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QUANTIFYING MOLLUSCAN BODY SIZE IN EVOLUTIONARY AND ECOLOGICAL ANALYSES: MAXIMIZING THE RETURN ON DATA-COLLECTION EFFORTS

MATTHEW A. KOSNIK,[1]* DAVID JABLONSKI,[2] ROWAN LOCKWOOD,[3] and PHILIP M. NOVACK-GOTTSHALL[4]
[1]School of Marine Biology & Aquaculture, James Cook University, Townsville, QLD 4811 Australia; [2]Department of the Geophysical Sciences, 5734 South Ellis Avenue, University of Chicago, Chicago, Illinois 60637, USA; [3]Department of Geology, College of William and Mary, Williamsburg, Virginia 23187, USA; [4]Department of Geosciences, University of West Georgia, Carrollton, Georgia 30118, USA
e-mail: mkosnik@alumni.uchicago.edu

ABSTRACT

How does the choice of size metric, specimen selection, and taxonomic level affect the results of macroevolutionary or ecological analyses? Four molluscan data sets are used to address this question as follows. First, the relationships among various size metrics are examined using a morphometric data set of Late Cretaceous–Oligocene veneroid bivalves. Second, the relationship between the size of bulk-sampled specimens and the size of species' type specimens is examined using bulk-sampled bivalves and gastropods from the Coffee Sand (Upper Cretaceous, Mississippi). Third, the same relationship is examined using mollusk-dominated field censuses from the type Cincinnatian (Upper Ordovician, Ohio, Indiana, and Kentucky). Fourth, the relationship between the size of the type species of a genus and median species size is examined using literature-derived measurements of bivalve type specimens from the recent eastern Pacific continental shelf. Together these data sets provide estimates of the biases imposed by measuring different kinds of specimens and using different methods of estimating body size. The geometric mean of length and height is highly correlated with more complex morphometrically based metrics and is our preferred bivalve size metric. Bulk or randomly sampled specimens are significantly smaller than species' type specimens for the Cretaceous dataset but significantly larger for the Ordovician dataset. Genus' type-species size is an unbiased estimate of median species size. These results suggest that large-scale studies can use the size of the type species of a genus as an unbiased proxy for a type-specimen size of a genus' median species, but that species' type-specimen size is a biased proxy for bulk or randomly sampled specimens. In addition, this study emphasizes the importance of using a single type of measurement within studies and suggests that combining multiple types of specimens (e.g., type specimens and bulk-sampled specimens) could lead to substantive errors.

INTRODUCTION

Body size is an important parameter in a wide range of ecological and evolutionary investigations. Macroevolutionary hypotheses such as Cope's rule are being actively tested (Jablonski, 1996, 1997; Alroy, 1998), and body size is frequently evaluated as a macroevolutionary correlate. Species survivorship appears to correlate with body size in some studies (Stanley, 1986; McKinney, 1997) but not in others (Budd and Johnson, 1991; Jablonski, 1996). The probability of surviving the end-Cretaceous (K/P) mass extinction was apparently unrelated to body size in bivalves (Jablonski and Raup, 1995; Jablonski, 1996; Lockwood, 2005), but post K/P recovery does appear to be size related (Lockwood, 2005). Macroecological relationships with body size include size of geographic range (Brown et al., 1996; Pryon, 1999), and local abundance and rarity (Pryon, 1999; but see McClain, 2004). Body size is considered to be an important determinant, or at least a correlate, of ecological community structure (Brown, 1995; Roy et al., 2000; Etienne and Olff, 2004).

Body size is also related to a wide variety of individual traits, including growth (Savage et al., 2004), reproductive output (Spight and Emlen, 1976; Angeloni et al., 2002; but see Styan and Butler, 2003), habitat breadth (Pryon, 1999; but see Hughes et al., 2000), metabolic rate (Vladimirova et al., 2003), feeding rates (Rajesh et al., 2001), resource requirements (Brown and Maurer, 1986; Gaston and Blackburn, 2000), and a taxon's vulnerability to exploitation (Ponder and Grayson, 1998). In addition, body size is a key determinant of specific sampling biases in paleontological studies including sieve-size effects (Kidwell 2001, 2002; Gage et al., 2002; Kowalewski and Hoffmeister, 2003), and size has been investigated both as a source of large-scale sampling bias (Valentine, 1989; Jablonski et al., 2003; Cooper et al., 2006; Valentine et al., 2006) and as general proxy for taphonomic durability (Behrensmeyer et al., 2005). Despite the importance of size to a wide array of ecological and evolutionary questions, there are relatively few studies confronting the methodological difficulties and biases inherent in measuring and inferring body size in fossils (e.g., Powell and Stanton, 1985; LaBarbera, 1989; Bookstein, 1991; Crampton and Maxwell, 2000; Krause et al., 2003, 2004).

There is no perfect measure of organismal size. The most ecologically meaningful measure of size is a measure of biomass, such as ash-free dry weight, but obtaining ash-free dry weight requires living material and is time and resource intensive, and of course biomass can be determined from fossil material only via correlation with another size measure (e.g., Powell and Stanton, 1985). Advances in computing and digital photography have made obtaining complex size metrics (e.g., area, centroid size) easier than ever, but simple caliper measurements of length, height, and width are still the easiest size measurements to obtain and are included in most taxonomic descriptions. Some authors simply use the maximum skeletal dimension as a size metric (e.g., Cooper et al., 2006), whereas others prefer to use geometric mean of length and height (e.g., Stanley, 1986; Jablonski, 1996, 1997; Jackson et al., 1996; Roy et al., 2000; Valentine et al., 2006). Fisheries biologists tend to use various definitions of length as a preferred measure of size and surrogate of age (e.g., Gervis and Sims, 1992). How different are the various size metrics?

At some point in nearly all paleontological and macroecological studies, a representative body size is extrapolated across numerous individuals, occurrences, or taxa from a variety of different samples, geographic areas, or stratigraphic intervals. Many faunal datasets exist as taxon lists without the original specimens or their measurements, and in most bulk samples specimens are broken, eliminating the possibility of obtaining direct measurements from all of the specimens in the sample. Because it is not possible to measure specimens that have not been archived and it is much more time efficient to measure representative specimens, generally a representative body size is based on a subsample, perhaps even a single specimen. If measuring every individual is impossible, what is the proper method for subsampling? Measurements for type material are often published, and type specimens can easily be measured from figures

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*Corresponding author.

