Two-phase increase in the maximum size of life over 3.5 billion years reflects biological innovation and environmental opportunity

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Edited by James W. Valentine, University of California, Berkeley, CA, and approved November 14, 2008 (received for review July 1, 2008)

The maximum size of organisms has increased enormously since the initial appearance of life >3.5 billion years ago (Gya), but the pattern and timing of this size increase is poorly known. Consequently, controls underlying the size spectrum of the global biota have been difficult to evaluate. Our period-level compilation of the largest known fossil organisms demonstrates that maximum size increased by 16 orders of magnitude since life first appeared in the fossil record. The great majority of the increase is accounted for by 2 discrete steps of approximately equal magnitude: the first in the middle of the Paleoproterozoic Era (≈1.9 Gya) and the second during the late Neoproterozoic and early Paleozoic eras (0.6–0.45 Gya). Each size step required a major innovation in organismal complexity—first the eukaryotic cell and later eukaryotic multicellularity. These size steps coincide with, or slightly postdate, increases in the concentration of atmospheric oxygen, suggesting latent evolutionary potential was realized soon after environmental limitations were removed.

body size | Cambrian | oxygen | Precambrian | trend

Despite widespread scientific and popular fascination with the largest and smallest organisms and numerous studies of body size evolution within individual taxonomic groups (1–9), the first-order pattern of body size evolution through the history of life has not been quantified rigorously. Because size influences (and may be limited by) a broad spectrum of physiological, ecological, and evolutionary processes (10–16), detailed documentation of size trends may shed light on the constraints and innovations that have shaped life's size spectrum over evolutionary time as well as the role of the body size spectrum in structuring global ecosystems. Bonner (17) presented a figure portraying a gradual, monotonic increase in the overall maximum size of living organisms over the past 3.5 billion years. The pattern appears consistent with a simple, continuous underlying process such as diffusion (18), but could also reflect a more complex process. Bonner, for example, proposed that lineages evolve toward larger sizes to exploit unoccupied ecological niches. For decades, Bonner's has been the only attempt to quantify body size evolution over the entire history of life on Earth, but the data he presented were not tied to particular fossil specimens and were plotted without consistent controls on taxonomic scale against a nonlinear timescale. Hence, we have lacked sufficient data on the tempo and mode of maximum size change to evaluate potential first-order biotic and abiotic controls on organism size through the history of life.

Here, we document the evolutionary history of body size on Earth, focusing on the upper limit to size. Use of maximum size allows us to assess constraints on the evolution of large body size and avoids the more substantial empirical difficulties in determining mean, median, or minimum size for all life or even for many individual taxa. For each era within the Archean Eon (4,000–2,500 Mya) and for each period within the Proterozoic (2,500–542 Mya) and Phanerozoic (542–0 Mya) eons, we obtained the sizes of the largest known fossil prokaryotes, single-celled eukaryotes, metazoans, and vascular plants by reviewing the published literature and contacting taxonomic experts. Sizes were converted to volume to facilitate comparisons across disparate taxonomic groups (see *Data and Methods*). The database is deposited in Data Dryad (www.datadryad.org) and can be accessed at http://hdl.handle.net/10255/dryad.222.

Results

The maximum body volume of organisms preserved in the fossil record has increased by ≈16 orders of magnitude over the last 3.5 billion years (Fig. 1). Increase in maximum size occurred episodically, with pronounced jumps of approximately 6 orders of magnitude in the mid-Paleoproterozoic (≈1.9 Gya) and during the Ediacaran through Ordovician (600–450 Mya). Thus, ≈75% of the overall increase in maximum body size over geological time took place during 2 geologically brief intervals that together comprise <20% of the total duration of life on Earth.

