

USING SIMPLE BODY-SIZE METRICS TO ESTIMATE FOSSIL BODY VOLUME: EMPIRICAL VALIDATION USING DIVERSE PALEOZOIC INVERTEBRATES

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ABSTRACT

Body size is one of the most significant organismal characteristics because of its strong association with nearly all important ecological and physiological characteristics. While direct body mass measurement (or estimation from other size metrics) is not feasible with most extinct taxa, body volume is a measurable and general proxy for fossil size. This study explores the reliability of several metrics that can be used to estimate the body volume of Paleozoic invertebrates of various sizes, shapes, taxonomic affinities, and ecological habits. The ATD model, based on the product of lengths of the three major body axes (anteroposterior, transverse, and dorsoventral), is simple and widely applicable. Models specific to particular morphological and taxonomic groups are slightly more accurate than this ATD model, but the advantages are minor. The ATD model is consistent with previous studies demonstrating widespread shape allometry—that is, small taxa tend to have globose geometries while large ones tend to be conical, even within the same taxonomic group. The ATD model successfully predicts the volume of 10 validation samples that were excluded from development of the original model. Because the linear measurements used to estimate volume are easy to obtain from specimens in the field or from published work, estimates of body volume can be incorporated into paleontological analyses, even those spanning multiple phyla.

INTRODUCTION

Body size ranks among the most fundamental organismal characteristics because of its strong association with abundance, geographic range, metabolic rate, reproductive rate, life span, mobile velocity, and most other ecological and physiological characteristics (Thompson, 1942; Damuth, 1981; Peters, 1983; Schmidt-Nielsen, 1984; Brown, 1995), and it has been widely used in paleontological studies. Representative examples include documentation of phyletic evolution (e.g., Raup and Crick, 1981; Arnold, 1983; Gingerich, 1985; Stanley and Yang, 1987; Millien and Jaeger, 2001), macroevolutionary trends (including Cope's Rule; e.g., McKinney, 1990; Jablonski, 1997; Alroy, 1998; Smith et al., 2004; Hunt and Roy 2006), paleoecology (especially for plants; Baker and DiMichele, 1997; Pryor and Gastaldo, 2000; Williams et al., 2003a, 2003b), macroecology (Roy et al., 2000), and size selectivity during and after mass extinctions (Stanley, 1986; Fraiser and Bottjer, 2004; Lockwood, 2005; Payne, 2005) and during background times (Smith and Roy, 2006). In such studies, size comparisons are usually restricted to taxonomically and morphologically similar taxa. Broader phylogenetic comparisons (e.g., among phyla) are constrained by the absence of a more generally useful body-size metric.

Neontologists are not so constrained. Body mass is an easily measured and biologically meaningful currency for living organisms (Blake et al., 1987; Hayek and Buzas, 1997) and has been the focus of much ecological theory (Brown, 1995; Siemann et al., 1999; Enquist and Niklas, 2001; Enquist et al., 2002; West et al., 2002). Recognizing this importance, paleontologists often choose size metrics known from empirical studies with living taxa to correlate with body mass (e.g., Golightly and Kosinski,

1981; Powell and Stanton, 1985; Damuth and McFadden, 1990; Tokeshi et al., 2000; Motani, 2001; Williams et al., 2003a, 2003b).

Several metrics are commonly used for shelled invertebrates. Length or other unidimensional linear shell measures (e.g., width, depth) are simple and broadly accurate (Niklas, 1994) estimates of size magnitude (Powell and Stanton, 1985; Tokeshi et al., 2000; Fraiser and Bottjer, 2004) but are potentially imprecise when comparing morphologically dissimilar taxa. More complicated measures incorporating two shell dimensions, such as cross-sectional area (Kosnik et al., 2006), geometric mean of shell length and width (Stanley, 1986; Jackson et al., 1996; Jablonski, 1997; Roy et al., 2000; Aberhan et al., 2006; Kosnik et al., 2006), or centroid size (Roopnarine and Beussink, 1999; Lockwood, 2005; Kosnik et al., 2006), have been used widely. Although empirical regressions allow conversion of all these measures to estimates of body mass, such conversions are only reliable for fossil taxa with representative living species.

Because of this constraint, body volume—which also can estimate body mass (Powell and Stanton, 1985; Henderson, 1999; Motani, 2001)—might offer a more general metric for use with extinct fossil taxa. As an overall measure of size, volume also might represent a greater range of three-dimensional forms than individual linear metrics (e.g., Dommergues et al., 2002). Volume typically is measured using geometric shape-specific approximations. For example, gastropods have been modeled as cones (Powell and Stanton, 1985; Payne, 2005) or prisms (Powell and Stanton, 1985), and cephalopods as cylinders (Dommergues et al. 2002). Volumes of more complex taxa—those not easily modeled as simple geometric shapes—have been estimated computationally from lateral and dorsal body outlines sliced transversely into ellipses or superellipses (Henderson, 1999; Motani, 2001); such methods have not been attempted for marine invertebrates, however.

This study makes a first attempt to validate volume estimation for Paleozoic invertebrates spanning a range of sizes, shapes, taxonomic affinities, and ecological habits. It uses regression analysis of various linear metrics, including many frequently used in paleontology, to predict the known body volume of well-preserved fossil invertebrates. The accuracy and precision of the optimal model is tested by predicting the volume of 10 validation samples that were excluded from the original regression model. Thus, this study evaluates which metrics are best for future size analyses and examines the validity of two widely held but untested claims—that volume is the most powerful measure of overall size and that geometric approximations are adequate proxies for volume.

MATERIALS

A total of 102 complete and well-preserved specimens (see Supplementary Data 1 and 2¹) were chosen from the invertebrate paleobiology collections at the National Museum of Natural History (Smithsonian Institution) to represent a variety of sizes, shapes, and taxonomic and ecological affinities. In order to represent the broad range of taxa found in typical benthic Paleozoic shelly assemblages, representatives of the following groups were included: brachiopods (Classes Rhynchonellata, Stro-

¹ www.paleo.ku.edu/palaios.

phenonata, and Lingulata), corals (Subclasses Rugosa and Tabulata), bivalves (Subclasses Paleotaxodonta, Pteriomorpha, Paleoheterodonta, Heterodonta, and Anomalodesmata), gastropods (Suborders Bellerophonitida, Euomphalida, and Murchisonida), monoplacophorans (Orders Cyrtoneidida and Tryblidiida), cephalopods (Subclasses Ammonoidea, Nautiloidea, Endoceratoidea, and Orthoceratoidea), and trilobites (Orders Asaphida, Phacopida, Ptychopariida, and Proetida). Such broad taxonomic coverage is necessary so that the resulting models capture the morphology of shelled invertebrates as a whole rather than phylogenetic correlation within a single group (Felsenstein, 1985; Harvey and Pagel, 1991). Specimens represented over five orders of volumetric magnitude (0.05–800 ml), a wide range of geometric forms (including cones, ellipses, frustrums, and cylinders), and a variety of ecological habits, including mobile mass or deposit feeders (e.g., Novack-Gottshall, 2007), sedentary filter feeders, swimming predators, and colonial microcarnivores. Because trilobites are commonly preserved enrolled, both prone and enrolled specimens were used. In order to measure the entire volume of a shelly fossil, including internal cavities, all specimens chosen were preserved with lithified infill but were free of surrounding rock matrix. In this sense, the volume of the entire fossil specimen was measured and not just the internal cavity or skeleton (used in the general sense here to refer to shells, exoskeletons, and other durable hard parts).

