range size, and genus duration while accounting for shared evolutionary history (Felsenstein 1985; Grafen 1989). PGLS is recommended even when individual traits exhibit little phylogenetic signal, because it is the phylogenetic correlation of the residuals from the regression model that are being accounted for and this cannot be determined by considering the phylogenetic signal of any single variable in isolation (Revell 2010; Hansen and Bartoszek 2012). PGLS models assuming Brownian motion were fit in R using the `gls` function in the `nlme` package, with the correlation structure given by the phylogenetic variance-covariance matrix, in which the off-diagonal elements are the phylogenetic distances separating the last common ancestor of any two tips from the root, and the diagonal elements are the phylogenetic distances separating each tip from the root.

Results

Taxonomic Results

Conventional taxonomic analyses recover a significant positive association between the aggregate geographic range size and genus duration, and between maximum geographic range size and genus duration (Table 1). These two measures of geographic range size are significantly positively correlated: across all 58 terebratulide genera with requisite data, the Spearman correlation coefficient is 0.93 ($p < 0.001$), and this correlation weakens only moderately when the partial correlation is calculated with duration held constant for the 18 genera with requisite data that were extant in two or more stages (Spearman rho = 0.85, $p < 0.001$); too few genera ($n = 3$) occur in more intervals to restrict the analysis to 3+ timers.

Body sizes measured from museum specimens (centroid size) vs. specimens figured in the *Treatise on Invertebrate Paleontology* (shell volume and area) are significantly positively correlated: centroid size vs. shell volume (Spearman rho = 0.74, $p < 0.001$), centroid

TABLE 2. Multiple regression results for the unique additive effects of body size and geographic range size on taxonomic duration, including and excluding genera restricted to a single geologic stage. Model 1 includes the aggregate geographic range whereas Model 2 includes the maximum geographic range. SE = one standard error. Statistically significant values are in bold.

Model	Predictor variables	Coefficient ± 1 SE	
		Including singletons	Excluding singletons
Model 1	Body size	-1.94 ± 1.23	-5.42 ± 3.48
	Aggregate geographic range size	6.29 ± 1.29***	14.40 ± 3.45***
Model 2	Body size	-2.22 ± 1.33	-6.90 ± 3.80
	Maximum geographic range size	6.99 ± 1.45***	12.54 ± 3.57**

* $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$.

size vs. shell area (Spearman rho = 0.73, $p < 0.001$). Similarly, shell area and volume are also significantly positively correlated (Spearman rho = 0.99, $p < 0.001$). Because of the redundancy of these various body size measures, for all subsequent analyses we use shell areas measured from the *Treatise on Invertebrate Paleontology* which enables us to include data for 39 additional genera for which we did not have direct measurements from museum specimens.

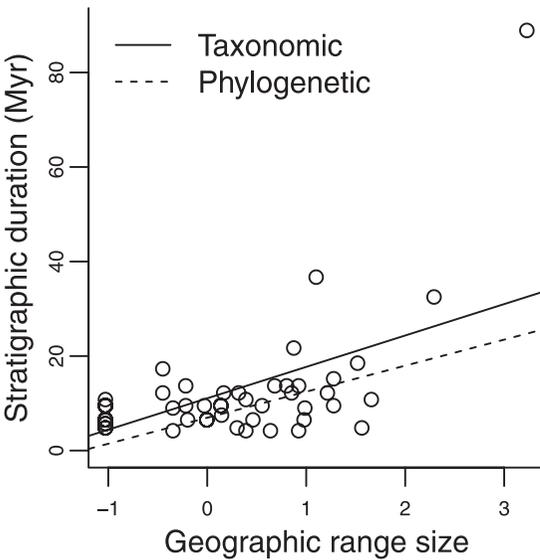


FIGURE 3. Association between geographic range size and taxonomic duration for Devonian terebratulide genera. Solid line is the least-squares regression line fit to the taxonomic data, the dashed line is the regression line from the phylogenetic generalized least-squares model. The aggregate geographic range size throughout the duration of each genus is used as the range size measure plotted here; Table 2 summarizes the association between geographic range size and stratigraphic duration for both geographic range measures.