Paleoproterozoic size increase occurs as a single step in Fig. 1, reflecting the presence of *Grypania spiralis* in the Paleoproterozoic (Orosirian) Negaunee Iron Formation of Canada (19). The taxonomic affinities of these fossils are controversial: Their morphological regularity and size suggest they are the remains of eukaryotic organisms (19, 20), but they have also been interpreted as composite microbial filaments (21). Possible trace fossils of similar age and comparable size occur in the Stirling Quartzite of Australia and the Chorhat Sandstone of India, suggesting Orosirian size increase may not have been confined to *Grypania* (22, 23). Slightly younger specimens of similar sizes from the Changzhougou and Changlinggou formations of China

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Author contributions: J.L.P., A.G.B., J.H.B., S.F., M.K., R.A.K., S.K.L., C.R.M., D.W.M., P.M.N.-G., F.A.S., J.A.S., and S.C.W. designed research, performed research, analyzed data, and wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

Freely available online through the PNAS open access option.

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This article contains supporting information online at www.pnas.org/cgi/content/full/0806314106/DCSupplemental.

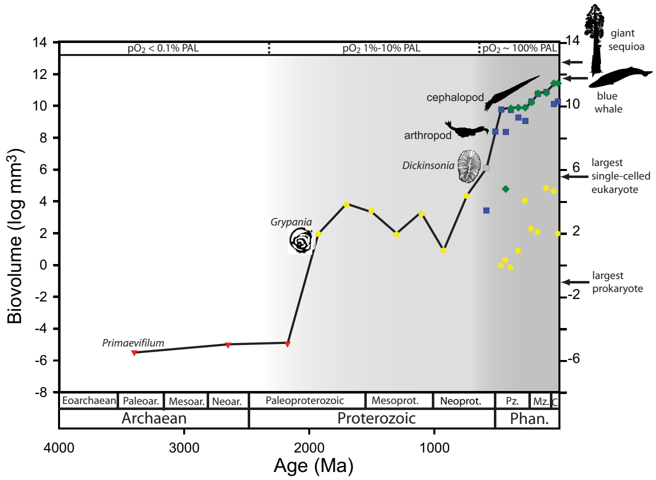

Fig. 1. Sizes of the largest fossils through Earth history. Size maxima are illustrated separately for single-celled eukaryotes, animals, and vascular plants for the Ediacaran and Phanerozoic. The solid line denotes the trend in the overall maximum for all of life. Increases in the overall maximum occurred in discrete steps approximately corresponding to increases in atmospheric oxygen levels in the mid-Paleoproterozoic and Ediacaran–Cambrian–early Ordovician. Sizes of the largest fossil prokaryotes were not compiled past 1.9 Gya. Estimates of oxygen levels from Canfield (38) and Holland (37) are expressed in percentage of PAL. Phan., Phanerozoic; Pz., Paleozoic; Mz., Mesozoic; C, Cenozoic. Red triangles, prokaryotes; yellow circles, protists; blue squares, animals; green diamonds, vascular plants; gray square, Vendobiont (probable multicellular eukaryote).

have also been interpreted as macroalgae, although some may be pseudofossils (24, 25). Specimens of *Grypania spiralis* in the ≈1.6 Gya Rohtas Formation of Vindhyan Supergroup in India exhibit clear annulations and represent the oldest uncontroversial eukaryotic macrofossils (26). Thereafter, maximum size remained approximately constant for >1 billion years (Fig. 1). If the Negaunee specimens are composite microbial filaments rather than eukaryotic (or prokaryotic) individuals, as suggested by Samuelsson and Butterfield (21), they would be excluded from our dataset because they would not be the remains of individual organisms. In this case, the size jump would shift forward in time to the first true eukaryotic macrofossil (the Vindhyan *Grypania* in the most extreme case), but the magnitude of the size jump and its association with the appearance of eukaryotic organisms would be essentially unchanged.

The second major increase in maximum size began with the appearance of the taxonomically problematic Vendobionts during the Ediacaran Period (635–542 Mya). These were followed in turn by larger Cambrian (542–488 Mya) anomalocariid arthropods and even larger Ordovician (488–443 Mya) nautiloid cephalopods. The largest Ordovician cephalopods were nearly 6 orders of magnitude larger than the largest pre-Ediacaran fossils.