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or museum collections. The proper representative size depends on the scale of the study, but approaches include the selection of type or figured material as a single point, in studies including a large number of taxa (e.g., Arnold et al., 1995; Jablonski and Raup, 1995; Roy et al., 2000; Valentine et al., 2006), or geographically or temporally dispersed representative samples in more detailed within-taxon studies (e.g., Wingard, 1993; Crampton and Maxwell, 2000; Roopnarine and Vermeij, 2000). While a wide range of selection criteria may be valid in particular cases, consistency within a study may be important, and careful thought needs to be put into scales of variance. How does specimen selection bias results?

Paleontological analyses take place at multiple taxonomic levels, and paleontologists have most commonly focused on taxonomic levels at the subgenus level and above, owing to the incompleteness of the fossil record and the relatively short duration of individual species. However, the ecological importance of body size is most clearly recognizable at the species level (Smith and Roy, 1999). Therefore, we face the problem of summarizing species-level patterns at higher taxonomic levels. How should a representative body size for a higher taxonomic level, such as subgenus or genus, be selected?

Four independent data sets are analyzed to address these four distinct but closely related questions relating to body size determination and estimation. First, the relationship between various size metrics is examined using a morphometric data set of Late Cretaceous–Oligocene veneroid bivalves. Second, the relationship between the size of bulk-sampled specimens and species' type-specimen size is examined using measurements of bulk-sampled bivalves and gastropods from the Coffee Sand (Upper Cretaceous, Mississippi). Third, the relationship between field-censused specimens and species' type-specimen size is examined using data from the type Cincinnatian (Upper Ordovician, Ohio, Indiana, and Kentucky). Fourth, the relationship between genus' type-species size and the median size of species within the genus is examined using literature-derived measurements of bivalve type specimens from the recent eastern Pacific shelf. Together these data sets provide insights into the biases imposed by different methods of body size estimation.

METHODS

Comparison of Size Metrics

A variety of size metrics were calculated for 390 bivalve specimens representing 153 species within the superfamilies Veneroidea, Arcticoidea, and Glossoidea. For simplicity these superfamilies are collectively referred to here as veneroids. Specimens were recorded from Upper Cretaceous to Oligocene deposits in North America and Europe and were sampled from both field and museum collections. For a more detailed description of systematics and sampling, see Lockwood (2004).

Specimens were digitally photographed in lateral and cross-sectional orientations. Traditional linear measurements (including shell length, height, and width; Fig 1A) were measured from these images, in addition to shell area in both orientations. Centroid size was determined for both the lateral and cross-sectional orientations by digitizing 100 equally spaced points around the outline using Optimas 5.2 for Windows and by calculating the square root of the sum of squared distances of these points from their centroid (Bookstein, 1991). Centroid size is the only measure of size that is uncorrelated with shape in the absence of allometry (Bookstein, 1991) and is increasingly used in morphometric studies of fossil taxa (e.g., Roopnarine and Beussink, 1999; Roopnarine and Vermeij, 2000; Anderson, 2001).

Square-root transformations were applied to shell-area measurements to linearize the expected relationship between areas and the other size metrics. The geometric mean of the two centroids and areas (lateral and cross section) were used as our morphometric measures. The three traditional linear metrics used were lateral length, the geometric mean of length and height, and the geometric mean of length, height, and width (Fig. 1A). The relationships among the traditional measures and the morphometric size metrics were examined using linear regression statistics and likelihood ratio tests. For the likelihood ratio tests only specimens that could be used in all comparisons were included ($n = 347$).

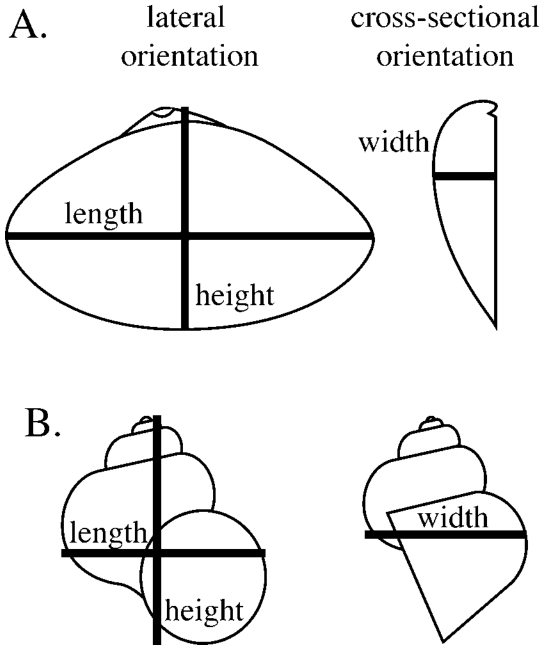

FIGURE 1—Shell diagrams indicating measurements of length, height, and width as used in these analyses. (A) Bivalve in lateral and cross-sectional view. (B) Gastropod in lateral and cross-sectional view.

Comparison of Type Specimen Versus Bulk-Sampled Specimens: Cretaceous

All unbroken specimens from four bulk samples collected from the Coffee Sand (Campanian, Mississippi) were measured to the nearest 0.1 mm using digital calipers (shell length, height, and width, Fig. 1). Measurements were obtained from the primary literature for type and figured specimens for the species recorded in the bulk samples. These data contain measurements from 460 specimens and 84 species. Additional information on the methods of sample collection and preparation are provided in Kosnik (2005), and the specimens are deposited at the Field Museum of Natural History, Chicago. Size was measured as the geometric mean of length and height (Fig. 1).