METHODS

Volumetric Measurement

Fossil volume was measured directly by (1) placing each specimen in a container known to overflow at a precise volume of water, (2) adding aliquots of water until the moment of overflow, and (3) subtracting the total aliquot volume added from this known overflow volume. This method is a variant of one commonly used by vertebrate paleontologists (Colbert, 1962; Henderson, 1999; Motani, 2001). The working table was stabilized and leveled, and water was maintained at room temperature to avoid fluctuations in density. Approximately one dozen containers were used to accommodate the variety of specimen sizes and shapes. The point of overflow was used as a standard reference volume because the varied containers were unequally precise and some lacked graduated marks altogether. To overcome these limitations, at least four (usually 6–10) independent overflow measurements were conducted for each container without specimens. The range of measurement error (Sokal and Rohlf, 1994) among containers was 0.026%–3.8%; the average container had an error of 0.94% (median = 0.64%, SD = 1.1%). Small containers were more prone to error; the smallest container, holding 3.8 ml (SD = 0.15 ml) of water, had the greatest error (3.8%), even after 15 repeated measurements. Final aliquots, both for these overflow calibrations and when measuring specimens, were added with a similarly calibrated water dropper (0.049 ml per drop, SD = 0.0014 ml-drop⁻¹). Although this immersion method is direct and simple, it is time intensive, somewhat imprecise (especially for specimens with volumes <0.25 ml), and not practical for very large specimens. Furthermore, it is not amenable to field use when specimens are incomplete, preserved as casts, or embedded in matrix or when measuring photographs of specimens (Kosnik, 2002; Krause et al., 2003, 2007; Kosnik et al., 2006).

Linear Measurements and Orientation of Specimens

Four measurements (with precision to 0.01 mm) were made on each specimen using a digital caliper (Fowler Ultra-Call Mark III). The maximum length (or major axis length) is the maximum distance between any two points on a specimen. Although this measure is useful for gauging the approximate size of a fossil, it is an inadequate estimator of volume because it cannot distinguish the many shapes found among benthic invertebrates. For example, the volume of a maximally 3-cm-long fossil can range from <1 ml to 14 ml depending on whether its shape is a cone or sphere (see equations 6–7 below). Three additional measures

were made in orthogonal orientations: anteroposterior length (A), transverse width (T), and dorsoventral depth (D). These measures were chosen to represent all three dimensions of the organism and to correspond to biologically relevant axes. While such measures often require a more complete specimen and a standard orientation, they can accommodate a great variety of organismal shapes when used in combination.

There are several reasons why measurements should be based on anatomy rather than pure geometry (e.g., major axis). First, it is difficult to interpret and compare results among specimens with different shapes when using only major axis, minor axis, or other nonhomologous measures. Because anatomical measurements are orthogonal, they are more likely to reflect the true volume of specimens, and body lengths can be estimated when specimens are incomplete; for example, the transverse width of a symmetrical bilaterian can be estimated when only one side is preserved. Anatomical measures also can be ecologically meaningful; for example, in many mobile benthic bilaterians, dorsoventral depth corresponds with the distance that an animal rests above the sediment.

Standard orientations (Table 1) were made following the guidelines for each taxonomic group from the *Treatise on Invertebrate Paleontology* (Moore, 1957, 1959, 1960, 1964, 1965, 1969; Teichert, 1981). For bilaterians, the choice of axes was generally self-evident. For corals and poorer preserved cephalopods in which such determinations were impossible, the transverse width was chosen as the maximum orthogonal to the more easily determined anteroposterior length or oral-aboral axis; this choice approximates the true morphology in many cephalopods. In all cases, axes were oriented orthogonally. All measures were made as the maximum distance between any two points in the plane described by the other two axes. Thus, the measurements define the smallest rectangular parallelepiped or cuboid that will contain the entire fossil when oriented along the ATD axes. These orientations are made with reference to the shell; in some cases, e.g., some gastropods and bivalves, these axes may not correspond with the biological orientations of the soft body. Table 1 explains additional guidelines for specific taxonomic groups.

Regression Models

Linear regression analysis was used to compare various combinations of these log-transformed linear measures to the log-transformed, observed body volume of 92 specimens (10 specimens were set aside to validate the model; see below). The simplest models used the maximum, A, T, and D measurements in isolation. Products of various combinations of measurements, excluding the maximum, were made to assess the accuracy of multidimensional models, especially those used in existing body-size studies. For example, area (Kosnik et al., 2006) is approximated here by the product of A and T. Several products are equivalent (through conversion using a square- or cube-root transformation; see below) to geometric mean size (Stanley, 1986; Jackson et al., 1996; Jablonski, 1997; Roy et al., 2000; Aberhan et al., 2006; Kosnik et al., 2006). The diagonal distance—also called the generalized hypotenuse or Euclidean distance (Van Valen, 1974)—also was tested for each combination. Multiple regression models were tested, treating A, T, and D as individual, independent predictors. Statistics were calculated using R, version 2.3.1 for Windows (R Development Core Team, 2006).

Although both volumetric and linear measures have error, model I regression was used because the measurement error for volume was about twice that using calipers (see below) and because body volume is the dependent variable to be predicted here (Sokal and Rohlf, 1994). Model selection was made by choosing the model with the minimum residual standard error of the regression (Sokal and Rohlf, 1994). In the face of equally predictive models, univariate models were considered more practical than multiple regression models.

To determine whether taxonomic and morphologic groups display different relationships, similar analyses were conducted for several groupings of specimens. Taxonomic comparisons were conducted for large groups (typically phylum or class level) and several subgroups (typically

TABLE 1—Orientation terminology for taxonomic groups measured. Each axis is oriented orthogonally to the other axes. Measures are the maximum distance between any two points in the plane described, following standard guidelines (Moore, 1957, 1959, 1960, 1964, 1965, 1969; Teichert, 1981). All measures are made with respect to the shell; in some cases, including some gastropods and bivalves, these measures may not correspond with the biological orientations of the soft body.

