CONSTRAINTS ON THE ADULT-OFFSPRING SIZE RELATIONSHIP IN PROTISTS

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The relationship between adult and offspring size is an important aspect of reproductive strategy. Although this filial relationship has been extensively examined in plants and animals, we currently lack comparable data for protists, whose strategies may differ due to the distinct ecological and physiological constraints on single-celled organisms. Here, we report measurements of adult and offspring sizes in 3888 species and subspecies of foraminifera, a class of large marine protists. Foraminifera exhibit a wide range of reproductive strategies; species of similar adult size may have offspring whose sizes vary 100-fold. Yet, a robust pattern emerges. The minimum (5th percentile), median, and maximum (95th percentile) offspring sizes exhibit a consistent pattern of increase with adult size independent of environmental change and taxonomic variation over the past 400 million years. The consistency of this pattern may arise from evolutionary optimization of the offspring size-fecundity trade-off and/or from cell-biological constraints that limit the range of reproductive strategies available to single-celled organisms. When compared with plants and animals, foraminifera extend the evidence that offspring size covaries with adult size across an additional five orders of magnitude in organism size.

KEY WORDS: Foraminifera, fusulinid, offspring size, proloculus, protist, reproductive strategy.

Size affects physiology on both the cellular and organismal scales. The volumes of many organelles and the DNA content of eukaryotic cells are proportional to cell size (Gregory 2001; Chan and Marshall 2010; Turner et al. 2012). Similarly, organ size typically scales with overall body size in animals (Schmidt-Nielsen, 1975). Because organelle and organ sizes impact physiology, body size places constraints on available ecological niches and is therefore an important determinant of organism fitness (Peters 1983; Clarke et al. 1999; Savage et al. 2007).

The relationship of offspring size to adult size directly reflects reproductive strategy in response to physiological and ecological constraints (Charnov and Ernest 2006). By definition, the maximum possible size of any individual offspring is limited by the size of the parent (i.e., the adult form). When offspring size is plotted against adult size the range of possible offspring sizes is thus bounded by a right-triangular envelope (Fig. 1). The lower bound-

ary of the triangle reflects a putative minimum size below which the organism is not able to function. Organisms with r-selected strategies (smaller organism and offspring) will be located toward the lower part of the triangle, while organisms with K-selected strategies (larger adult and offspring) will be located in the upper right of the triangle.

Animals and plants exhibit a diversity of reproductive strategies, which are reflected in the relationship between adult and offspring size. Some taxa, such as teleost fish and plants, include species spanning a wide range of possible strategies and fill out most of the right-triangular envelope of reproductive strategies (Duarte and Alcaraz 1989; Moles et al. 2005; Grubb et al. 2005). However, adult and offspring sizes are more tightly correlated in mammals, birds, reptiles, amphibians, insects, and crustaceans, which rarely employ the large adult-small offspring strategy space in the lower right corner of the envelope (Blueweiss et al. 1978;
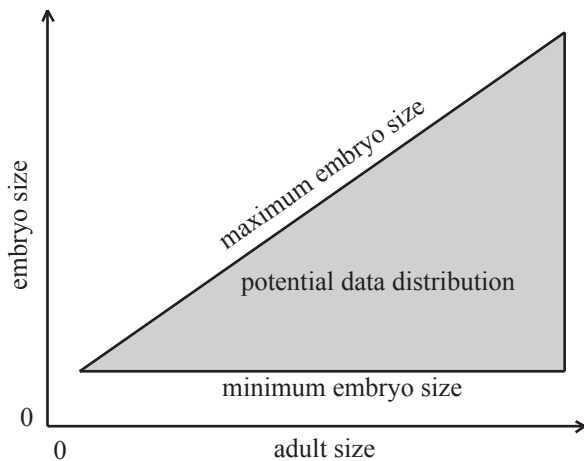
Figure 1. Potential data distribution. Viable embryos must be larger than some minimum size and smaller than the adults that produce them through multiple fission.