We observed no association between body size and genus duration (Table 1). Body size is also uncorrelated with either measure of geographic range size (Spearman rho using the aggregate range = -0.04, $p = 0.76$; Spearman rho using the maximum range in a stage = 0.01, $p = 0.94$). Because the two predictor variables do not covary, results of a multiple regression model are comparable to the associations inferred from the separate rank order correlations (Table 2), with a significant positive association between geographic range size and duration (Fig. 3) and no association between body size and duration (Fig. 4).

Excluding genera restricted to a single stage strengthens, rather than weakens, the associations that geographic range size and body size have with duration, although the association between duration and body size remains indistinguishable from zero at the level of $\alpha = 0.05$ (Tables 1, 2). This result runs counter to the general expectation in the literature that singleton genera may artificially strengthen the relationship between measures of rarity, such as geographic range size, and extinction risk (e.g., Liow 2007; Payne and Finnegan 2007; Harnik et al. 2012b), and may be attributable to variation in the durations of Devonian stages. Because genus durations were calculated assuming that genera ranged from the base of the stage in which they first occurred to the top of the stage in which they last occurred, the durations of singletons vary with stage duration, from a minimum of 4.2 Myr in the Pragian stage to a maximum of 10.8 Myr in the Frasnian; the mean and median durations of Devonian stages contain-

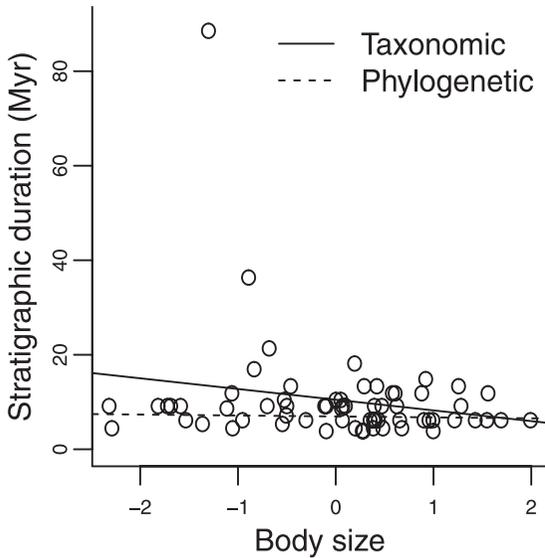


FIGURE 4. Association between body size and taxonomic duration for Devonian terebratulide genera. Solid line is the least-squares regression line fit to the taxonomic data, the dashed line is the regression line resulting from the phylogenetic generalized least-squares model.

ing singletons are 6.9 and 6.1 Myr, respectively.

Phylogenetic Results

Considering body size, geographic range size, and duration in a phylogenetic framework reveals substantial support for each trait evolving under Brownian motion (Table 3, Fig. 5). Models in which λ is set equal to zero (i.e., in which trait values change independently of

the phylogeny) have negligible support when all genera, including singletons, are considered. The one exception is when the maximum geographic range observed in a stage is considered, for which the $\lambda = 0$ model has the greatest support. Furthermore, models in which λ is set equal to unity have no support, indicating that other factors, not included in the Brownian motion model of trait evolution, contribute to the variation in trait values observed among terebratulide genera. In general, excluding singletons substantially weakens support for models with estimated values of λ greater than zero; this may be due to the reduced sample size of genera included in those analyses, as estimated λ values are comparable between the full data set and the data set in which singletons are excluded (Table 3).

We use phylogenetic regression models to account for shared evolutionary history (Table 4). These models corroborate the general results of our taxonomic analysis, with a significant positive association observed between range size and duration (Table 4, Fig. 3), and no association between body size and duration (Table 4, Fig. 4). The estimated range size–duration relationship is moderately weaker in the phylogenetic vs. taxonomic analysis owing to the down-weighting of closely related genera such as *Cranaena* and *Globithyris*, which were both broadly distrib-