Group	Anteroposterior (AP) length	Transverse (RL) width	Dorsoventral (DV) depth
Enrolled trilobites ¹	Enrolled exoskeleton length	Enrolled exoskeleton width	Enrolled exoskeleton height
Prone trilobites	Exoskeleton length	Exoskeleton width	Exoskeleton height
Monoplacophorans ²	Shell length	Shell width	Shell height
Isostrongic gastropods ³	Shell length	Shell width	Shell height
Anisostrophic gastropods ³	Shell height (coiling axis)	Shell diameter (apertural plane)	Shell diameter
Bivalves ⁴	Shell length (hinge axis)	Shell width	Shell height
Straight cephalopods ⁵	Conch length	Conch width	Conch height
Coiled cephalopods ⁶	Conch length	Conch width	Conch height
Solitary rugose corals ⁷	Proximodistal corallum height	Maximum corallum diameter	Corallum diameter
Massive tabulate corals ⁷	Proximodistal corallum height	Maximum corallum diameter	Corallum diameter
Brachiopods	Shell length	Shell width	Shell height (thickness)

¹ Enrolled trilobites oriented with ventral margin of the cephalon horizontal; dorsoventral depth passes through both cephalic and thoracic segments.

² Monoplacophorans and isostrophic gastropods oriented with the aperture horizontal; coiling axis is parallel to, and may correspond with, transverse width.

³ Anisostrophic gastropods measured so that transverse width is perpendicular to coiling axis and passes through a point on the apertural margin (often in the apertural plane); this measurement often corresponds with maximum shell diameter. Dorsoventral depth is perpendicular to the other two axes and often corresponds with minimum shell diameter.

⁴ Bivalves oriented with hinge axis horizontal, so that shell length is parallel to hinge axis, which may not correspond with the biological orientation of the soft body.

⁵ Straight (i.e., longiconic and orthoconic) cephalopods oriented with the hyponomic sinus in a ventral position.

⁶ Conch length in coiled cephalopods is the length of the coiled conch, not the length of the conch if uncoiled. Conch height is the maximum length in a plane parallel with the aperture, conventionally with the peristome in a ventral position.

⁷ Transverse width for rugose and tabulate corals equals maximum diameter of the corallum, which often is nearly equal to the perpendicular dorsoventral depth.

subclasses, orders, or suborders). All specimens were also grouped into one of three morphological groups (depressed, conical, and globose) prior to analysis to determine whether standardizing for overall shape would improve predictability. Depressed forms include convolute, open-coiled, concavo-convex, and geniculate specimens, those gastropods with an open umbilicus, and some solitary coral calyces. Conical forms include conical, pyramidal, and beaked specimens, those with a flat bottom, those with markedly projecting ornament in a single axis, and those, such as prone trilobites, that can be described as half ellipsoids because the volume of a cone is mathematically equivalent to half an ellipsoid. Globose forms include ellipsoidal, spheroidal, and evolute specimens and those in the shape of frustums. These group designations are labeled in Supplementary Data 1 and 2¹.

Validation Data Sets

After volumetric and linear measurements were made for all 102 specimens, 10 specimens were selected at random to represent a validation data set (Sokal and Rohlf, 1994). These specimens were set aside prior to analysis of the regression models to test the predictability of resulting models. In this test, the predicted volumetric value (\hat{y}) was determined by substituting the known value of the observed linear independent variable (x_i) into the optimal regression model. Standard error (s_y) and confidence intervals (CI) for each predicted volumetric value were made according to equations 1 and 2, respectively (Sokal and Rohlf, 1994, p. 471–472):

$$s_y = \sigma \sqrt{1 + \frac{1}{n} + \frac{(x_i - \bar{X})^2}{\sum x^2}} \quad (1)$$

$$CI = \hat{y} \pm t_{a/2} s_y \quad (2)$$

where σ is the residual standard error of the regression model, n is the number of specimens in the regression model, \bar{X} is the mean independent variable value in the regression model, and $\sum x^2$ is the sum of squares for the independent variable in the regression model.

Because this study uses a wide range of taxa, shapes, and sizes, it is possible that the optimal model offers little predictability in practice, due to the fact that standard error depends on the range of values in the dependent variable (which here covers five orders of magnitude) and

because the log-scale can conceal appreciable linear differences. To assess the actual predictability of the model, the percent prediction error (%PE, equation 3) was used (Smith, 1984, p. R155):

$$\%PE = \frac{(y_i - \hat{y})}{\hat{y}} \times 100\% \quad (3)$$

where y_i is the observed volumetric value and \hat{y} is the predicted value, with both values converted to linear scale. Good models will have percent prediction errors close to 0%. Determination of acceptable error, in practice, depends on the question being asked and the precision required to answer it.

RESULTS AND DISCUSSION

Measurement Error

Measurement error in both volume and length was assessed for 10 specimens at random. Volume was more variable, with 1.8%–11.9% error (mean = 5.6%) on repeated measurement of the same specimen. Larger error occurred with specimens <1 ml in volume because the immersion method is constrained by individual drops of water (~0.05 ml); such errors are acceptable, however, because they are unbiased measurements and because of the vast size range among specimens. Caliper measurements were more precise, with 0.04%–2.3% error (mean = 1.1%). To compare this mean error with that obtained using volume, the error must be propagated as a three-dimensional measure; this converted error, 3.3%, is about half the 5.6% mean error observed for volume. Using a caliper is clearly preferable to immersion and has the advantages of efficiency and ease of measurement in the field. This lesser error also supports the choice of volume as the dependent variable for these regression analyses.

Linear Regression Models

The results of regression analyses for 16 combinations of linear measures, with volume as the dependent variable, are listed in Table 2. In Tables 2–5, the intercept is reported in the log-linear form; the proportionality coefficient is the antilogarithm of this intercept. Among single measures, maximum length (max) and anteroposterior length (A) are the best predictors, which is expected because these lengths best capture the overall extent of body size, especially for bilaterians. Products

TABLE 2—Linear regression models for various combinations of measures. Models discussed in text are highlighted in bold. Here and in Tables 3–5, the intercept is reported in the log-linear form. Models refer to the maximum length (max) in any orientation, anteroposterior length (A), transverse width (T), and dorsoventral depth (D). The dependent variable in models with multiple variables (i.e., ATD) is the product of measures; those with a plus sign (i.e., A+T+D) are multiple regression models with multiple, independent variables. Model selection was based on minimizing residual standard error. Standard error in parentheses. Multiple regression has a slope parameter for each independent variable.