Kaplan and Salthe 1979; Kiorboe and Sabatini 1995; Berrigan 1991). In a metaanalysis, Hendriks and Mulder (2008) showed that the relationship between offspring and adult size varies substantially across clades of plants and animals: terrestrial homeotherms tend to employ K-selected strategies; aquatic heterotherms tend to employ r-selected strategies; and teleost fish and plants employ the full range of strategies.

Although the reproductive strategies employed by animals and plants are beginning to be delineated, the distribution of reproductive strategies in protists has not been systematically examined. Protist strategies are of particular interest because they may reflect distinct constraints associated with single-celled life.

Foraminifera, a diverse and abundant clade of marine protists, are an ideal study group with which to examine the relationship between adult and offspring size in single-celled organisms. Several major subclades of foraminifera produce mineralized shells (tests) that occur abundantly in marine sediments and as fossils. Embryo size in living and fossil foraminifera can be estimated from the diameter of the proloculus, the interior-most chamber of the test (Rottger and Kruger 1990). The final test size provides a measure of the size of the adult cell at the time of reproduction, which is co-incident with the death of the adult cell in semelparous organisms such as most foraminifera. In addition, the foraminiferan fossil record is exceptionally diverse (>40,000 species) and spans from the Cambrian (∼540 million years ago) to the present (Loeblich and Tappan 1982), presenting an unusual opportunity to determine if and how the offspring-adult size relationship has changed across geological time.

Despite the long-recognized potential to identify protist adult-offspring size relationships through the study of foraminifera, there has been little previous work to systematically document and interpret these patterns. Schenck (1944) compared proloculus and adult size in 48 species from multiple orders. However, likely due to the limited sample size and nonrandom sampling, the data do not show a strong relationship between proloculus and test size. Focused studies on individual species and small subclades have suggested a positive correlation between adult and offspring size. For example, proloculus size scales positively with adult size within the fusulinid species *Triticites cullomensis* (Koepnick and Kaesler 1974) and with chamber count in the family Miogypsinidae (Drooger 1963). However, most recent work on the adult-proloculus size relationship has instead focused on within-species variation of a population mean, which reflects the ratio of microspheric (diploid) to megalospheric (haploid) individuals and is a proxy for local environmental conditions (Nigam and Rao 1987; Seiglie 1975). To more systematically investigate the adult-offspring size relationship in protists, we report here our measurements and analysis of adult and offspring size for more than 3000 foraminiferan species.

Materials and Methods

We focused our study on fusulinid foraminifera (Order Fusulinida) due to their easily distinguished proloculus, large range of adult test sizes (maximum dimension <1 mm to >10 cm), and abundance and diversity in the fossil record. Fusulinids originated late in the Mississipian Epoch (∼325 Mya) and nearly all fusulinids perished in the mass extinction at the end of the Permian Period (∼252 Mya), with the last representatives of the order going extinct during the subsequent Triassic Period. Fusulinids evolved to some of the largest sizes ever observed for eukaryotic cells (Payne et al. 2009); some individuals exceeded 10 cm in maximum dimension (Stevens 1989). Each fusulinid secreted an intricate, multiple-chambered test with an easily distinguishable proloculus at the center.

We also measured a representative subset of species from the orders Miliolida and Rotaliida to determine whether or not the adult-offspring size relationship in fusulinids is likely to be representative of all foraminifera. Miliolids and rotaliids originated ∼300 Mya and ∼200 Mya, respectively, and each order contains more than 1000 living species. Like fusulinids, rotaliids, and miliolids are "larger foraminifera" (i.e., typically more than 1 mm in maximum dimension) with a trimorphic life cycle (BouDagher-Fadel 2008).

To examine the relationship between embryo and adult size in the foraminiferan orders Fusulinida, Rotaliida, and Milioliida, we assembled a dataset of proloculus size, overall test size (i.e., adult size), and geological age from illustrations and descriptions of type material in the Ellis and Messina catalog of foraminiferan species. We used the original catalog and all its updates through 2006 (Ellis and Messina 1940–2006).