The continuing diversification of terrestrial and marine life since the Ordovician has resulted in comparatively minor increase in the sizes of the largest species. The maximum size of animals has increased by only 1.5 orders of magnitude since the Ordovician; the giant sauropods of the Mesozoic and even the extant blue whale add comparatively little to the size range of animals (Fig. 1). The largest living individual organism, the giant sequoia, is only 3 orders of magnitude bigger than the largest Ordovician cephalopod and one and a half orders of magnitude bigger than the blue whale (Fig. 1).

Discussion

Several lines of evidence indicate that our record of maximum size accurately reflects both the fossil record and the actual history of maximum size at the taxonomic and temporal scales addressed. Larger fossils and larger fossil species tend to be remarked upon in the paleontological literature; genus and species names with roots meaning "large" or "giant" are commonly applied to particularly sizeable taxa, making them easy to identify in the literature. Because we treat size data on a logarithmic scale, even moderate sampling biases are unlikely to cause observed maxima to vary by >1 or 2 orders of magnitude. In contrast, species in the maximum size dataset span >16 orders of magnitude, and the sizes of all living organisms span >22 orders of magnitude (27). Although the upper bound error bars for the individual data points cannot be readily estimated, these errors are likely to be negligible given the size range addressed in our study. For example, it is unlikely that dinosaurs, whales, or cephalopods >10 times the size of the largest known specimens have ever existed. That the largest living plant and animal species are not much bigger than the largest known fossils (Fig. 1) suggests fossils reliably sample not only trends but also absolute values of maximum size at the temporal and taxonomic scales considered in this study. Trends in trace fossil sizes are generally concordant with the body fossil record (28), indicating that the apparent size increase from the Ediacaran through Ordovician does not merely reflect an increase in preservation potential of large animals. Moreover, large-bodied fossils occur in both well-fossilized clades (e.g., cephalopods) and taxa that are preserved only under exceptional circumstances (e.g., anomalocariids, Vendobionts).

The episodic pattern of size increase is not predicted under the simplest null model of diffusion away from a small starting size, which has commonly been invoked to account for the tendency of maximum size to increase through time within clades (18, 29, 30). If size evolves in a manner analogous to diffusion, size increase and decrease would be equally likely for any lineage in any time interval and, given constant diversity, the typical maximum size would be expected to increase with the square root of time elapsed. Based on the diffusive model alone, one would predict initially rapid increase in maximum size early in the history of life, followed by a gradual decrease in this rate. Any divergence from this pattern would suggest other causes at work. In particular, the observed episodes of dramatic increase suggest the origins of key evolutionary innovations, the removal of environmental constraints, pulses of diversification, or more likely, some combination of these. The relative stability in maximum size between these episodes of increase suggests the encountering of new environmental or biological upper bounds. The existence of such boundaries is also consistent with the observation that the historical maxima for numerous well-fossilized animal phyla and plant divisions differ by only 2 orders of magnitude (Fig. 2). Ongoing diversity increase and improved sampling likely contribute to the continuing, albeit slow, increase observed in the overall maximum size of plants and animals through the Phanerozoic.

Increases in organismal complexity, first the eukaryotic cell and later eukaryotic multicellularity, appear to have been prerequisites for increase in maximum size. The Paleoproterozoic jump in maximum size reflects the first appearance of eukaryotic body fossils rather than the evolution of larger prokaryotes. The apparent abruptness of the size increase from prokaryotic cells to *Grypania* may reflect, at least in part, the limited preservation and sampling of fossils of this age. However, even the largest known prokaryote—the extant giant sulfur bacterium *Thiomargarita namibiensis* (27)—does not approach the size of the oldest eukaryotic macrofossils, perhaps in part because simple diffusion of nutrients into or within the cell becomes inefficient at larger sizes (27). Moreover, *Thiomargarita* and other giant bacteria consist of thin films of cytoplasm surrounding a hollow interior; the metabolically active portion of their volume is relatively small (27). Similarly, the Ediacaran–Ordovician jump