Relationships between bulk-sampled specimens and species' type specimens effectively weight the results by taxon abundance. In addition to the specimen-level analyses, species-level mean and maxima were also examined, which effectively weights species equally. In addition to raw measurements, bulk-sample specimen measurements were standardized by dividing the specimen measurement by the type-specimen measurement. These standardized measurements were used to examine size-dependent variation in the relationship between bulk and type specimens and to estimate a bias factor between specimen types. The $\log_2$ transformation of this standardized measure has the desirable property of being multiplicatively scaled from unity, so that 0.5 and 2 are both two-fold away from 1.0. If type specimens are an unbiased sample of bulk-sampled specimens, then the expected value for the standardized measurements is zero; values greater than zero indicate that bulk-sampled specimens are larger than type specimens, whereas values less than zero indicate that bulk-sampled specimens are smaller than type specimens.

Comparison of Type Specimen Versus Field-Censused Specimens: Ordovician

Field-censused specimens from several formations from the type Cincinnatian (Late Ordovician: Ohio, Indiana, and Kentucky) were measured

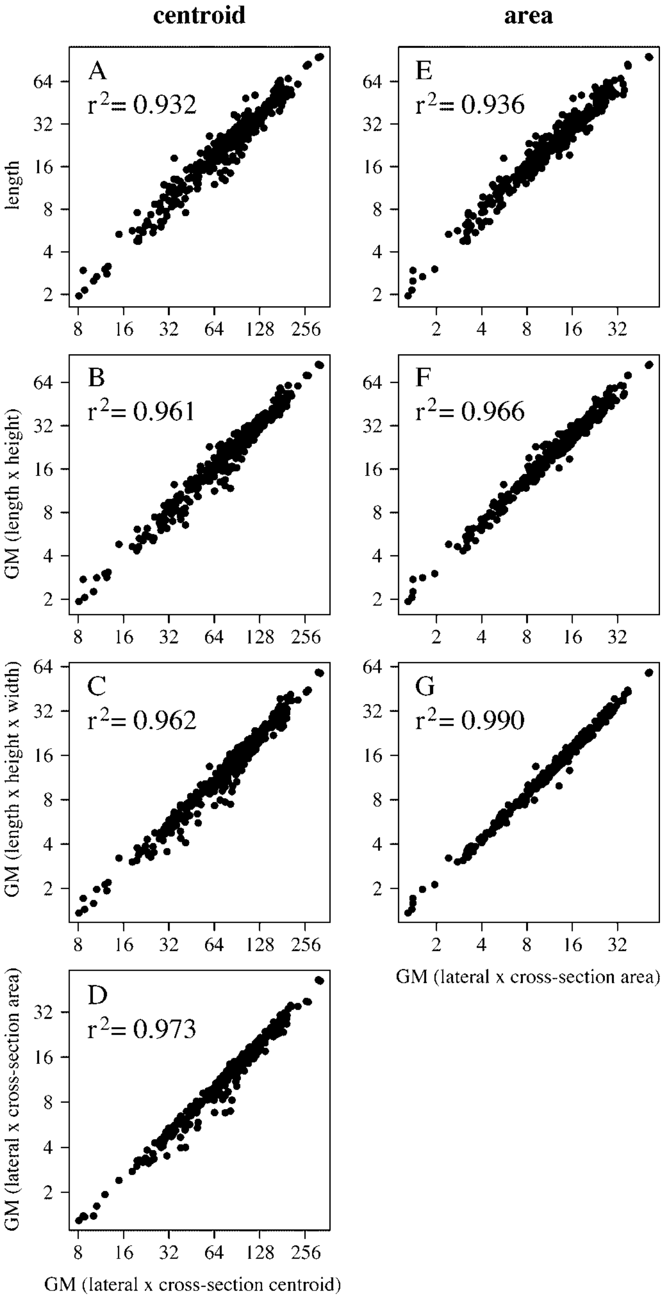

FIGURE 2—The relationships between traditional linear measures and morphometric measures of size in Late Cretaceous and Early Tertiary veneroid bivalves. All units of measure are millimeters; axes are log units. (A) Length vs. centroid size, $r^2 = 0.932$, LL $= -892.5$. (B) Geometric mean (GM) of length and height versus the centroid size, $r^2 = 0.961$, LL $= -796.7$. (C) Geometric mean (GM) of length, height, and width versus centroid size, $r^2 = 0.962$, LL $= -787.6$. (D) Shell area versus centroid size, $r^2 = 0.973$, LL $= -721.5$. (E) Length versus shell area, $r^2 = 0.936$, LL $= -238.1$. (F) Geometric mean (GM) of length and height versus shell area, $r^2 = 0.966$, LL $= -129.4$. (G) Geometric mean (GM) of length, height, and width vs. shell area, $r^2 = 0.990$, LL $= -76.6$.

along standardized axes (maximum length, height, and width) and reported by Frey (1987). Although these samples were dominated by bivalves, they also included data on intact specimens from the entire fauna, including brachiopods, trilobites, cephalopods, and gastropods. The size of the largest field-censused specimen of each species was compared to the size of type or figured material of the same species. Digital calipers were used to obtain corresponding measurements from the primary literature for type and figured specimens for the species present in the bulk samples (Knight et al., 1960; Cox et al., 1969; Pojeta, 1971; Wahlman, 1992; Feldmann, 1996). These data contain measurements from 45 specimens and 31 species, of which about half (21 specimens and 17 species) were gastropods or bivalves. This data set was subjected to the same analyses as the Cretaceous bulk sampled data set.

Generic Type Species Versus Median Species

The length and height of the largest known specimen were compiled for 915 of the ~950 species of marine bivalves recorded from the North American eastern Pacific continental shelf (depth < 200 m) through an extensive search of the primary literature and from major museum collections (see Roy et al., 2000, and references cited therein for additional information on this data set). The size of the type species was compared to the median species size for each genus. Size was measured as the geometric mean of length and height (Fig. 1A).

Our analysis of the relationship between the median size of a species for a genus and the size of the type species of that genus weights each genus equally. It should be explicitly stated that these two measurements are not strictly independent, because the type species of the genus is one of the species contributing to the median for about a third of the genera. Genera with only a type species measurement were excluded from these analyses. In addition to raw measurements, measurements were standardized by dividing the species measurement by the genus measurement and performing a $\log_2$ transformation. Again, these standardized measurements allow us to examine size-dependent variation in the relationship between type species and median species and to estimate a bias factor. If type species are an unbiased estimate of the median species, then the expected value for the standardized data is zero; values greater than zero indicate that type species are larger than median species, and values less than zero indicate that the median species is smaller than type species of the genus.