Many larger foraminifera switch between haploid and diploid generations as part of a dimorphic or trimorphic life-cycle, with the haploid generations typically being more common than the diploid generations (Armstrong and Brasier 2004). The haploid individuals typically have larger proluculi and smaller adult tests than the diploid individuals and the haploid individuals are typically much more common in the geological record (Armstrong and Brasier 2004). Consequently, we restricted our analyses to megalospheric specimens because of the limited catalog data for microspheric specimens. Due to a lack of data, we were unable to analyze microspheric forms. Beyond showing relatively smaller proloculus size relative to adult size, we see no reason to expect that the general scaling relationship between proloculus size and test size to differ substantially for microspheric versus megalospheric forms.

Geological ages were assigned from the geochronological age given for the type material following the time scale of Ogg et al. (2008). Species were assigned to families using the higher taxonomic classification of Loeblich and Tappan (1989). All fusulinid species illustrated in the Ellis and Messina catalog were measured. Representative subsets of rotaliid and miliolid species were measured with a goal of capturing the entire range of adult sizes and geologic ages present within their respective orders. Rotaliid and miliolid specimens were also selected at the size ranges typical of fusulinids to permit thorough comparison of the adult-offspring size relationship between orders. We measured 2692 fusulinid species and subspecies representing 213 genera, 295 rotaliid species and subspecies representing 42 genera, and 44 milioliid species and subspecies representing 10 genera. All of the data analyzed in this study are archived at Dryad (doi:10.5061/dryad.6n385).

Because proloculi are typically close to spherical, we treated embryos as spheres whose diameters were the measured inside diameters of the proloculi (Fig. 2A). Adult size was calculated assuming that the full test was a three-dimensional ellipsoid (volume $= 4/3 \times \pi \times a \times b \times c$) where a, b, and c are the radii in the x, y, and z dimensions (Fig. 2B, C). Specimens without adult or proloculus size measurements were excluded from analysis. Because the proloculus is small even in magnified images, and we are estimating a species relationship from a single data point, we expect our measurement error to be approximately twofold. However, because proloculus size ranges over about eight orders of magnitude within each order, our measurement error is small relative to the overall distribution of proloculus sizes used in the analyses and will not affect any of our conclusions. Similarly, size variation within foraminiferan species is small relative to size variation among species (Rego et al. 2012) and so the uncertainty introduced by using a single specimen to approximate a species will be small at the scale of the present analysis, which includes species spanning eight orders of magnitude in biovolume. Impor-
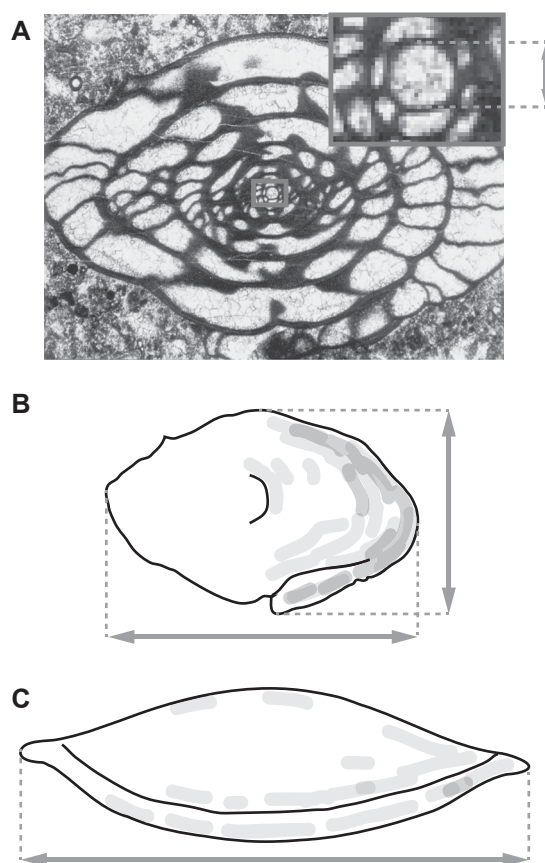