Model	Residual standard error	r ²	Intercept	Univariate		Multivariate	
				Slope	Slope (A)	Slope (T)	Slope (D)
max	0.342	0.853	−0.632 (±0.057)	2.326 (±0.102)			
A	0.442	0.754	−0.357 (±0.064)	2.038 (±0.123)			
T	0.490	0.697	−0.090 (±0.061)	2.194 (±0.153)			
D	0.505	0.678	0.114 (±0.056)	1.867 (±0.136)			
AT	0.286	0.897	−0.372 (±0.040)	1.305 (±0.047)			
AD	0.325	0.867	−0.217 (±0.042)	1.183 (±0.049)			
TD	0.348	0.848	−0.065 (±0.041)	1.245 (±0.056)			
ATD	0.216	0.941	−0.265 (±0.028)	0.896 (±0.024)			
Euclidean AT	0.307	0.881	−0.841 (±0.057)	2.469 (±0.096)			
Euclidean AD	0.319	0.872	−0.727 (±0.056)	2.357 (±0.095)			
Euclidean TD	0.357	0.839	−0.574 (±0.058)	2.522 (±0.116)			
Euclidean ATD	0.260	0.915	−1.034 (±0.053)	2.548 (±0.082)			
multiple A+T	0.287	0.897	−0.376 (±0.041)		1.338 (±0.101)	1.267 (±0.114)	
multiple A+D	0.322	0.871	−0.255 (±0.046)		1.354 (±0.118)		1.019 (±0.114)
multiple T+D	0.347	0.850	−0.078 (±0.043)			1.385 (±0.137)	1.128 (±0.119)
multiple A+T+D	0.210	0.946	−0.302 (±0.031)		1.025 (±0.082)	0.981 (±0.089)	0.701 (±0.080)

of these lengths are better predictors because they capture additional information on overall body size. Capturing all three dimensions, the volumetric product, ATD (Fig. 1), is the best predictor, with a residual standard error of 0.216; this simple model accounts for >90% of the variation in the data ($r^2 = 0.941$). Each of these product models can be converted to a model for the corresponding geometric mean by multiplying the slope (and associated standard error) by the number of lengths; in other words, the slope for the geometric mean of the AT, AD, and TD models is twice that for its product, while the slope for the geometric mean of the ATD model is three times that for its product. The Euclidean models are similar but slightly less powerful than these product models.

The smallest residual standard error, 0.210, is found in the multiple regression model, in which the three measures are treated independently. This model, however, offers only minimal improvement over the simpler ATD model. Another reason for preferring the ATD model is that it is the only supported model that accommodates errors in specimen orientation. In other words, it does not matter whether the dorsoventral depth is confused with the transverse width in practice as long as each corresponds to one of the fundamental biological axes.

Equation 4 (Table 2; Fig. 1) is recommended as a general allometric model for predicting Paleozoic, shelly invertebrate body volume:

$$\text{volume} = 0.544(\text{ATD})^{0.896} \quad (4)$$

Re-written in its linear form (equation 5):

$$\log(\text{volume}) = 0.896 \log(\text{ATD}) - 0.265 \quad (5)$$

Note that A, T, and D are measured in centimeter units such that the product (in cm³) can be converted directly into milliliters. A slope of <1.0 (95% confidence interval; 0.850–0.942) might be expected because the ATD model is a maximum estimate of volume; all specimens of a particular ATD product value must have a true volume less than or equal to this product. A consequence of this slope value is that the three-dimensional shape of large organisms, measured as ATD, must have a different shape than small organisms. Because of the increasing offset from a slope of unity, larger organisms must take up proportionally less ATD volume compared to small ones, which should increasingly approximate ATD at the smallest sizes. This shape allometry can be verified by comparing the trend in Figure 1 to isometric relationships for known shapes. To demonstrate this, consider the equations for the volume of an ellipsoid (equation 6) and cone (equation 7), shapes approximated by invertebrates, where the radius, r, has been rewritten in terms of the appropriate body axis measures A, T, and D:

$$V_{\text{ellipsoid}} = \frac{4}{3}\pi \left(\frac{A}{2} \frac{T}{2} \frac{D}{2} \right) = \frac{\pi}{6}(\text{ATD}) \quad (6)$$

$$V_{\text{cone}} = \frac{1}{3}\pi \left(A \frac{T}{2} \frac{D}{2} \right) = \frac{\pi}{12}(\text{ATD}) \quad (7)$$

It is important to note that because all geometric models are isometric, their exponent will equal unity; different geometric models differ solely in their proportionality coefficient. When these models are superimposed

TABLE 3—Linear regression models for various large taxonomic groups using the ATD product as independent variable. n = number of specimens used in regression; in the case of the monoplacophorans, small sample size prevented meaningful analysis. Bold = models that were better than the ATD model, based on smaller residual standard error. Standard error in parentheses. ATD = product of anteroposterior length (A), transverse width (T), and dorsoventral depth (D). NA = standard error is meaningless in this instance.

Taxonomic group	n	Residual standard error		Intercept	Slope
Anthozoa	10		0.314	−0.395 (±0.139)	0.943 (±0.084)
Bivalvia	19		0.141	−0.229 (±0.045)	0.788 (±0.041)
Brachiopoda	17		0.243	−0.143 (±0.067)	0.785 (±0.059)
Cephalopoda	15		0.119	−0.293 (±0.043)	1.024 (±0.029)
Gastropoda	15		0.159	−0.374 (±0.050)	0.955 (±0.046)
Monoplacophora	2		NA	−3.811	8.997
Trilobita	14		0.161	−0.196 (±0.050)	0.864 (±0.0627)

TABLE 4—Linear regression models for various taxonomic subgroups using the ATD product as independent variable. n = number of specimens used in regression; in some cases, small sample size prevented meaningful analyses. Nautiloidea includes several subclasses that have been placed within this single subclass at one time (Moore, 1964). Bold = models that were better than the ATD model, based on smaller residual standard error. Standard error in parentheses. ATD = product of anteroposterior length (A), transverse width (T), and dorsoventral depth (D). NA = standard error is meaningless in this instance.

Taxonomic group	n	Residual standard error	Intercept	Slope
Ammonoidea	3	0.182	−0.270 (±0.148)	0.964 (±0.092)
Anisostrophic gastropods	11	0.174	−0.432 (±0.075)	1.001 (±0.061)
Articulata	15	0.194	−0.086 (±0.058)	0.766 (±0.049)
Bellerophontida	4	0.050	−0.326 (±0.025)	0.851 (±0.036)
Bivalvia	19	0.141	−0.229 (±0.045)	0.788 (±0.041)
Enrolled Trilobita	8	0.132	−0.119 (±0.059)	0.729 (±0.070)
Inarticulata	2	NA	−0.535	0.045
Monoplacophora	2	NA	−3.810	8.997
Nautiloids	12	0.111	−0.302 (±0.044)	1.045 (±0.031)
Prone Trilobita	6	0.125	−0.245 (±0.054)	1.035 (±0.076)
Rugosa	5	0.485	−0.332 (±0.296)	0.871 (±0.196)
Tabulata	5	0.093	−0.455 (±0.060)	0.998 (±0.034)

on the ATD model (Fig. 2), it is apparent that the equation for an ellipsoid (proportionality coefficient = $\pi/6$) approximates that found for small specimens (<~25 ml), while the equation for a cone (or half ellipsoid; proportionality coefficient = $\pi/12$) approximates that found for larger specimens (see discussion of morphological models below). This could be a sampling artifact of the specimens chosen in the study; the five largest specimens—including several cephalopods (*Cyrtoceras* and *Manticoceras*), a high-spined gastropod (?*Hormotoma*), and massive, colonial corals (*Favosites* and *Cystiphyllum*)—could be described as cones, while the smallest specimens—including brachiopods (*Dicoelosia* and *Zygospira*), mollusks (*Deceptrix* and *Phragmolites*), and an enrolled trilobite (*Greenops*)—could be described as globose. Such a bias is unlikely here because the sampling within each taxonomic group was chosen to span the same range of sizes. Large specimens in this study are not generally biased toward individual taxonomic groups (see discussion of Fig. 3 below).