Statistics

All statistics were calculated and graphs plotted using R 2.1.0 for MacOSX (R Development Core Team, 2005, http://www.r-project.org). Least-squares regressions were performed using the linear models function, and log likelihood (LL) values were calculated using the formulas in Burnham and Anderson (1998).

RESULTS

How Do Size Metrics Compare?

Not surprisingly, all of the size metrics examined here are highly correlated with one another. Shell length was highly correlated with centroid size ($r^2 = 0.932$, LL $= -892.5$, Fig. 2A). The relationship between the geometric mean of length and height and centroid size was slightly stronger ($r^2 = 0.961$, LL $= -796.7$, Fig. 2B), but including width does not substantially improve the relationship ($r^2 = 0.962$, LL $= -787.6$, Fig. 2C). Shell length is highly correlated with shell area ($r^2 = 0.936$, LL $= -238.1$, Fig. 2E). The relationship between area and the geometric mean of length and height was stronger ($r^2 = 0.966$, LL $= -129.4$, Fig. 2F), and including width further improves the correlation ($r^2 = 0.990$, LL $= -76.6$, Fig. 2G).

Relative fit of the correlation coefficients was assessed using likelihood ratio tests (LRT). In each case the fit of the linear measures to the geometric mean of lateral and cross-sectional shell area or centroid was superior to the fit to the lateral shell area or centroid (the sole exception being the superior fit of the geometric mean of length and height to lateral shell area relative to geometric mean of lateral and cross-sectional shell area). In each case the relationship between the linear shell dimensions and shell area was stronger than the relationship between the linear shell dimensions and shell centroid size. The model fit to shell centroid size improves with each additional linear shell measure (Fig. 2, column 1), but adding width improves the LRT value by only 18 ($\mathrm{LRT}_{\mathrm{LH}} = 18$,

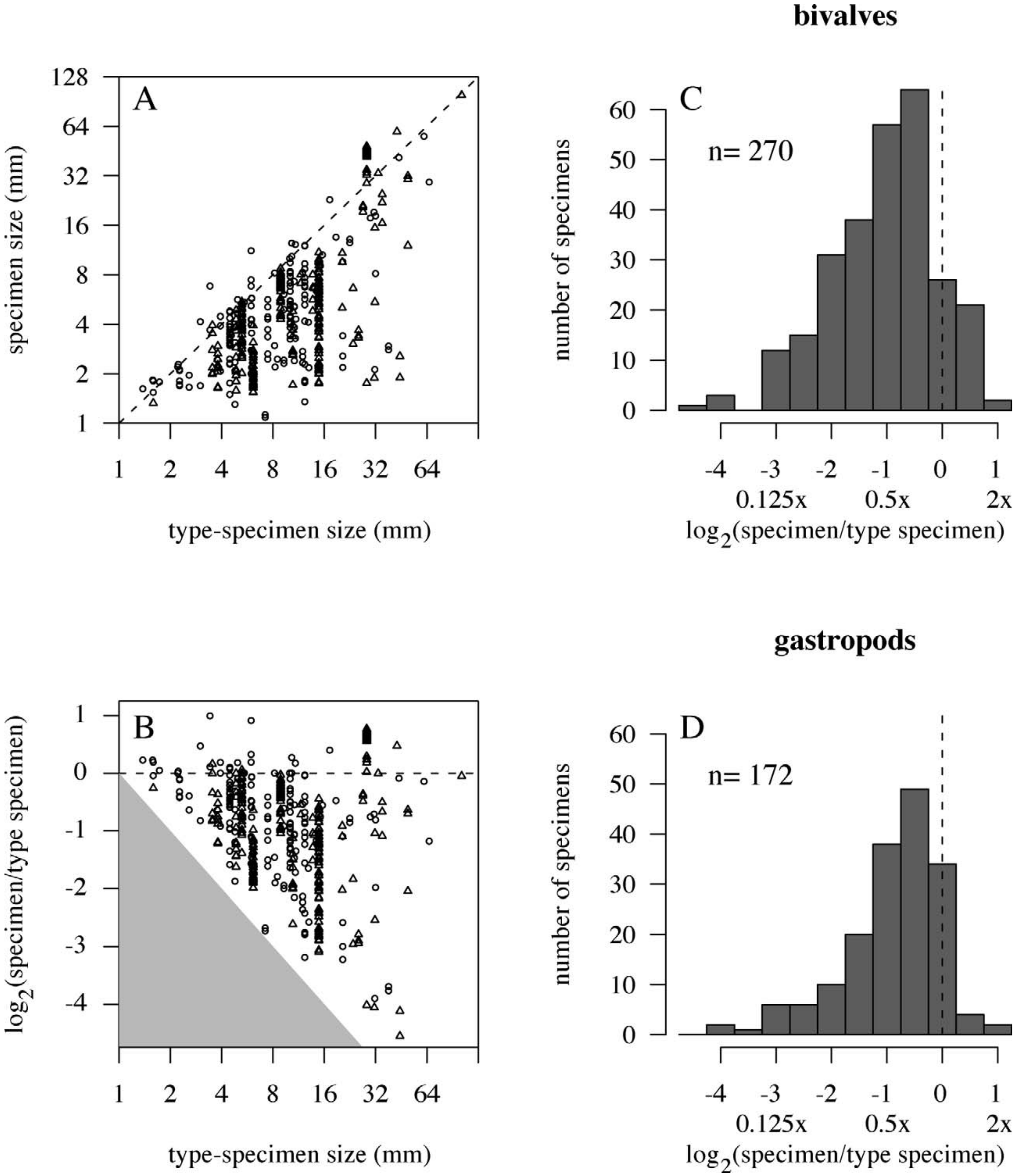

FIGURE 3—The relationship between the size of Late Cretaceous bulk-sampled specimens and species' type specimens (geometric mean of length and height). triangles = bivalves; circles = gastropods. (C, D) Note that nearly all specimens are smaller than the type specimens. (A) Bulk-sampled specimen size vs. size of species' type specimen with 1:1 line (log axes). (B) Bulk-sampled specimen size standardized by type-specimen size ($\log_2$) vs. type-specimen size (log axis) with a zero line; nearly all points fall below the zero line. Gray area = unsampled (specimens < 1 mm in diameter). (C) Histogram of bulk-sampled bivalve specimen sizes standardized by type-specimen size ($\log_2$). (D) Histogram of bulk-sampled gastropod specimen sizes standardized by type-specimen size ($\log_2$).