Figure 2. Measurement of proloculus and body size. A, the inside diameter of the proloculus is measured in cross section. The region around the proloculus is magnified for clarity (red rectangle). B, C, line drawings of a typical fusulinid adult test. B, measurement along the *x* and *y* axes of the adult test. A and B are oriented identically. C, measurement along the *z* axis of the adult test.

tantly, the proportional error in size measurements should not vary significantly with proloculus or test size because images of specimens are magnified to approximately the same size in the Ellis and Messina catalog. This fact eliminates any systematic trend in proportional measurement error with test and proloculus size that would otherwise lead to larger proportional error at smaller sizes. All statistical analysis was performed in R (version 2.15.0; R Development Core Team 2012) and some of the plots were produced with the "ggplot2" package (version 0.9.1; Wickham 2009). We chose standardized major axis regression ("lmodel2" package; version 1.7–1; Legendre 2013 and "smatr" package; version 2.0; Warton 2012) for its advantages over ordinary least squares regression in characterizing relationships within bivariate data.

Results

Figure 3 illustrates the relationship between offspring (i.e., proloculus) and adult size across species within each of foraminiferan
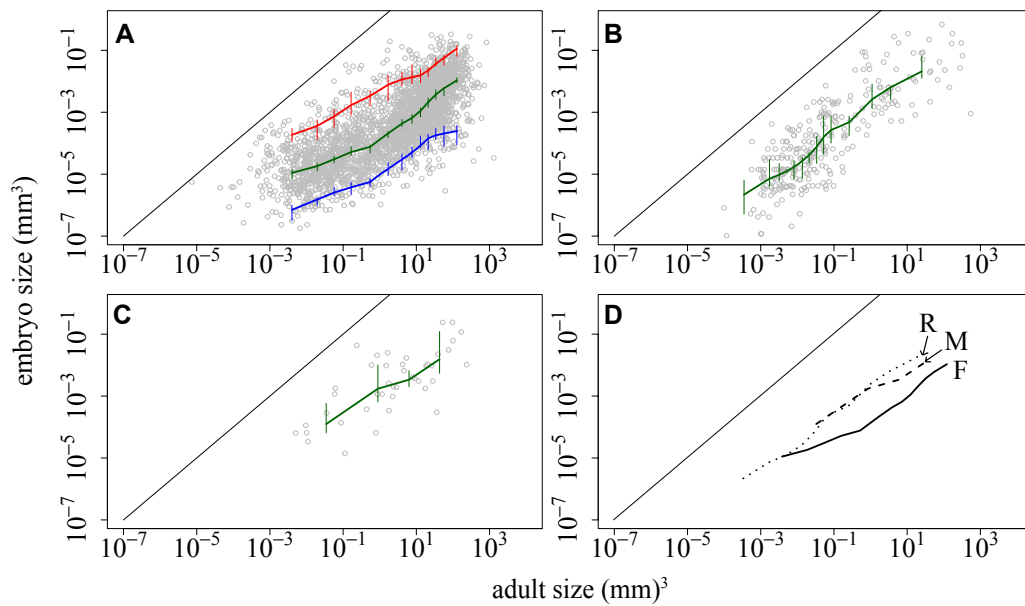
Figure 3. Embryo versus adult size in three foraminiferan orders indicates dependence of minimum embryo size on adult size. Gray points are measurements for single holotype specimens from the orders Fusulinida, Rotaliida, and Miliolida in A, B, and C, respectively. Colored dashed lines are smoothed through quantiles of binned data. Red line 95% quantile, green line 50% quantile, blue line 5% quantile. Vertical lines are 95% confidence intervals computed by bootstrapping within each bin. Black dashed lines indicate an upper bound with a scaling slope of one and a constant lower bound. D: superimposed medians (50% quantiles) for fusulinid (F), rotaliid (R), and miliolid (M) orders.

order. Despite vast differences in geological age and adult size, all three orders exhibit similar relationships between offspring and adult size. The relationship between adult and offspring size appears largely insensitive to changes in global environmental conditions over geologic time, as well as to differences among foraminiferan orders in the ecosystems they occupy and the ecological strategies they employ. Median offspring size in each order follows a similar trend relative to adult size (Fig. 3D).