TABLE 3. Maximum likelihood estimate of Pagel's λ for each trait using the time-scaled terebratulide phylogeny. Results are presented for the full data set (including singletons) and with singletons excluded. Weight is the Akaike weight for the model in which λ is estimated relative to two other models, one in which $\lambda = 1$ and another in which $\lambda = 0$. Pagel's λ values closer to unity indicate that the trait is evolving under pure Brownian motion with more closely related lineages exhibiting greater similarity in trait values, and λ values closer to zero indicate that the trait is evolving more independently of the phylogeny (i.e., little phylogenetic signal). Akaike weights summarize the relative support for each model among the set of models under consideration, with values closer to unity indicating substantial support for that model. All models in which $\lambda = 1$ have a weight equal to zero and thus lower weights in the table indicate greater support for the model in which $\lambda = 0$. For aggregate geographic range size, for example, the weight of the model in which λ is estimated is 0.93, the weight of the model in which $\lambda = 0$ is 0.07, and the weight of the model in which $\lambda = 1$ is 0. N is the number of genera with measures of that trait included in that analysis. Weights ≥ 0.90 are in bold. When singletons are excluded, Akaike weights decline for the models of body size and aggregate geographic range size evolution in which λ is estimated; this may be due to the substantially reduced sample size of genera included in those analyses.

	Including singletons			Excluding singletons		
	λ	Weight	N	λ	Weight	N
Body size	0.39	1	65	0.27	0.35	18
Aggregate geographic range size	0.48	0.93	63	0.62	0.55	19
Maximum geographic range size	0	0.27	58	0	0.27	18
Duration	0.59	0.92	71	0.54	0.90	19