$LRT_L = 210$). This minor improvement in support indicates that the geometric mean of length and height alone is an adequate model of centroid size. The model fit to shell area size improves with each additional linear measure (Fig. 2, column 2), and no model other than the geometric mean of length, height, and width received strong support ($LRT_{LH} = 106$, $LRT_L = 323$). In the case of lateral centroid size, the best-fit model is the geometric mean of length and height, with no other model having strong support ($LRT_{LHW} = 81$, $LRT_L = 52$). The same is true for shell lateral area, with only the geometric mean of length and height receiving strong support ($LRT_{LHW} = 281$, $LRT_L = 297$). Shell-width data improve the model fit if the geometric mean of shell lateral area and cross-sectional area is the measure of interest, but not if the shell lateral area or shell centroid size are the measures of interest.

Overall, model selection using likelihood ratio tests indicates that the

TABLE 1—Bulk-sampled specimen size relative to the type specimen size. In all cases the Cretaceous bulk-sampled specimens are significantly smaller than the type specimen.

	All Specimens	Largest Specimen
Gastropod mean	55%	62%
median	63%	69%
Bivalve mean	48%	55%
median	52%	67%

relationship between linear measures and centroid size is not greatly improved by the addition of shell width, and the relationship between linear measures and shell lateral area decreases with the inclusion of width. Shell width is generally the hardest linear measure to obtain from monographs, because it cannot be measured from most published figures, which generally illustrate shells only in lateral view (see Fig. 1A). Thus, the extra collection efforts required to obtain width measurements can be justified only when linear measures are expected to be a proxy for the geometric mean of shell lateral area and shell cross-sectional area.

How Do Cretaceous Bulk-Sampled Specimens Compare To Type Specimens?

All specimens: Most species have specimens ranging in size from the limit of sampling (1.0 mm sieve) through the size of the type specimen (Fig. 3A). Standardizing by the size of the type specimen shows that no specimens are more than twice the size of the type specimen but that nearly half the specimens are less than half the size of the type specimen (Fig. 3B). The shaded area in Figure 3B represents the boundary imposed by sampling (filling that space would require specimens less than one millimeter in size). This suggests that, given the constraints imposed by sieve size (as well as inherent limits to organism size), bulk-sampled specimens fill the available size space, and type specimens are drawn from a subset of larger specimens (Wilcoxon paired test, $p < 0.0001$ for both bivalves and gastropods).

Specimens from bulk samples are nearly always smaller than the type specimen of the species (Table 1). The mean bivalve specimen is 48% of the size of type specimen, and the median specimen is 52% of the type (Fig. 3C). The mean gastropod specimen is 55% of the size of the type specimen, and the median gastropod specimen is 63% of the type specimen (Fig. 3D). Both distribution means are significantly less than zero (Wilcoxon unpaired tests, $p < 0.0001$). The means differ significantly from each other (Wilcoxon unpaired test, $p = 0.018$), but the bivalve distribution (Fig. 3C) is drawn from a population whose standardized sizes are smaller than the gastropod distribution (Fig. 3D; Kolmogorov-Smirnov test, $D = 0.1439$, $p = 0.0257$).

Largest specimen: Similar results are seen using the mean, median, or maximum bulk-sampled specimen per species. The mean and median specimens in bulk samples were found to be smaller than the type specimens, so using the largest bulk-sampled specimen for each species should minimize the differences between the bulk-sampled specimens and the type specimens. The largest bivalve and gastropod specimens found in the bulk samples are still generally smaller than the type specimens (i.e., fall below the dotted line in Fig. 4A, B, Table 1, Wilcoxon paired tests: bivalve $p = 0.0018$, gastropod $p < 0.0001$). The mean maximum bivalve specimen is 55% of the size of the type specimen, and the median maximum specimen is 67% (Fig. 4C). The mean maximum gastropod specimen is 62% of the size of the type specimen, and the median maximum specimen is 69% (Fig. 4D). The distributions of differences between bulk-sampled and type-specimen means are significantly less than zero (Wilcoxon test $p < 0.001$). Bivalves and gastropods are not significantly different from each other (Wilcoxon unpaired test $p = 0.657$; Kolmogorov-Smirnov test $p = 0.831$). Using the largest specimen has a bigger effect on bivalves (median maximum of 67% versus median all specimens, 55%) than on gastropods (median maximum of 69% versus median all specimens, 63%). The difference is fairly small, but it does explain why the all-specimen distributions are different while the maximum-specimen distributions are not.

How Do Ordovician Field-Censused Specimens Compare To Type Specimens?

The sizes of field-censused Cincinnatian specimens and the sizes of the species' type-specimens are strongly correlated and do not show the same tendency to fill in the areas under the unity (dashed) lines in Figures 5A and B as the Cretaceous data (Figs. 4A, B). Maximum field-censused specimen size is strongly correlated with type-specimen size ($r^2 = 0.8738$, $p < 0.0001$, Fig. 5A), but field-censused specimens are not consistently larger or smaller than type specimens (Wilcoxon paired test $p = 0.747$). When gastropods and bivalves are analyzed separately from the other invertebrates, a strong correlation remains ($r^2 = 0.8774$, $p < 0.0001$, Fig. 5A), but field-censused specimens are larger than the type specimens (Wilcoxon paired test $p = 0.006$). Standardized specimen size is significantly correlated with type-specimen size for the entire fauna ($r^2 = 0.2927$, $p < 0.0001$, Fig. 5B) but not for the gastropods and bivalves ($r^2 = -0.0245$, $p = 0.4792$, Fig. 5B).