This shape allometry furthermore has been predicted generally (McMahon, 1973; Wainwright, 1988; Vogel, 1994, 2003) on the principle that larger, mobile organisms ought to be more streamlined than smaller ones. This principle seems to transcend taxonomic groups and locomotory abilities (cf. Niklas, 1994). Specifically, McMahon (1973) argues that animals larger than ~1 g (volume of 1 ml, assuming equal density to water) ought to approximate a stretched cylinder, a result predicted on theoretical considerations of body proportions, surface area, and elastic criteria for structurally sound organisms. The empirical results in Figure 2 compare quite favorably with these predictions and are consistent with results of an empirical survey of the mass of 753 unicellular and multicellular algal, plant, and animal species spanning 22 orders of magnitude (Niklas, 1994).

Several other regression models are worth considering for some uses. Although maximum length is a useful proxy for the absolute size of a specimen (Niklas, 1994), it is not the best model for predicting overall volume. Its residual standard error is nearly 160% greater than that of

the ATD model (Table 2). As a measure of overall length, however, it is a better estimator than anteroposterior length. This result is not surprising because maximum length, made in any orientation, always captures overall size better than a measure made in a single, standard orientation. Another model with some support is the product of A and T, which models organisms as a sheet and can distinguish many shapes. This product and a related measure, the geometric mean of A and T lengths, have been used frequently in body-size studies (Stanley, 1986; Jackson et al., 1996; Jablonski, 1997; Roy et al., 2000; Aberhan et al., 2006; Kosnik et al., 2006) and can be suitable when they are the only two measures available. For example, these two measures are the most commonly figured in taxonomic monographs, especially for bivalved invertebrates (e.g., bivalves, brachiopods, and ostracodes).

Taxonomic Models

If the ATD model is biased by the taxonomic identity of organisms used to develop it, then a different model for each taxonomic group may produce more accurate results. This possibility was considered for various taxonomic groups and subgroups (Tables 3, 4; Fig. 3) and the two preservation states of trilobites, enrolled and prone. Accuracy of the ATD model increases for most of these groups, sometimes substantially. The slope in most groups, however, is still similar to the broader ATD model—that is, it is slightly less than 1; variation is more widespread in the value of the proportionality coefficient. Such general correspondence across taxonomic groups in the slope but variation in the proportionality coefficient is consistent with the prediction of broadly similar shape allometry (McMahon, 1973; Wainwright, 1988; Niklas, 1994; Vogel, 1994, 2003). All taxonomic groups display nearly equal degrees of allometry, but different groups may have a different shape at a particular size. The exception seems to be enrolled trilobites, whose volume may be prone to error because of sediment or cavities held within the enrolled state. These allometric equations may prove useful when the focus of study is

TABLE 5—Linear regression models for various morphological groups using the ATD product as independent variable. n = number of specimens used in regression. Bold = models that were better than the ATD model, based on smaller residual standard error. Standard error in parentheses. See text for assignment to morphological groups; the final model combines globose and depressed forms. ATD = product of anteroposterior length (A), transverse width (T), and dorsoventral depth (D).

Morphological group	n	Residual standard error	Intercept	Slope
Conical	37	0.211	−0.379 (±0.047)	0.997 (±0.035)
Depressed	17	0.223	−0.230 (±0.059)	0.882 (±0.059)
Globose	38	0.176	−0.182 (±0.036)	0.786 (±0.035)
Depressed + Globose	55	0.192	−0.204 (±0.031)	0.818 (±0.029)

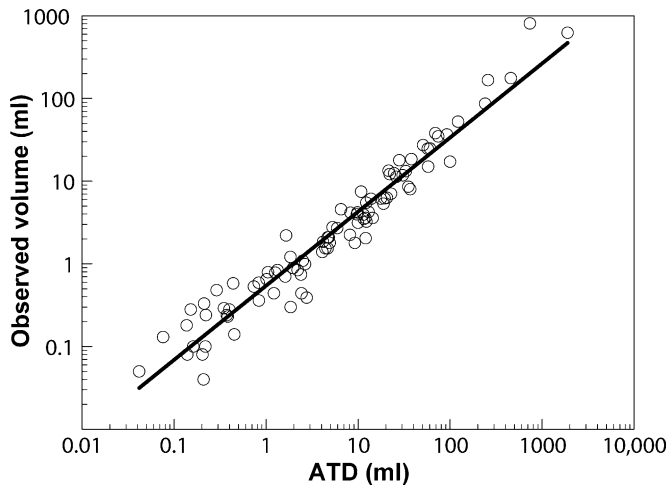


FIGURE 1—Regression of observed volume versus measured body size using the ATD model. The independent variable is the product of the anteroposterior length (A), transverse width (T), and dorsoventral depth (D).

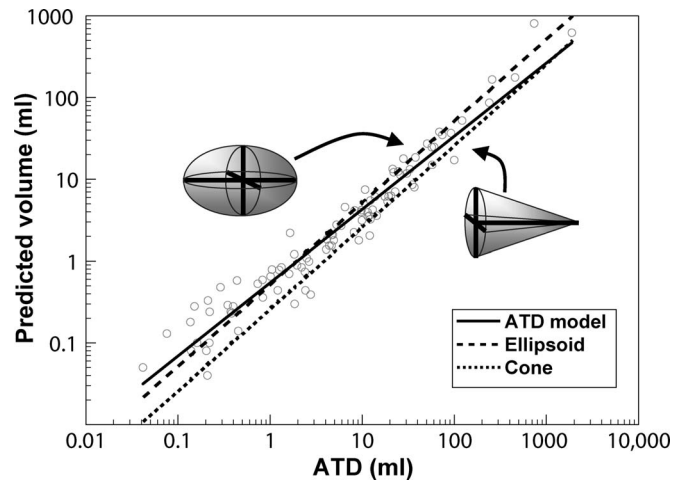


FIGURE 2—Comparison of the ATD model with ellipsoid and cone models, with specimen data from Figure 1 for comparison. Small specimens can be approximated by the equation for ellipsoids, and larger specimens by the equation for a cone. Dark lines = ATD measures. ATD = anteroposterior length (A), transverse width (T), and dorsoventral depth (D).