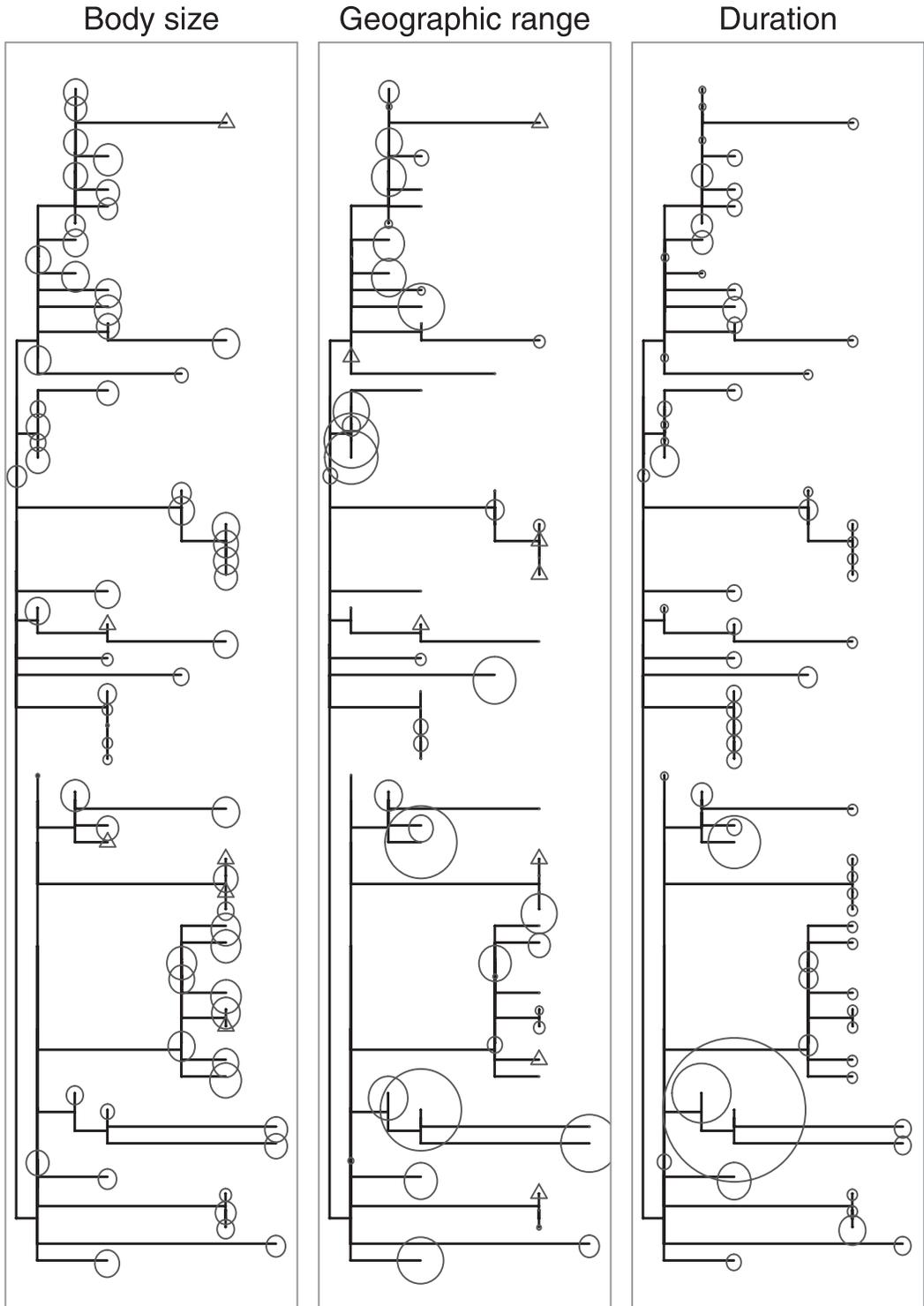


FIGURE 5. Time-scaled phylogeny for Devonian terebratulide brachiopods with the body sizes (left), geographic range sizes (center), and stratigraphic durations (right) of genera plotted at the tips. Note that tips correspond to taxon first occurrences. Circle size is proportional to trait values. Triangles denote genera missing data for a given trait.

TABLE 4. Phylogenetic regression results for the unique additive effects of body size and geographic range size on taxonomic duration while accounting for shared evolutionary history, including and excluding genera restricted to a single geologic stage. Model 1 includes the aggregate geographic range whereas Model 2 includes the maximum geographic range. λ is the estimated phylogenetic signal in the residuals for the model. SE = one standard error. Statistically significant values are in bold.

Model	Predictor variables	Including singletons		Excluding singletons	
		Coefficient \pm 1 SE	λ	Coefficient \pm 1 SE	λ
Model 1	Body size	-0.20 \pm 1.29	0.50	-2.92 \pm 2.49	0.65
	Aggregate geographic range size	5.51 \pm 1.18***		11.93 \pm 2.28***	
Model 2	Body size	-0.45 \pm 1.36	0.45	-5.86 \pm 2.22*	0.91
	Maximum geographic range size	6.06 \pm 1.27***		13.92 \pm 2.22***	

* $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$.

uted and long lived (Fig. 2). Although the change in slope is in the expected direction given the phylogenetic correlation of these traits, the slope derived from the phylogenetic regression is not significantly different from the least-squares regression model that ignored phylogenetic relationships, indicating that the pattern of geographic range selectivity in this clade is largely independent of phylogeny. However, because the residuals of these models exhibit significant phylogenetic structure (i.e., $\lambda > 0$), phylogenetic regression is still warranted.

As in our taxonomic analyses, excluding genera restricted to a single stage strengthens, rather than weakens, the associations of geographic range size and body size with duration estimated using PGLS (Table 4). When singletons are removed, body size also exhibits a significant inverse association with duration, with larger-bodied genera persisting for shorter periods of geologic time. It is important to note that although many of the analyses show a weak inverse relationship between body size and duration (Tables 1, 2, and 4), this association emerged as statistically significant only in one data treatment (i.e., the model excluding singletons that used the maximum geographic range size measure) and thus should not be over-interpreted.

The long-lived terebratulide genus *Cranaena* is a notable outlier in Figures 3 and 4. *Cranaena* first occurs in the Emsian stage of the Devonian and last occurs in the Serpukhovian stage of the Mississippian (Fig. 2), and is present in collections spanning paleolatitudes from 85°S to 45°N. To determine the robustness of the results presented above, all analyses were rerun excluding *Cranaena*.