As in most other taxa, the foraminiferan adult-offspring size relationship can be expressed as an allometric scaling relationship of the form $y = ax^b$ where y is offspring size, x is adult size, and a and b are scaling constants. In log space, allometric scaling becomes linear with the slope given by the scaling exponent b: $\log(y) = \log(a) + b*\log(x)$. For fusulinids, the best-fit scaling exponent (b) is 0.84 and the best-fit intercept ($\log(a)$) is −3.66 (Table 1). Fusulinids exhibit smaller offspring size than miliolids and rotaliids across most of the adult size range, suggesting a more r-selected reproductive strategy.

Fusulinids do not occupy the entire space of geometrically permissible reproductive strategies. Notably, the lower right hand corner of the triangle denoting potential strategies in Figure 1 is vacant. The smallest offspring of large species are two or more orders of magnitude larger than the smallest offspring of small species, which is comparable to the differences in adult sizes. The 5th percentile of embryo size in fusulinids and miliolids

increases with adult size in parallel with the median embryo size (Fig. 3).

To test whether differences in the adult-offspring size relationship arise from a systematic change across periods of geologic time or across families and genera, we examined a fusulinid dataset stratified by geologic time interval and family assignments. Figure 4A illustrates the embryo-adult size relationship from the origin of fusulinids in the Late Devonian through their decimation in the end-Permian mass extinction event. Standardized major axis regressions by epoch reveal only small variations in scaling slopes over geologic time (Tables 1 and 2). The size range of species within each geologic epoch overlaps most of the overall size range of species present in the fusulinid dataset, suggesting that embryo size scaling varied little, despite the dramatic global environmental change over the timescale of fusulinid existence (e.g., the transition from a greenhouse world to glaciation, and the variation in atmospheric oxygen from <20% to >30% of the atmosphere). A trend toward smaller intercepts in later intervals suggests fusulinids became slightly more r-selected over time (Fig. 4A). Relative to variation across time, variation in offspring-to-adult size scaling across families is in some cases large and statistically significant, with larger sized families exhibiting more diverse slopes (Fig. 4B; Tables 1 and 3). The family Neoschwagerinidae represents an exceptional case in which embryo size is inversely associated with adult size (Fig. 4B; Table 1).

Table 1. Summary of standardized major axis regressions calculated for each order, family, and epoch in log–log space. Slopes and intercepts are given with 95% confidence intervals.