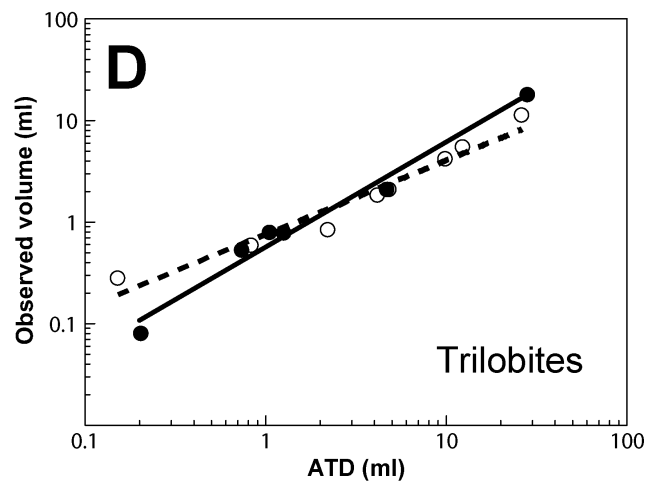
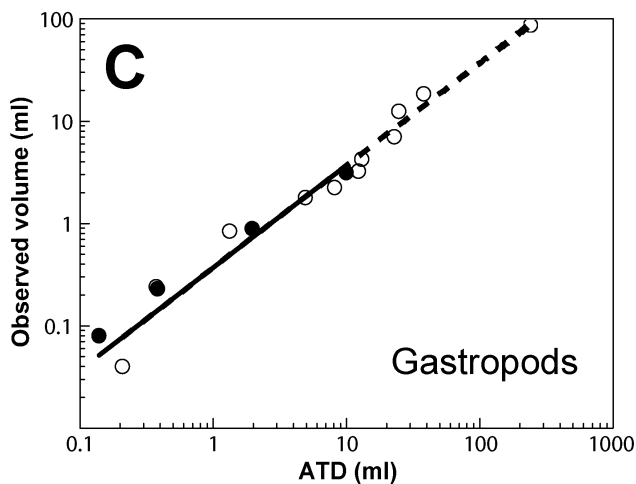
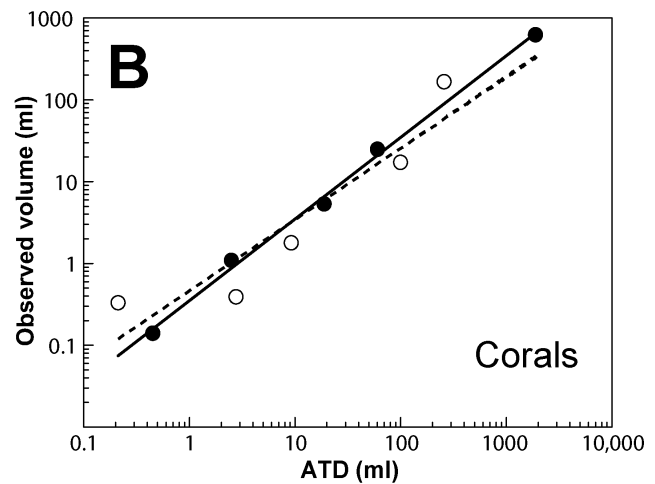
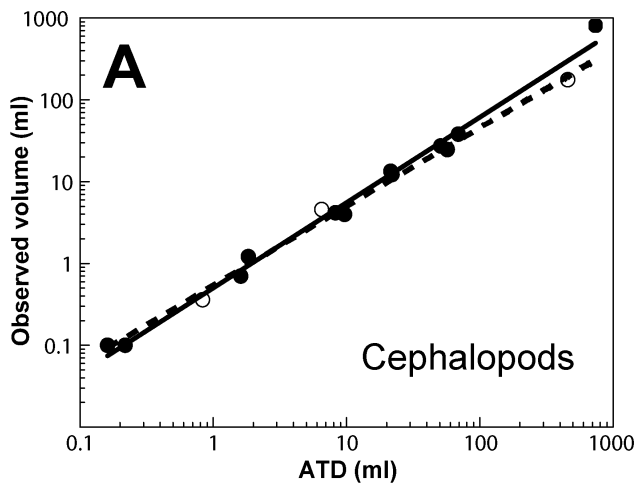


FIGURE 3—Regressions for representative subgroups of Paleozoic classes using the ATD product as independent variable. A) Ammonoid and nautiloid cephalopods. B) Rugose and tabulate corals. C) Anisotropic and bellerophonitid gastropods. D) Enrolled and prone trilobites. Empty circles and dotted, best-fit lines represent the first subgroup of each pair. ATD = anteroposterior length (A), transverse width (T), and dorsoventral depth (D).

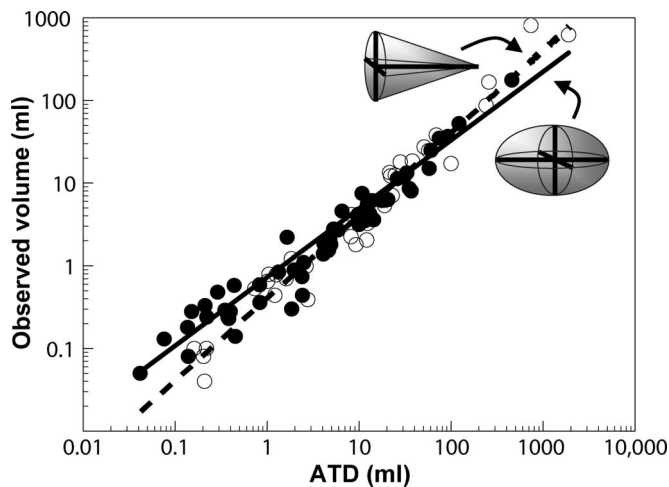


FIGURE 4—Regressions of Paleozoic invertebrates as two simple shapes using the ATD product as independent variable. Empty circles and dotted, best-fit line represent conical morphologies; closed circles and continuous, best-fit line represent globose (including depressed) morphologies. Dark lines in illustrated shapes = ATD measures. ATD = anteroposterior length (A), transverse width (T), and dorsoventral depth (D).

a single taxonomic group, but because sampling is generally sparser at this scale, the models should be validated using larger sample sizes. The ATD model is still recommended when the focus is on Paleozoic and, possibly, post-Paleozoic (see below), invertebrate assemblages.

Morphological Models

The final group of models viewed organisms polyphyletically in terms of their general morphological shape determined *a priori*, whether globose, conical (or half ellipsoid), or depressed (i.e., having some marked concavity). Such geometric-model approximations have also been used frequently in paleontology (e.g., Powell and Stanton, 1985; Dommergues et al. 2002; Payne, 2005). All of the models (Table 5) except the depressed form offer improvements over the ATD model, but the improvement is less than when considering taxonomy. The final model combines the globose and depressed groups; the relationship using conical and globose (including depressed) morphologies is shown in Figure 4. As discussed earlier (equations 6–7), the relationship for globose shapes has a larger proportionality coefficient than does the relationship for conical shapes. The use of these models requires some arbitrariness in the designation of shapes, however, and the ATD model remains a better general model. The ATD model is also preferable because isometric models are not consistent with general shape allometries known to exist in nature (McMahon, 1973; Wainwright, 1988; Niklas, 1994). In other words, all isometric models likely underestimate the volume of small taxa while overestimating the volume of large ones.