When *Cranaena* is excluded, there is equivocal support for phylogenetic signal in genus durations; the maximum likelihood estimate of λ is 0.1, and this model of trait evolution has equivocal support (Akaike weight = 0.62) over a model in which duration evolves independently of phylogeny ($\lambda = 0$, Akaike weight = 0.38); all other results are unchanged.

Discussion

Similarities in extinction risk among closely related lineages have been documented across a diversity of groups including frogs (Cooper et al. 2008), birds (Bennett et al. 2005), bivalves (Roy et al. 2009a), ammonites (Hardy et al. 2012), and brachiopods (this study). This correlation between phylogeny and extinction risk can be explained by similarities among closely related lineages in the biological characteristics that affect the vulnerability of lineages to changing ecological and environmental conditions. Such characteristics may include organismal traits such as gestation period and fecundity, as well as emergent (i.e., group-level) traits such as geographic range size and population size. Teasing apart the relative contributions of individual and group-level traits to extinction risk has been a central focus of much research in paleobiology, macroecology, and conservation biology (e.g., Cardillo et al. 2008; Jablonski 2008a; Davidson et al. 2009; Crampton et al. 2010; Lee and Jetz 2010; Harnik 2011). However, the evolutionary context for understanding changes in these different types of traits over deep time has received much less attention. This oversight exists in part because some group-level characteristics such as population size traditionally have been assumed to be

highly dynamic and thus a reflection of contemporary rather than historical processes (Purvis et al. 2005). It exists also because most analyses of extinction selectivity that have used the marine fossil record have not been conducted in a phylogenetic context.

Although the relationship between range size and duration has been observed in many previous studies (Rode and Lieberman 2004; Kiessling and Aberhan 2007; Payne and Finnegan 2007; Jablonski 2008a; Crampton et al. 2010; Harnik 2011; Harnik et al. 2012b; Foote and Miller 2013; Nürnberg and Aberhan 2013, among others), with few exceptions (Crampton et al. 2010; Hopkins 2011) phylogeny has not been accounted for. In our analysis we find that accounting for shared evolutionary history can moderately weaken the positive association between range size and duration, due to the down-weighting of closely related genera that had broad geographic distributions and long stratigraphic durations. The effect that accounting for phylogeny has on the range-duration relationship is to be expected given the similarities in trait values of closely related lineages. However, it is notable that the pervasive association between range and duration observed in so many previous macroevolutionary analyses is robust when phylogeny is accounted for and, furthermore, that the strength of association (as measured by the slope of the regression model) does not differ significantly from a phylogenetically uninformed, taxonomic analysis.

Phylogenetic conservatism of geographic range size might seem unlikely given that most models of speciation predict that newly established lineages will initially be narrowly distributed (Coyne and Orr 2004), and thus more likely to show range-size asymmetry when compared with their closest relatives. Furthermore, range sizes have been shown to vary systematically over the geologic history of lineages (Foote 2007; Foote et al. 2007; Liow and Stenseth 2007; Liow et al. 2010; Tietje and Kiessling 2013), with many lineages exhibiting protracted intervals of range expansion and contraction separated by short-lived peaks in range size, which could also result in little phylogenetic structure to range size. Among

Devonian terebratulide genera, however, we show that the distribution of geographic range sizes over the phylogeny is consistent with that expected if range size was evolving under Brownian motion over the Devonian history of the clade. Phylogenetic conservatism of range size has been observed in studies of extant and extinct lineages across a diversity of clades (Jablonski 1987; Taylor and Gotelli 1994; Hunt et al. 2005; Jones et al. 2005; Hopkins 2011), and presumably reflects heritable aspects of physiology (e.g., thermal tolerance) and life history (e.g., dispersal mode) that give rise to the observed geographic ranges of taxa (Roy et al. 2009b and references therein).

Among Devonian terebratulides we find that body size was also phylogenetically structured (as indicated by the support for the Brownian motion model of body size evolution), with more closely related genera tending to be more similar in size. For example, *Micidus*, the smallest Devonian terebratulide, was sister to *Adrenia* and *Cydimia*, which were also considerably smaller than the median body size for the clade, whereas the subclade that includes *Stringodiscus* and *Pseudobornhardtina* consisted primarily of genera that were considerably larger than the median body size for the clade (Fig. 2). Because Carlson and Fitzgerald's (2008b) phylogeny is based on synapomorphies and not body size, we can rule out the possibility that the phylogenetic correlation of body size observed here is an artifact of size being used as a character used in phylogeny reconstruction.