| Taxon/epoch	N	Slope	Intercept	R^2
Fusulinida	3353	0.84 ± 0.02	-3.66 ± 0.01	0.58
Miloilida	84	0.83 ± 0.2	-2.84 ± 0.09	0.53
Rotaliida	451	1.10 ± 0.01	-2.60 ± 0.09	0.69
Archaediscidae	81	1.17 ± 0.2	-2.56 ± 0.5	0.04
Biseriamminidae	17	1.02 ± 0.4	-2.71 ± 0.6	0.10
Endothyridae	201	1.15 ± 0.1	-2.78 ± 0.2	0.27
Fusulinidae	667	1.00 ± 0.06	-3.81 ± 0.03	0.54
Neoschwagerinidae	73	-1.24 ± 0.3	-1.54 ± 0.4	0.0005
Ozawainellidae	115	0.98 ± 0.2	-3.71 ± 0.2	0.16
Schubertellidae	102	0.89 ± 0.1	-3.79 ± 0.1	0.23
Schwagerinidae	838	1.47 ± 0.1	-4.68 ± 0.1	0.30
Tournayellidae	8	0.80 ± 0.5	-3.31 ± 1.3	0.001
Verbeekinidae	6	3.32 ± 2.2	-6.91 ± 7.7	0.11
Late Devonian	18	1.20 ± 0.4	-1.66 ± 1.1	0.18
Mississipian	453	1.10 ± 0.08	-2.87 ± 0.1	0.25
Pennsylvanian	1025	0.88 ± 0.04	-3.84 ± 0.01	0.45
Early Permian	759	1.03 ± 0.05	-3.93 ± 0.1	0.46
Middle Permian	123	1.20 ± 0.2	-4.16 ± 0.2	0.38
Late Permian	116	0.82 ± 0.1	-3.52 ± 0.01	0.41
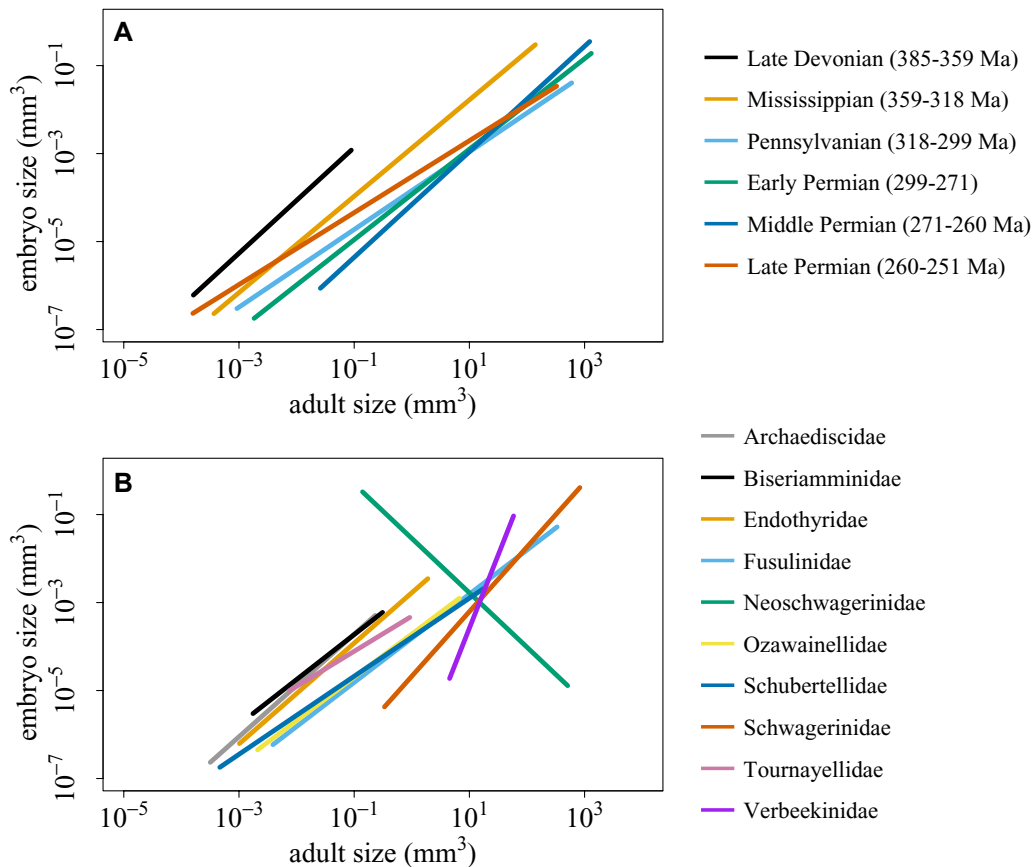
Figure 4. Allometric scaling of adult and embryo size within geologic epochs and fusulinid families. Slopes from standardized major axis regression within epochs (A) exhibit small but statistically significant differences while slopes within families (B) exhibit larger, statistically significant differences. Summary data for regression analyses are presented in Table 1 and pairwise comparisons of slopes in Tables 2 and 3.

Table 2. Results of pairwise comparison of slopes between geological epochs using the analysis of variance (AOV) test.

	L. Dev.	Miss.	Penn.	E. Perm.	M. Perm.	L. Perm.
L. Dev.	NA	*	*			
Miss.		NA	*	*		*
Penn.	*	*	NA	*	*	*
E. Perm.	*	*	**	NA	*	*
M. Perm.			*	*	NA	
L. Perm.		*	*	*		NA

L. Dev. = Late Devonian; Miss. = Mississippian; Penn. = Pennslyvanian; E. Perm. = Early Permian; M. Perm. = Middle Permian; L. Perm. = Late Permian.
*indicates *p*-value < 0.05.