Validation Data Sets

Ten validation specimens of known volumes, which had been excluded from model development, were used to test the accuracy of these models (see Supplementary Data 2¹). The ATD (Fig. 5A), taxonomy-based (Fig. 5B), and morphology-based models (Fig. 5C) succeeded at predicting the body volume of these validation specimens. Error bars for the ATD model (Fig. 5A) were calculated from equations 1 and 2 using the statistics in Tables 2 and 6; summary statistics (sample size, mean, and sum of squares) for other models are not presented but can be calculated using Supplementary Data 1¹. In all cases, the observed and expected values are close to the 1:1 line, which designates a perfect prediction, and well within the 95% confidence intervals predicted for each specimen. Error bars in Figure 5B are rather large for some specimens owing to small

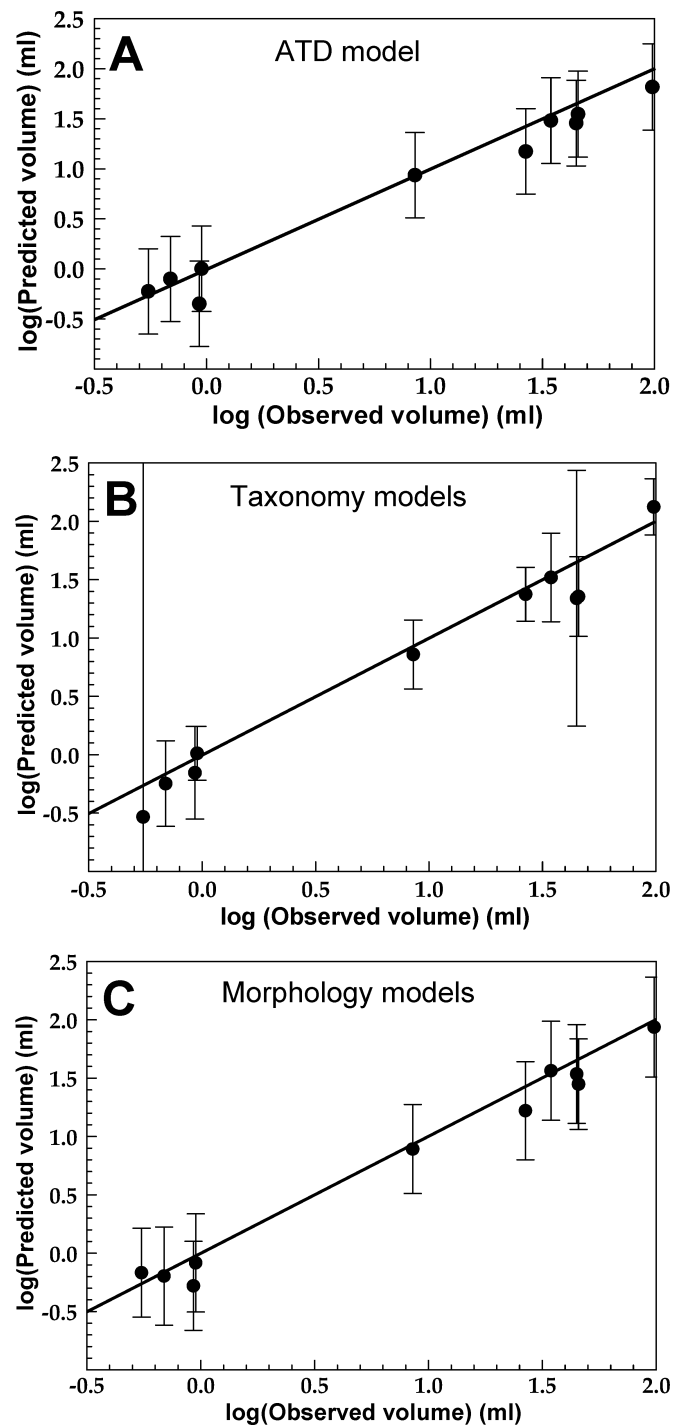


FIGURE 5—Validation tests of the models for 10 random specimens. Error bars = 95% confidence intervals based on: A) ATD model, B) taxonomic subgroup models, and C) morphological models. Straight line designates where specimens would fall if the volumes were predicted exactly. ATD = anteroposterior length (A), transverse width (T), and dorsoventral depth (D).

sample sizes of the taxonomic subgroup models; even in this case, however, the observed and average predicted body volumes are concordant. Overall, the general ATD model still predicts volume nearly as well as, or better than, the other, more complicated models.

Because confidence intervals are plotted on a logarithmic axis, it is possible that the accuracy of these estimates is still inadequate in practice. Table 7 lists the observed and predicted volumes using the ATD model in linear scale, as well as the percent prediction error (equation 3). Av-

TABLE 6—Statistics for ATD model used to calculate standard error and confidence intervals for validation data set. All calculations were made using the log-transformed data and equation 2. See text for details. ATD = product of anteroposterior length (A), transverse width (T), and dorsoventral depth (D).

Statistic	Value
Residual standard error (σ)	0.216
Number of specimens (n)	92
log (\bar{X})	.724
log (ΣX^2)	83.666
Slope	0.896
Intercept	-0.265

erage error (using absolute values to focus on the magnitude and not the direction of the error) is 36%, and all estimates but one are within a factor of two of the observed volume. Given the broad taxonomic and size coverage of the sampling and the convenience of a single allometric equation, such errors are reasonable, especially for large-scale applications (e.g., macroecology and macroevolution) involving diverse shelly taxa spanning a wide range of sizes.

BROADER APPLICATIONS OF THE ATD MODEL

This study rests on the assumption that fossil body volume is an important biological variable, one potentially as important as body mass. There are several reasons to question this assumption. In particular, it is hard to equate body volume (including skeleton and internal cavity) of a meaty clam, the corallum of a colonial coral, and the primarily hollow cavity of cephalopod conchs and brachiopod shells physiologically. Potentially more important variables than volume might include proportional volume of soft tissues or considerations of productivity, growth, and assimilation. While such estimates are possible for fossils with living representatives (e.g., Powell and Stanton, 1985), such estimates are significantly more difficult to make for extinct lineages (but see Payne and Finnegan, 2006). Volume, at least, can serve as a starting point toward constraining several of these other factors in various lineages.

There are good reasons to think that these simple measures of fossil body volume have merit beyond the argument that they are the best size metric extinct taxa have to offer. Body volume is a valid measure, albeit indirect, of the energy allocated to construct and maintain a skeleton over the course of an organism's life. Powell and Stanton (1985), for example, demonstrated that shell volume, body cavity volume, and biomass (population-wide body mass) were directly related in living gastropods and bivalves. Although they estimated volume using a different method than the present one, their allometric equations might prove useful for estimating body mass, especially for mollusks. Henderson (1999) and Motani (2001) discuss similar estimations for vertebrates. Such conversion methods, even if approximate, might be possible for extinct taxa. It has been demonstrated that skeletal mass generally scales with total (skeletal plus visceral) body mass, regardless of taxonomy, mobility, habitat, or type of skeleton (e.g., Anderson et al., 1979; Prange et al., 1979) and that the slope is constant (~ 1.1) for mollusks, arachnids, terrestrial and marine mammals, birds, and even bird eggs. Given these relationships, it seems probable that a general correlation exists between total body volume and mass.