Body size was largely decoupled from extinction risk with only a weak (and nonsignificant) tendency for larger-bodied terebratulide genera to have shorter durations, a pattern observed in at least one other group of epifaunal marine invertebrates (i.e., bivalve species in the Pectinoida [see Harnik 2011]). The decoupling of body size and extinction risk among terebratulides is in agreement with two recent studies that have shown that across marine invertebrates there is no general association between body size and extinction risk (Finnegan et al. 2009), and that among ecological groups the

relationship between size and longevity can vary dramatically in direction as well as strength (Harnik 2011). These results imply that if body size is important in determining extinction risk in terebratulides it emerges as such only at even finer phylogenetic and/or ecological scales.

All told, the results of our phylogenetically informed analyses of extinction selectivity largely corroborate those inferred from analyses in which taxa are assumed to be independent despite their common history. Other recent studies that have attempted to examine the effect of accounting for phylogeny on extinction selectivity patterns, especially those involving geographic range, have also found taxonomic results to be remarkably robust (Crampton et al. 2010; Hopkins 2011). This finding is encouraging, because it suggests we can tease apart some of the biological correlates of extinction risk using the counts and occurrences of taxa in the fossil record even when phylogenetic hypotheses are lacking. Alternatively, the congruence between taxonomic and morphological phylogenetic analyses in Devonian terebratulides could reflect the fundamental reliance of both approaches on morphology, and this association cannot, unfortunately, be investigated further in clades consisting largely of extinct organisms for which we lack molecular data.

Although certain patterns of extinction selectivity are in effect phylogenetically independent (e.g., the association between range size and duration observed in this study), delving further into the ecological and evolutionary underpinnings of the biological traits thought to affect extinction benefits considerably from the rich context offered by phylogeny. For example, and counter to some expectations, we show here that among terebratulides both individual-level organismal traits (body size) and emergent group-level traits (geographic range) exhibit strong phylogenetic signal. Considering the evolutionary lability of such traits has implications that extend beyond studies of extinction selectivity to elucidating the processes underlying broad-scale macroevolutionary trends in both organismal and emergent traits.

Conclusions

The fossil record provides substantial empirical support for associations between traits and extinction risk over geologic time scales. However, few paleobiological studies have considered the effect of phylogeny on these macroevolutionary patterns. Beyond simply violating statistical assumptions about the independence of data points (i.e., species or genera in taxonomic analyses), failing to account for phylogeny leaves unresolved much broader questions such as the lability of organismal and emergent traits over evolutionary history. A growing set of comparative phylogenetic methods allows us to investigate the evolution of traits in a phylogenetic framework as well as the associations between traits and extinction risk. Here we show that closely related lineages of terebratulide brachiopods tended to be at similar risk of extinction through the Devonian due, in part, to the phylogenetic distribution of geographic range sizes that confer greater resilience and consequently longer geologic durations. We show that the range size–duration relationship observed in many previous macroevolutionary analyses weakens moderately in this group when phylogeny is accounted for, owing to the down-weighting of closely related lineages that both were geographically widespread and had long stratigraphic durations, although this change in slope is not statistically significant. In contrast, both taxonomic and phylogenetically informed analyses indicate that body size had little effect on the durations of terebratulide genera. Lastly, using a Brownian motion model of trait evolution we show that both individual (body size) and group level (geographic range) traits are phylogenetically correlated in this group, with more closely related lineages exhibiting considerable similarity in trait values. The overall congruence in the results of our taxonomic and phylogenetic analyses of Devonian terebratulides suggests that phylogenetic history may not obscure (or artificially produce) the extinction selectivity patterns reported previously from taxonomic data. However, attempts to further elucidate the evolutionary histories of the traits associated

with patterns of differential extinction and origination require phylogenetic approaches, and stand to benefit greatly from the rich lens on history that phylogeny has to offer.

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