In general, however, our results show that the pattern of correlation between offspring and adult test size is broadly consistent across both geological time and higher taxa.

Discussion

Our data illustrate a significant positive allometric scaling relationship between adult size and embryo size in three diverse orders of larger foraminifera, comparable to the relationship previously reported in animals. The large variation in embryo size scaling across families relative to that across geological epochs suggests that taxon-specific specialization may be the predominant evolutionary driver of fusulinid reproductive strategy. In contrast to the expectation that the allometric scaling slopes would vary systematically as a function of taxonomic level or geological time interval, we observe that scaling within families and epochs are nearly indistinguishable from those across all fusulinids. The constraints we observe are therefore likely to be acting universally on all fusulinids rather than being the result of evolutionary specialization within taxa or environmental and ecological differences across time periods. The consistency of our comprehensive results for fusulinids with representative data for miliolids and rotaliids suggest that the fusulinid pattern may be representative of foraminifera more broadly.

In addition to the positive allometric relationship between median size of adults and embryos, we note a coordinated increase of maximum and minimum offspring size with adult size leading to an approximately constant range of offspring sizes available for each specific adult size. One possible explanation for this constant range of offspring sizes is that physiological constraints specific to unicellular life limit the ratio between adult and embryo size. Fusulinid adults and embryos both consist of a single cell even though they may be a thousand-fold different in size. This biological constraint requires cellular organelles to operate over an extensive range of cell size to which there may be a limit. There may also be a limit on the range of cell sizes that can be optimally controlled by the genome. Consistent with this idea, genome size increases linearly with cell volume across all eukaryotic species suggesting an optimal cytoplasm-to-DNA ratio (Gregory et al. 2000; Cavalier-Smith 2005). Although the number of copies of the genome per cell can be controlled by endoreduplication, this process is often associated with terminal differentiation and may have limits as the number of examples where cells have >1000 copies of the genome are relatively rare (Nagl 1978). Alternatively, ecologically determined mass-specific mortality rates could vary over a certain range corresponding to the different types of environments occupied by fusulinids. The set of evolved offspring sizes would therefore fall within a certain range for any specific adult size. Thus, cell physiology or the variety of ecological conditions could limit the range of reproductive strategies adopted by foraminifera and other single-celled protists.

Table 3. Results of pairwise comparison of slopes between fusulinid families using the analysis of variance (AOV) test.

	Arch.	Biser.	Endo.	Fusul.	Neo.	Ozaw.	Schub.	Schwag.	Tour.	Ver.
Arch.	NA		*	*				*		
Biser.		NA								
Endo.	*		NA		*			*		
Fusul.	*			NA	*			*		
Neo.			*	*	NA	*	*	*		
Ozaw.						NA		*		
Schub.					*		NA	*		
Schwag.	*		*	*	*	*	*	NA		
Tour.									NA	
Ver.										NA

Arch. = Archaediscidae; Biser. = Biseriamminidae; Endo. = Endothyridae; Fusul. = Fusulinidae; Neo. = Neoschwagerinidae; Ozaw. = Ozawainellidae; Schub. = Schubertellidae; Schwag. = Schwagerinidae; Tour. = Tournayellidae; Ver. = Verbeekinidae.
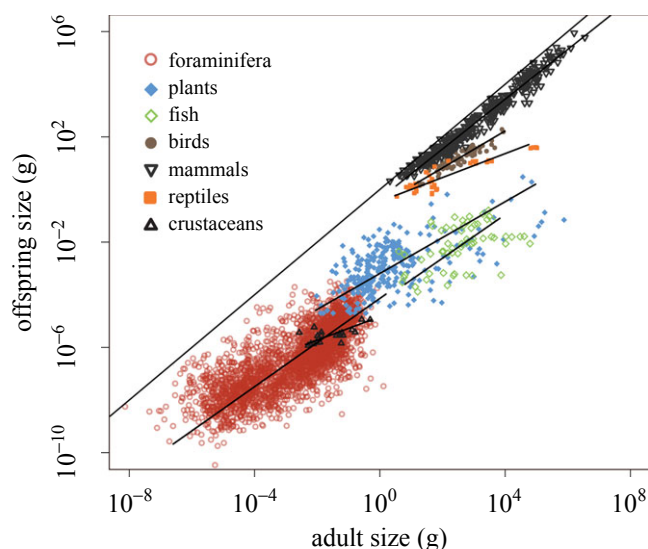*indicates *p*-value < 0.05.

