Body Size Evolution Across the Geozoic

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Keywords

Abstract

The Geozoic encompasses the 3.6 Ga interval in Earth history when life has existed. Over this time, life has diversified from exclusively tiny, single-celled organisms to include large, complex multicellular forms. Just how and why this diversification occurred has been a major area of interest for paleontologists and evolutionary biologists for centuries. Here, we compile data on organism size throughout the Geozoic fossil record for the three domains of life. We describe canonical trends in the evolution of body size, synthesize current understanding of the patterns and causal mechanisms at various hierarchical scales, and discuss the biological and geological consequences of variation in organismal size.

1. INTRODUCTION

The Geozoic, the ~3.6 Ga period of Earth history when the planet has supported life, began with the origin of living things and has subsequently been characterized by an enormous diversification of body form, complexity, and function. While the earliest organisms were small, single-celled prokaryotes, life on Earth today spans approximately 23 orders of magnitude in size (Payne et al. 2009, Smith & Lyons 2013), from bacteria at 0.2 μm (10^{-11} mm^3) to the giant sequoia tree at >115 m (10^{12} mm^3) (**Table 1**). Moreover, life inhabits all mediums—aquatic, terrestrial, and air—in a bewildering array of habitats from deep-sea thermal vents to the upper atmosphere. Scientists have long been intrigued by this incredible diversity in lifestyles, shapes, and sizes of organisms (Aristotle 347–334 BC [1984]; Galileo 1638; Haldane 1928; Thompson 1942; Simpson 1953; Bonner 1988, 2006; Payne et al. 2009). Accordingly, considerable research within biology and paleontology has been focused on how and why organisms evolve certain body masses, on the constraints imposed by the medium in which they live, and on characterizing the biotic and abiotic consequences and trade-offs of various lifestyles and sizes (McMahon 1973; Alexander 1982; Peters 1983; Calder 1984; Schmidt-Nielsen 1984; Downhower & Blumer 1988; Charnov 1993; McShea 1994; Brown 1995; Jablonski 1997; Alroy 1998; Smith et al. 2004, 2010a; Bonner 2006; Payne et al. 2009; Smith & Lyons 2011, 2013; Evans et al. 2012; Saarinen et al. 2014).

The size of an organism is not only readily measurable (see the sidebar Measuring Size), but it is undeniably also one of its most basic properties. Many fundamental mechanical, geometric, and physical principles constrain how the structure and function of organisms vary with body mass at various temporal and spatial scales (Thompson 1942, McMahon 1973, Alexander 1982, Peters 1983, Calder 1984, Schmidt-Nielsen 1984, Bonner 2006) (**Figure 1**). To begin with, size influences how organisms interact with their abiotic and biotic environment. This is particularly true for simple prokaryotic life, whose interactions with the physical environment are influenced

Table 1   Body size variation across domains of life

Domain	Kingdom	Smallest taxon			Largest taxon			Biovolume range[c]	References
		Name	Length	Biovolume (mm^3)[a]	Name	Length	Biovolume (mm^3)[a]		
Bacteria	—	*Mycoplasma genitalium*	200 nm	8×10^{-12}	*Epulopiscium fishelsoni*	0.7 mm	3.8×10^{-3}	8.7	Smith & Lyons 2013
Archaea	—	*Thermodiscus* sp.	200 nm	8×10^{-12}	*Staphylothermus marinus*	15 μm	3.4×10^{-6}	5.6	Schulz & Jørgensen 2001
Eukarya	Protista	*Chaetoceros* sp.	<9 μm	7.3×10^{-4}	Giant kelp (*Macrocystis pyrifera*)	45 m	4.5×10^{6}	9.8	Gomi et al. 2010, Steneck et al. 2002
	Fungi	*Rozella* sp.	30 μm	2.7×10^{-2}	*Fomitiporia ellipsoidea*	1,085 cm	4.1×10^{9}	11.2	Held 1981, Dai & Cui 2011
	Plantae	*Ostreococcus tauri*	0.97 μm	4.8×10^{-10}	Redwood (*Sequoia sempervirens*)	115 m	9×10^{12b}	22.3	Fry & White 1938, Courties et al. 1994
	Animalia	*Myxobolus* sp.	20 μm	8×10^{-6}	Blue whale (*Balaenoptera musculus*)	31 m	1.9×10^{11b}	16.4	Yokoyama et al. 2003, Smith & Lyons 2013

[a]Biovolume was calculated according to methods described in the sidebar Measuring Size.
[b]Biovolume was taken from Payne et al. (2009).
[c]Orders-of-magnitude difference in biovolume between smallest and largest taxon.