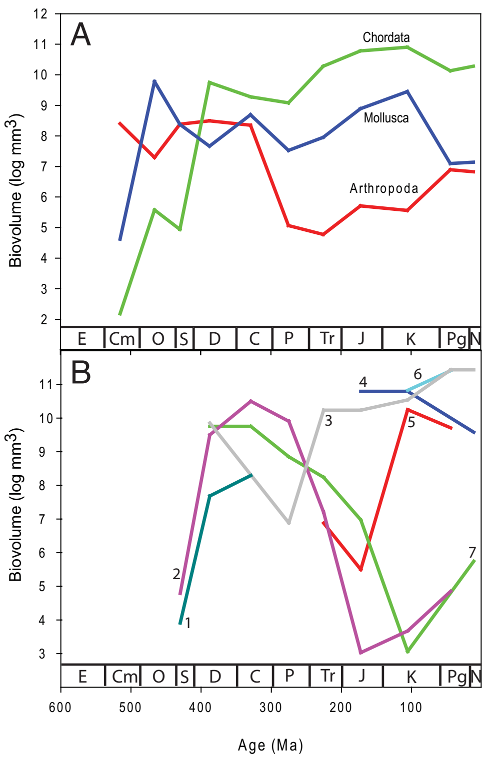

Fig. 2. Phanerozoic trends in size maxima for selected animal phyla and plant divisions. (*A*) Animal phyla. (*B*) Vascular plant divisions. Historical maxima differ by <2 orders of magnitude among phyla and divisions, although the timing of those historical maxima differs across clades. 1, Pteridophyta; 2, Lycopodiophyta; 3, Pinophyta; 4, Ginkgophyta; 5, Cycadophyta; 6, Magnoliophyta; 7, Equisetophyta; E, Ediacaran; Cm, Cambrian; O, Ordovician; S, Silurian; D, Devonian; C, Carboniferous; P, Permian; Tr, Triassic, J, Jurassic; K, Cretaceous; Pg, Paleogene; N, Neogene.

in maximum size occurred exclusively within multicellular eukaryotes. Notably, the largest multicellular eukaryotes during the Ediacaran and early Paleozoic were not chordates or vascular plants, demonstrating that the size increase was not simply tied to the structural or biomechanical properties of vertebrates or trees. Rather, these size increases occurred within higher taxa different from those that now contain the largest species. No fossil or living single-celled eukaryote approaches the size of the largest plants and animals (Fig. 1). This absence may reflect the metabolic inefficiency of having a large cell with a single nucleus and the inadequacy of diffusion as the primary transport process within such a large organism (17).

Delays between innovation and size increase suggest that increased organizational complexity alone was not sufficient to drive increase in maximum size. Steranes (organic molecular fossils) likely produced by stem-group eukaryotes have been reported to occur indigenously in rocks that predate the earliest macroscopic eukaryotic fossils by as much as 800 My (31, 32). However, the time gap between the oldest preserved steranes and the oldest eukaryotic body fossils could reflect the sparse nature of the Archean and early Proterozoic body fossil record or contamination of the Archean rocks by biomarkers from younger organic matter (33). Delay between the advent of eukaryotic multicellularity and subsequent size increase is more clearly defined. The oldest definitive fossil of a multicellular eukaryote—a red alga ≈1,200 Myr old (34)—predates the initial Ediacaran increase in maximum size by ≈600 Myr. If older specimens of *Grypania* or coeval producers of trace fossils were multicellular (22), then the delay may have been even longer.

Explicitly testing other hypothesized biological and environmental constraints on the evolution of maximum size is beyond the scope of our data, but we note that the 2 most rapid increases in maximum size correspond closely with the 2 primary episodes of increase in the concentration of atmospheric oxygen (35–40). That oxygen availability could potentially have limited maximum size is indicated by the correlation of maximum size with ambient oxygen concentrations in fossil and recent organisms (41–43). Increases in atmospheric oxygen concentrations have long been hypothesized as triggers for the Late Archean origin of the eukaryotic cell and the Cambrian radiation of animals (44–50). Increased oxygen concentrations have been also linked implicitly (45) and explicitly (46, 51) to associated size changes, but the magnitude of maximum size increase during these episodes and their importance relative to size changes during intervening times has not previously been assessed quantitatively.