Unlike the Coffee Sand bulk samples, the mean specimen from Cincinnatian field-census samples is 110% longer than the type specimen, while the median specimen is 119% longer. (Fig. 5C). These size differences are slightly larger, 117% for mean and 120% for median, when considering only the gastropods and bivalves (Fig. 5D). Both means are significantly greater than zero (Wilcoxon test: all $p = 0.0310$, gastropods and bivalves $p = 0.0063$).

Generic Type Species Versus Median Species

As expected, the size of the median species is strongly correlated with the size of the type species of the genus in the eastern Pacific data set ($r^2 = 0.8016$, $p < 0.0001$, Fig. 6A), and the correlation between the standardized size and type-species size, while significant, again explains little of the variance ($r^2 = 0.0378$, $p = 0.0001$, Fig. 6B). Generic type species are an unbiased representation of the median species size (Wilcoxon paired test $p = 0.2762$). The mean median species is 95% of the generic type species, while the median median species is 100% (Fig. 6C). Although excluding the generic type species when determining the median species size may be statistically more appropriate, most scientists want to use the type species as a proxy for the sizes of all the species within a genus, rather than for the sizes of all species except the type. However, this further analysis shows that the type species will be an adequate size proxy, even for congeners occurring outside the spatial or temporal ranges of the type.

The most distant outlier in this analysis is the living eastern Pacific species of *Bathyarca*. As the name suggests, *Bathyarca* is essentially a deep-sea genus. The deep-sea species are almost all small, and the small Pliocene type species is in fact from a bathyal deposit. In very high latitudes, however, a few of the species emerge into shallow water. The Arctic species, *Bathyarca glacialis*, occurs in the Beaufort Sea (northern coast of Alaska) at depths as shallow as 23 meters, ranging south in the eastern Pacific no further than the Bering Strait (Coan et al., 2000). A more comprehensive sample of *Bathyarca* species (Oliver and Allen, 1980; Coan et al., 2000) suggests that the type species is not as poor a proxy as suggested by its extreme position in the eastern Pacific analyses ($n = 10$, yields a mean standardized length that is 2.3 times the size of the type specimen and a median standardized length that is 1.5 time the size of the type specimen). While an even more complete sample reduces the impact of these outliers, *Bathyarca* is an excellent example of the noise inherent in the way that regional studies subsample the global biota.

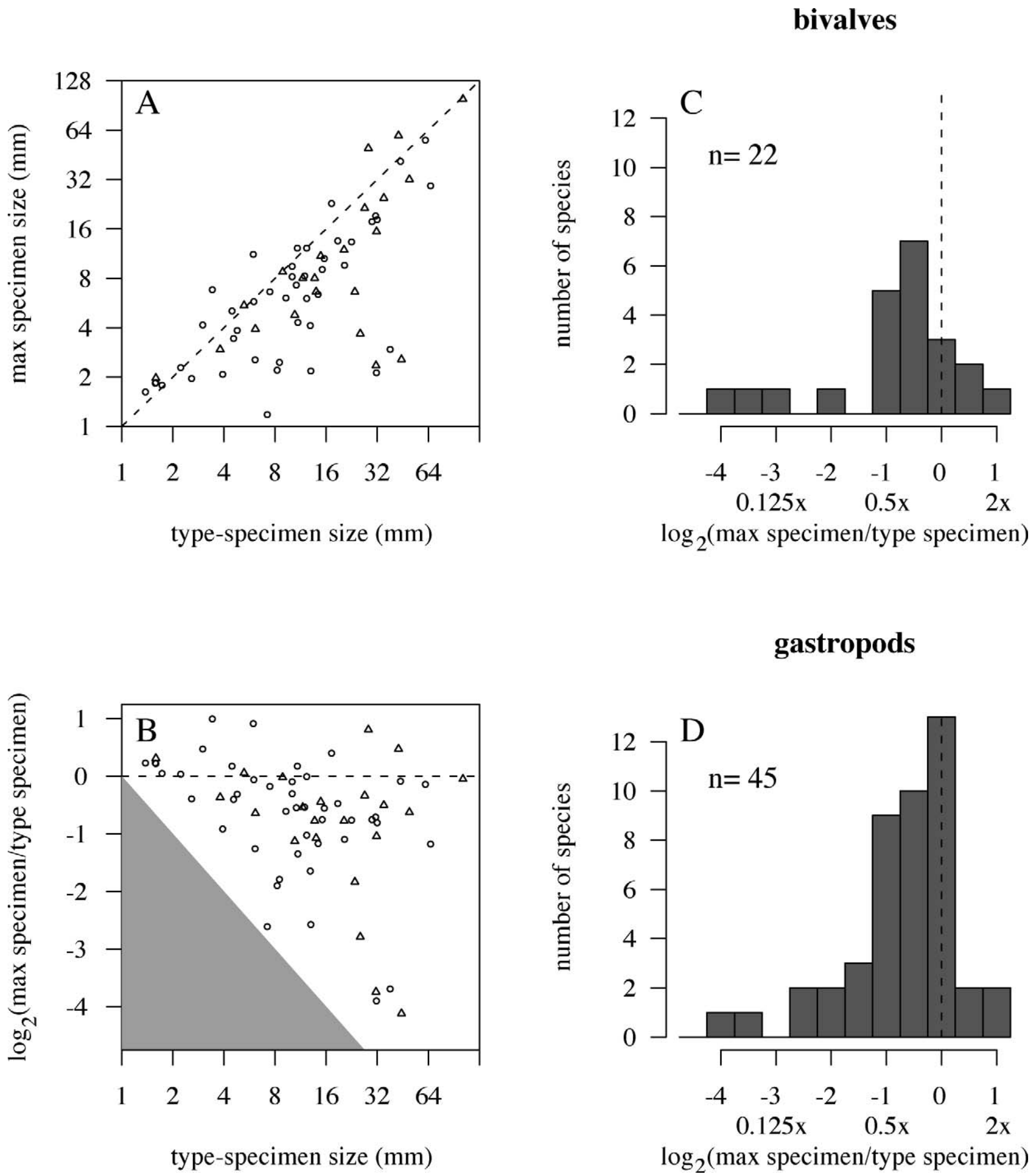

FIGURE 4—The relationship between the size of largest Late Cretaceous bulk-sampled specimens and species' type specimens (geometric mean of length and height). triangles = bivalves; circles = gastropods. (C, D) Note that nearly all specimens are smaller than the type specimens. (A) Largest bulk-sampled specimen size vs. size of species' type specimen with 1:1 line (log axes). Nearly all points fall below the 1:1 line. (B) Largest bulk-sampled specimens standardized by type-specimen size ($\log_2$) vs. type-specimen size (log axis) with a zero line; nearly all points fall below the zero line. Gray area = unsampled (specimens < 1 mm in diameter). (C) Histogram of the largest bulk-sampled bivalve specimens standardized by type-specimen size ($\log_2$). (D) Histogram of the largest bulk-sampled gastropod specimens standardized by type-specimen size ($\log_2$).