GLOSSARY OF TERMS

Allometric: From the Greek *allos*, meaning different, and *metron*, meaning measure. A scaling relationship that is nonlinear with body mass with a slope less than or greater than 1. The term was coined by Julian Huxley and Georges Teissier in 1936. Many traits scale as power functions of the form $Y = aM^b$, where M represents body mass; b, the scaling coefficient (or slope of the relationship in log-log form); and a, the taxon-specific normalization or proportionality constant (the intercept in log-log form when $M = 1$).

Bacteria: Diverse group of prokaryotic (having cells lacking a nucleus) organisms that are typically unicellular (microscopic), asexual in reproduction, and diverse in their biochemical processes. Divided into two domains: Bacteria, which include most well-known bacterial strains, and the relatively recently discovered Archaea (Archaebacteria), which include prokaryotes with rather unusual biochemical pathways, often enabling them to live in extreme environments.

Biogenic: Characterized by the existence of morphological structures consistent with living things and/or evidence of biochemical products.

Bioturbation: The disturbance of sediments by living organisms, especially plants (via roots) and animals (by creating burrows, digging, and other reworking activities). This process, first evident during the Cambrian Period, provides an important relationship between organismal ecology and evolution and nutrient, chemical, and geological cycles. The prevalence, depth, and intensity of bioturbation have increased across Phanerozoic time, along with the sizes of organisms.

Bergmann's rule: An ecogeographic pattern that, within a broadly distributed taxonomic genus, species of larger size are found in colder environments and smaller ones in warmer areas (Bergmann 1847); also found for populations within a species (Millien et al. 2006). Although originally formulated for vertebrates, it holds for many ectotherms and is broadly supported (>70% of investigated studies) among diverse endothermic taxa (Millien et al. 2006).

Biovolume: The body volume of an organism, measured directly or using geometric approximations. Mass is the primary way biologists measure the size of living organisms, but it is not typically possible or practical to measure mass directly with many organisms, including dead/extinct organisms, large trees, and microscopic cells. Biovolume provides a proxy for mass for such organisms, and its suitability has been validated in numerous studies (Payne et al. 2009).

Clade (monophyletic group): A genealogical group of organisms that includes an ancestor and all of its descendants. The clade is the basic unit of the phylogenetic field of cladistics and is used to hypothesize evolutionary relationships among groups of organisms (taxa).

Cope's rule: An empirical pattern of lineages evolving larger body sizes over time, in its strictest sense resulting from size increase within lineages. Recent work (Heim et al. 2015a) suggests Cope's rule may be widely supported over many taxa and broad timescales.

Geozoic: From the Greek *Geo*, meaning Earth, and *zoic*, meaning life. The interval of Earth history when the planet has supported life; the lower and upper boundaries are defined by the first and last appearance of life, respectively (Kowalewski et al. 2011).

Homeothermy: From the Greek *homoios*, meaning similar, and *thermē*, meaning heat. Maintaining a nearly constant or stable internal body temperature. While mammals and birds maintain homeothermy through increased metabolism, other vertebrates maintain a constant body temperature through behavioral modifications (e.g., basking).

Island rule: First described by Foster (1964), after whom the rule is sometimes named, it describes a consistent pattern of body size evolution on islands. Large taxa tend to become dwarfed (such as pygmy mammoths) presumably because of reduced resource availability, whereas small taxa tend to become larger (such as rodents and Galapagos tortoises) because of reduced predation pressures (Lomolino 1985, Smith 1992).