Eukaryotes require oxygen for respiration, but the availability of oxygen may also have mediated the transitions to eukaryotic and multicellular organizations through other pathways, such as the action of oxygen on communication-related transmembrane proteins (52). Although the biosynthesis of sterols, which control fluidity of the cell membrane in eukaryotes, may have been possible even in the absence of oxygen (53, 54), aerobic metabolism does not occur at oxygen concentrations <1–2% of the present atmospheric level (PAL) (55). Even higher concentrations may be required to maintain nitrate levels in the oceans high enough for eukaryotic primary producers (which cannot fix nitrogen) to compete effectively with nitrogen-fixing cyanobacteria (47). The evolution of large animals with greater demand for oxygen probably required still higher oxygen concentrations, consistent with geochemical data suggesting oxygen was at least 10% PAL by the beginning of the Cambrian (37, 56). Vascular plants require similar ambient oxygen concentrations to respire effectively (57). The minimum oxygen requirements of the earliest animals are difficult to state exactly because they would have depended on the extent to which they acquired oxygen via diffusion versus through elaborated respiratory and circulatory systems (49, 51).

Conclusions

Although increase in maximum size over time can often be accounted for by simple diffusive models (18, 29, 30), a single diffusive model does not appear capable of explaining the evolution of life's overall maximum size. Approximately 3/4 of the 16-orders-of-magnitude increase in maximum size occurred in 2 discrete episodes. The first size jump required the evolution of the eukaryotic cell, and the second required eukaryotic multicellularity. The size increases appear to have occurred when ambient oxygen concentrations reached sufficient concentrations for clades to realize preexisting evolutionary potential, highlighting the long-term dependence of macroevolutionary pattern on both biological potential and environmental opportunity.

Data and Methods

Data on the sizes of fossil organisms were compiled from our own existing databases, extensive searches of the primary and secondary literature, and consultation with taxonomic experts. We attempted to represent the evolution of maximum size of all of life over all of geological time. We only included data on fossil prokaryotes for the Archaean and early Paleoproterozoic when they were the largest known living organisms. Data were restricted to organisms that can be considered individuals at the appropriate level of organizational hierarchy following McShea (58) to facilitate the greatest possible comparability; we did not include the sizes of colonies or more loosely integrated associations of individuals. Body volume, calculated by application of simple geometric models (e.g., ellipsoids and cones), was used as a standard measure of body size because it is both biologically meaningful and methodologically practical when comparing such morphologically and ecologically diverse taxa (59). Although such estimates only approximate actual body volume, associated errors are unlikely to bias results, considering the reported size trends span 16 orders of size magnitude. The observed data and the geometric approximations used to calculate volume for individual fossil specimens are included as Table S1.

Although our database contains only 93 recorded observations, the amount of implicit information recorded is much larger. For example, it is widely agreed that a specimen of *Parapuzosia seppenradensis* is the largest ammonite fossil ever collected (60), and thus, each of the thousands (if not millions) of ammonites ever seen in the field or collected for study must have been smaller than this specimen. By extension of this argument, the database places upper bounds on the sizes of many millions of fossil specimens collected over the past several centuries.

The full database analyzed in this study is deposited in Data Dryad (www.datadryad.org) at http://hdl.handle.net/10255/dryad.222.

ACKNOWLEDGMENTS. This study is a product of the working group on body size evolution (principal investigators: J.L.P., J.A.S., and M.K.) funded by the National Evolutionary Synthesis Center (NESCent), National Science Foundation Grant EF-0423641. We thank N. Butterfield, M, Carrano, W. DiMichele, L. Dong, R. Feldmann, P. Gensel, J. Huntley, P. Janvier, A. Logan, S. Low, S. Lucas, R. Lupia, W. Manger, K. Niklas, W. Ou, S. Porter, C. Schweitzer, H. Steur, R. Taggert, B. Tiffney, S. Truebe, S. Wing, and S. Xiao for advice and assistance in data compilation; J. Denton and especially S. Porter for comments on previous drafts of the manuscript; and G. Hunt and 2 anonymous reviewers for constructive and thoughtful suggestions.

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