DISCUSSION

Selecting a Size Metric

All the various metrics of body size investigated here are strongly correlated. Given that the simple linear dimensions are the easiest measurements to obtain, they would seem to be the natural choice for a size metric. Length is a good choice given its ease of collection (e.g., Powell and Stanton, 1985). The geometric mean of length and height shows an improved fit to both centroid size and shell area, suggesting that geometric mean of length and height is a better proxy for either size than length alone. Adding a third dimension (width) increased the correlation with shell area and modestly improved the correlation with shell centroid

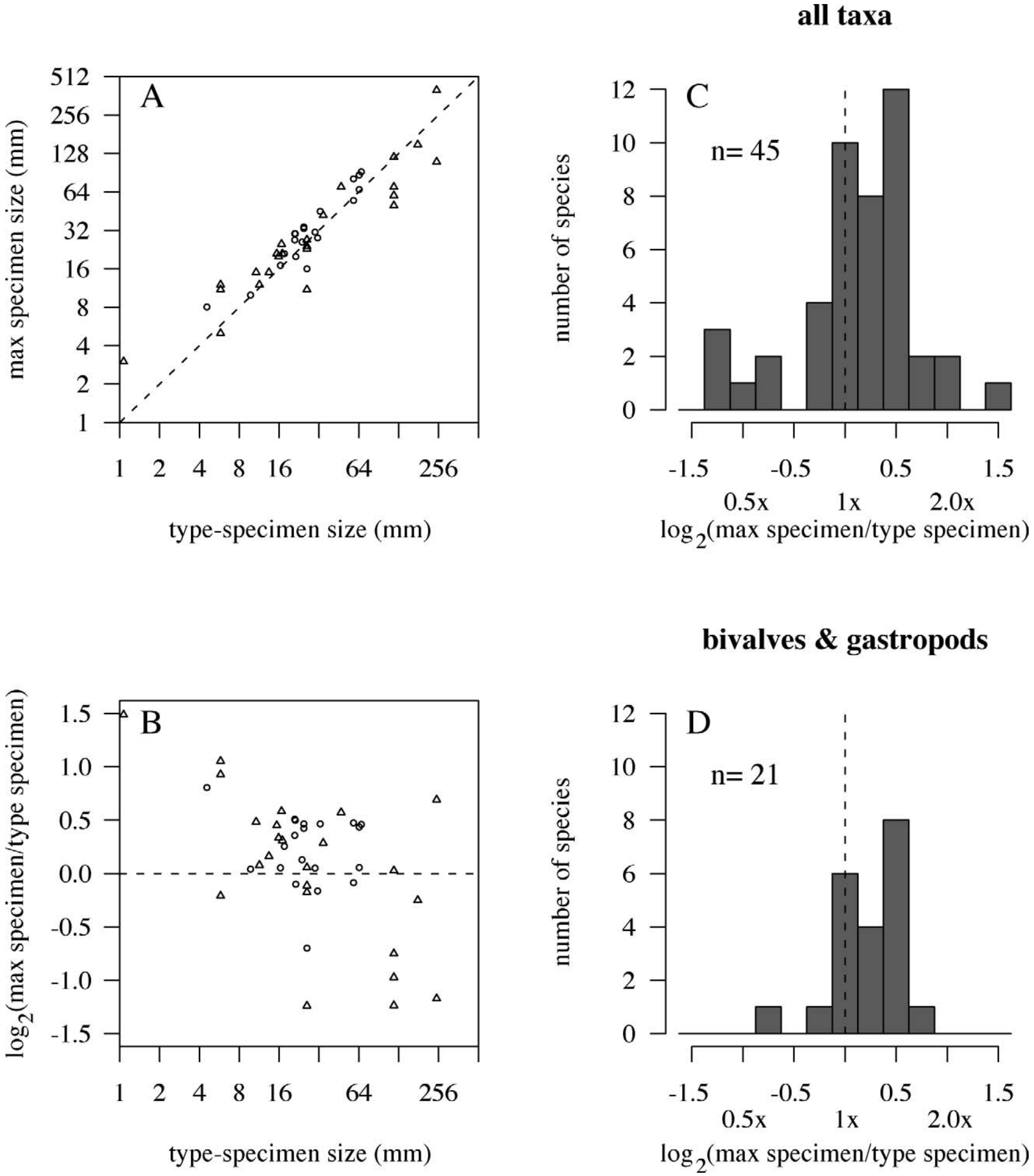

FIGURE 5—The relationship between the size of Ordovician field-censused specimens and species' type specimens (maximum dimension); circles = mollusks; triangles = nonmollusks. (C, D) Note that field specimens tend to be larger than the type specimen. (A) Maximum field-censused specimen size vs. size of species' type specimen with 1:1 line (log axes); nearly all points fall above the 1:1 line. (B) Maximum field-censused specimen size standardized by type-specimen size ($\log_2$) vs. type-specimen size (log axis) with a zero line; nearly all points fall above the zero line. (C) Histogram of maximum field-censused specimen sizes standardized by type-specimen size ($\log_2$). (D) Histogram of maximum field-censused mollusk specimen sizes standardized by type-specimen size ($\log_2$).

size. The improved fit associated with adding shell width is much less than the improvement seen when height is added, suggesting that the third dimension is much less important for estimating body size. Given the relative ease of obtaining length and height measurements from illustrations, species descriptions, or museum collections, as well as the minor improvement in the correlations with morphometric measures, the relatively time-efficient approach of using the geometric mean of length and height is recommended.