Body volume by itself is an important variable that directly reflects how organisms occupy space in a community. Larger-volume organisms may have a greater influence on species composition in a community because of increased surface area for epibionts (Sparks et al., 1980; Peters and Bork, 1998) or through postmortem taphonomic feedback (Kidwell and Jablonski, 1983). In this case, volume (and other measures of size) may have important bearing on species richness and evenness, especially in the manner defined by Hurlbert (1971), who interpreted these attributes as probabilities of individual physical encounters within an assemblage. Body volume may also be correlated with other important autecological

TABLE 7—Predictive ability of the ATD model against observed volume for the 10 validation specimens, in linear scale. Percent prediction error is calculated from equation 3. The values of percent prediction error reported here have been rounded from raw observed and predicted values. ATD = product of anteroposterior length (A), transverse width (T), and dorsoventral depth (D). NA = standard error is meaningless in this instance.

Species	Observed volume (ml)	Predicted volume (ml)	Percent prediction error
<i>Lingula</i> sp.	0.55	0.60	-7.72
<i>Onniella meeki</i>	0.93	0.45	107.53
<i>Sactoceras</i> sp.	0.95	1.00	-5.35
<i>Sactoceras fosteri</i>	98.00	65.59	49.41
<i>Dawsonoceras</i> sp.	26.65	14.91	78.80
<i>Streptelasma rusticum</i>	44.82	28.57	56.88
<i>Asaphus expansus</i>	8.54	8.64	-1.10
<i>Phacops rana</i>	45.60	35.14	29.76
<i>Subulites gigas</i>	34.50	30.29	13.88
<i>Lophospira</i> sp.	0.69	0.79	-13.19

characters, such as burrow shape and diameter, microhabitat, and prey size and capture rate (see Hansen et al., 1994; Novack-Gottshall, 2007).

Volume has other benefits for paleoecological studies. As a source of size data, shell volume may be a more appropriate measure of ecological dominance than abundance data (Ausich, 1984; Wiedman, 1984; Powell and Stanton, 1985; Staff et al., 1985; Li and Droser, 1997, 1999; Payne and Finnegan, 2006), at least for macroscopic specimens (Cummins et al., 1986; Kidwell and Bosence, 1991; Kidwell, 2002; Cooper et al., 2006). For example, a species of rare but massive bivalves may have a greater influence in the ecological economy of a benthic assemblage than does a species of ubiquitous but tiny brachiopods. Such questions can only be addressed when combining abundance data with size data.

Can this model be applied to other organisms and other time periods? There seems to be no barrier to application to Mesozoic brachiopods, mollusks, and other morphologically and taxonomically similar animals. If the ATD model reflects basic allometric relationships of benthic animals in general, it might be reasonable to apply it to other animals from other time periods. Future analyses can certainly test this claim.

Additional caution may be needed when applying the ATD model to significantly larger or smaller animals than those included here (e.g., ostracodes or foraminiferans) or those with different morphologies and anatomical structure (e.g., echinoderms). The model's predictions (Fig. 2) should be consistent, however, as ostracodes and foraminiferans are basically globose and pelmatozoans conical. The model of a cone may seem to break down for very long-stalked pelmatozoans (>1 m tall); a cone may overestimate volume because columns are typically much longer and thinner than calyces. Careful consideration of the allometric nature of the ATD model, however, shows that this apparent geometric failing supports the rule. The model suggests that an elliptical hyperboloid with a predicted proportionality coefficient of $\pi/24$ (cf. other shapes in Fig. 2) might offer a better geometric model for such pelmatozoans. Such consistency with basic allometric constraints on invertebrate biomechanics, if true, might allow broader use for other shelly invertebrates.

With the ATD model, body volume can be assessed easily in the field using calipers. Previous attempts to include body volume (Ausich, 1984; Weidman, 1984), although useful, have had only limited success because of the difficulties involved in sieving bulk samples, especially when the sediments are lithified or diagenetically altered. The measures used here can be made on incomplete specimens or matrix-embedded specimens. In cases where complete measurements are not possible, the less accurate models (Table 2) offer useful alternatives. Using ATD data, body volume can be incorporated into ongoing occurrence-based fossil compendia (e.g., Krebs et al., 1996; Alroy et al., 2001; Budd et al., 2002). Although it is often impossible to measure body size retroactively for some taxa represented in these databases (some data represent field measurements

only), recent analyses (Kosnik, 2002; Krause et al., 2003, 2007; Kosnik et al., 2006) of body-size data for Ordovician, Silurian, Cretaceous, and Neogene marine assemblages demonstrate that body size of type collection specimens is strongly correlated with specimens measured in field samples. Thus, a simple, accurate, and broadly applicable method for measuring body size of marine invertebrates has the benefit not only of expanding the ecological significance of field research, but also of allowing body size to be included in analyses of large-scale ecological and evolutionary patterns throughout the Phanerozoic (e.g., Novack-Gottshall, 2008).

CONCLUSIONS

Although body size is an important ecological trait, its use in paleontological studies has been restricted to comparisons of taxonomically and morphologically similar taxa, primarily because of the lack of a standardized and biologically meaningful size metric for extinct taxa that could serve as a reliable proxy for body mass. Broader comparisons, those encompassing entire marine biotas, would be tremendously useful for a variety of paleoecological and macroevolutionary questions. For example, Vermeij (1987, 1995, 1999), Bambach (1993, 1999; Bambach et al., 2002), and others (Van Valen, 1976; Martin, 1996; Payne and Finnegan, 2006) have predicted increases in both individual and assemblage-wide biomass (the population-level expression of body mass) through time. The difficulty of estimating fossil body mass has hindered validating such claims empirically. The current study presents an efficient and accurate method, using ATD measurements, to obtain body-size data for organisms that vary widely in taxonomic affinity, size, shape, and ecological habit and explicitly recommends body volume as a common currency for fossil size.

The ATD model is a simple allometric equation that estimates volume using the product of three major body axes—the anteroposterior length, transverse width, and dorsoventral depth. This model has the virtue of being somewhat insensitive to the orientation of an organism and is consistent with known shape allometries in diverse organisms. The model does as well as more complicated models restricted to individual taxonomic groups or to particular morphologies. Although restricted models might be warranted when particular groups are the focus of study, such taxon-specific models here are based on limited numbers of specimens, and additional effort should be undertaken to confirm these results. All three models successfully predicted the volume of validation specimens excluded from the regression models. The broad generality of the ATD model allows for an efficient way to include body size in a wide range of paleontological studies.

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