Figure 5. **Comparison of adult-offspring size relationships in foraminifera, plants, fish, birds, and mammals with standardized major axis regression slopes. Plant and mammal data are used with permission from Falster et al. (2008). Fish and bird data were acquired from Blueweiss et al. (1978) using Data Thief software (Tummers 2006). Mammalian offspring mass is given as mass at weaning to account for the influence of adultal care. Bird offspring mass is mass at hatching. Fish offspring mass is approximated by multiplying the volume of the egg by the density of water. The mass of the proloculus is approximated analogously.**

Our data expand existing knowledge of adult-offspring size scaling relationships by more than five orders of magnitude in adult size. Importantly, we cross the gap between single-celled and multi-celled organisms to find a surprising degree of commonality in adult-offspring size trends. Figure 5 shows the adult-offspring size relationship and the standardized major axis regression slope in fusulinids alongside the relationships in plants, fish, crustaceans, birds, reptiles, and mammals. Across this enormous range of sizes, spanning 16 orders of magnitude in both adult and offspring size, several phenomena become clear. First, eukaryotes as a whole do not come close to filling the full right-triangular space of geometrically permissible adult-offspring size pairings. Instead, the range of offspring sizes at any given adult size is far smaller than the overall range of offspring sizes. Second, the allometric trend in the adult-offspring size relationship in foraminifera overlaps that of plants and is nearly continuous with those of plants and fish, suggesting unanticipated common constraints.

Foraminifera, like multicellular organisms, evolve optimal offspring sizes in response to ecological context (Smith and Fretwell 1974). Unlike many multicellular organisms, most foraminifera only reproduce once at the end of their lives. However, the evolution of foraminiferan offspring still involves the

fundamental biological trade-off between offspring size and number (Hallock 1985). In this trade-off, the number of surviving offspring must be maximized in the context of ecologically determined, size-dependent juvenile mortality (Hallock 1985; Kiflawi 2006; Falster 2008). The shape of the adult-offspring size relationship within species is also influenced by the scaling relationships of reproductive effort (Falster 2008) and growth rate (Kiflawi 2006) with adult size. Despite some universal constraints on life history evolution, it is therefore remarkable that the foraminiferan adult-offspring size relationship is partially continuous with the adult-offspring size relationships of multicellular taxa whose offspring receive little adult care.

Although the adult-offspring size trend is common to all eukaryotes, the amount of variability in offspring size for a particular adult size differs. The scatter of offspring size at a given adult size in foraminifera, plants, and fish spans about three orders of magnitude (Falster 2008). By comparison, all tetrapods (mammals, birds, and reptiles) are strongly K-selected as indicated by the tighter correlation and larger offspring for any given body size. This result agrees with a model for optimal offspring size (Falster 2008) that predicts more scatter among species about the general adult-offspring size relationship for taxa with high mortality rates during offspring settlement and unpredictable juvenile recruitment opportunities.

Despite substantial variation in offspring size at a given adult size, data from foraminifera clearly demonstrate that the trend of allometric scaling of offspring size with adult size within eukaryotes extends to single-celled organisms. Physiological constraints on single-celled development may produce a trend in foraminifera similar to the ecologically driven trends in multicellular organisms. Alternatively, basic ecological constraints on life history evolution may act similarly in foraminifera and multicellular organisms.

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