Selecting Specimens to Measure

Type specimens of Late Cretaceous species tend to be about twice the size of randomly sampled bivalve and gastropod mollusks. It is intuitive

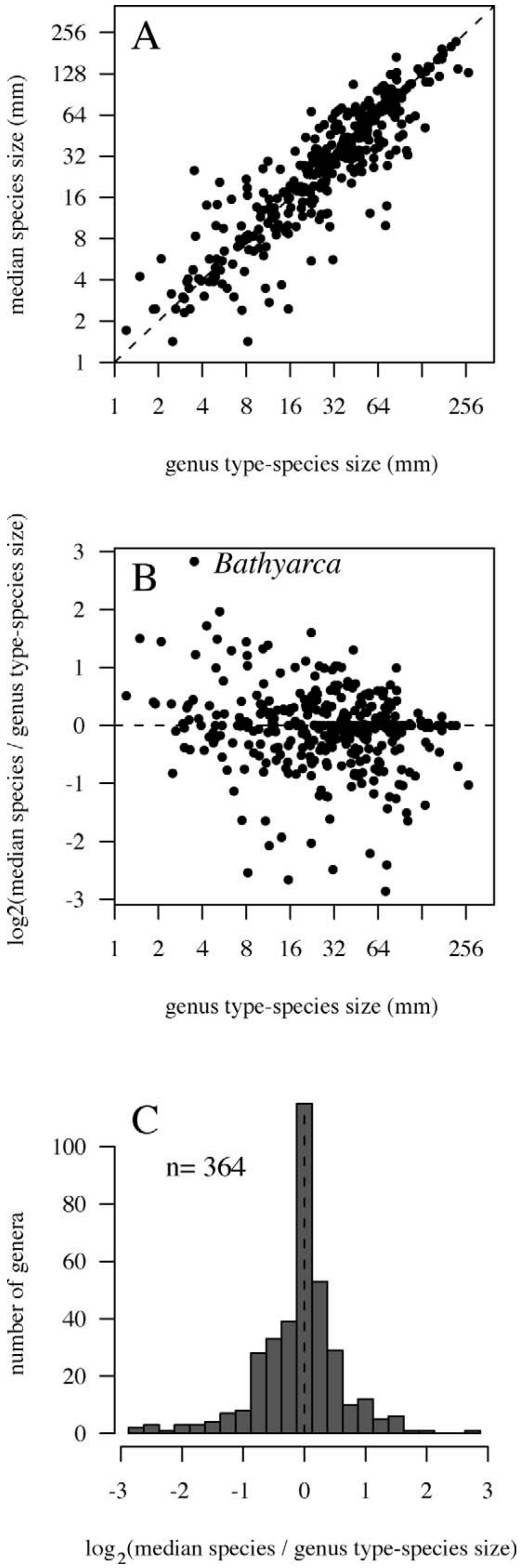

FIGURE 6—The relationship between the size of the median species vs. generic type species in living Eastern Pacific bivalves (size = geometric mean of length and height). (A) Median species vs. generic type species with a 1:1 line (log axes). (B) Median species standardized by generic type species ($\log_2$) vs. generic type species (log axis) with a zero line. (C) Histogram of the median species standardized by generic type species ($\log_2$), with mode of zero indicating that the median species is the same size as the type species of the genus.

to suggest that larger specimens might be selected as types because they are easier to handle, they tend to be better preserved, and systematists tend to avoid selecting immature specimens as types. It is also possible that types are randomly selected (with respect to size) from surface collections, but these data cannot test that hypothesis. Bulk or randomly sampled gastropods tend to be closer in size to the type specimen than bivalves. This suggests a potential bias in comparing bivalves to gastropods using these sorts of estimators, although a larger data set should be investigated before strong inferences are made. Using the largest specimen found in a bulk sample did not improve the comparison, because type specimens were still much larger than the bulk-sampled specimens. If these results are more broadly applicable, using bulk-sampled measurements for one datum point and type-specimen measurements for another datum point could lead to a two-fold difference between data points that derives entirely from the methods used to estimate size.

In contrast to the Cretaceous results and those using Neogene bivalves (Krause et al., 2003), the Cincinnatian species' type specimens tend to be smaller than field-censused specimens. These results contradict the Cretaceous results but have a smaller effect size (1.2x vs. 0.5x). The contrast could be related to the method of collection, because the Coffee Sand samples were sieved from unconsolidated sediments, whereas the Cincinnatian specimens were sampled from lithified mudstones and limestone tempestites and thus were unlikely to include very small, fragile growth stages. Additional study is needed to confirm whether the bias for Ordovician samples differs from that seen in the Cretaceous samples, or whether these results are due to differences in sampling methods (field-census versus sieved bulk samples), lithological or environmental differences, or represent a special case. If these results hold in other investigations, they raise an interesting potential bias in Phanerozoic-scale analyses of body size.

The size of the type species of a genus is an unbiased estimate of median species size. This strongly suggests that the generic type-species measurements can be used as a proxy for median species' type-specimen size in studies in which the loss of within-genus variance is not important. It is intuitively appealing that congeneric species should be similar in size relative to the members of other genera, and congeneric similarity in body size has also been found in mammals (Smith et al., 2004).

CONCLUSIONS

The geometric mean of length and height is selected as the preferred size metric. Cretaceous species' type specimens are found to be approximately twice the size of randomly sampled specimens found in bulk samples, but Ordovician type specimens are found to be slightly smaller than field-censused specimens. Generic type-species size is found to be an unbiased measure of median species' type-specimen size, suggesting that the type species of the genus can be a reasonable proxy for median species size. On the other hand, our results warn against mixing body sizes derived from type material with body sizes derived from bulk-sampled material.

These results are good news for researchers working with large data sets who cannot measure all possible specimens and to researchers working at higher taxonomic levels. Statistically reliable large-scale studies of body size can be achieved using relatively small samples and numbers widely available in the literature. However, these results raise a number of concerns of which paleoecologists estimating body sizes from bulk samples must be aware.

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