Mass-specific metabolic rate: Metabolic rate of animals and plants often scales allometrically with body mass to the power of approximately three-fourths (Peters 1983, Calder 1984, Schmidt-Nielsen 1984). Mass-specific metabolic rate provides a measure of metabolism relative to amount of living tissue and is usually measured physiologically as milliliters of O_2 consumed per gram of organismal mass per second. Although larger animals have larger absolute metabolic rates than smaller animals, larger animals convert proportionally less oxygen into carbon dioxide per unit mass.

Passive trend (neutral drift, random walk): A pattern that operates by diffusion away from an initial starting point, in contrast to an active/driven/directional trend where there is a tendency for movement in certain directions. When the starting point is small body size, it can be challenging to distinguish passive from driven trends because mean and maximum body size increase in both cases.

Protist: General term for a diverse group of eukaryotes (organisms with nucleated cells) that are neither plant, nor fungus, nor animal. The group includes unicellular amoebae and phytoplankton, terrestrial slime molds, and multicellular (often large) seaweeds.

Rhizaria: Clade of unicellular amoeboid protists that include testate (shelled) foraminiferans and radiolarians.

MEASURING SIZE

The simplest and most easily applied method to quantify organism size is via linear measurement of the major axis of the organism. Biomass is, of course, a more ideal measure that incorporates three-dimensional shape and correlates more directly with metabolic demand. It is highly correlated with maximum linear dimension when considering organisms spanning at least an order of magnitude in length (Novack-Gottshall 2008b). For tetrapods, measurements of limbs or molars are typically used; these are converted to mass or biovolume using known scaling relationships with closely related modern taxa. When biovolume cannot be measured directly, reasonable estimates can be obtained using linear and geometric (ellipsoid, conical, etc.) approximations. Because nearly all organisms are within a few percent of the density of water, biovolume and biomass are essentially interchangeable when considering body sizes spanning an order of magnitude or more.

directly by cell size because transport of nutrients occurs passively by diffusion through the cell membrane. Larger organisms such as invertebrates and mammals are slightly more buffered from their environment, but nonetheless, virtually all aspects of their life history, physiology, ecology, and evolution are also influenced by their body mass. For example, the thickness of the limbs of a terrestrial animal or the diameter of a redwood tree represent trade-offs between being strong enough to support the organism against the force of gravity, but not so large as to interfere with efficient locomotion or the transport of water and nutrients through a tree's xylem. Thus, the dimensions of organisms change in regular and predictable ways with body size (Thompson 1942, McMahon 1973, Peters 1983, Calder 1984, Bonner 2006). Similarly, the relative effect of Earth's
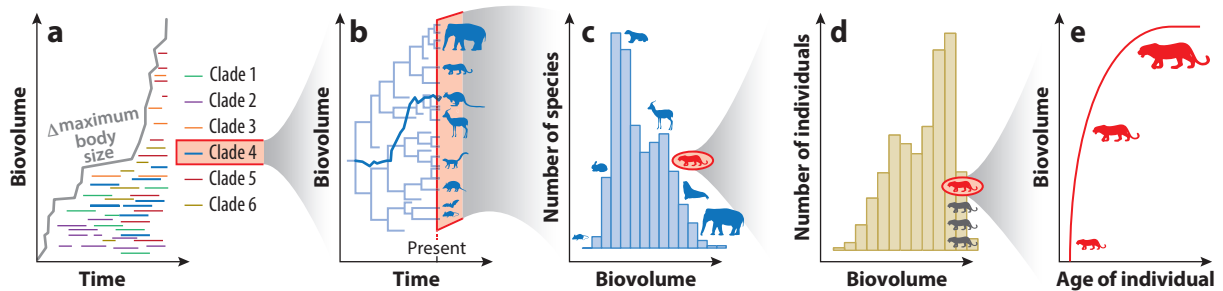
Figure 1

Conceptual depiction of temporal and phylogenetic scales over which evolution of body size can be investigated. (*a*) Evolution of body size for all life. The gray line depicts changes in the maximum body size of life throughout the entire history of life on Earth (the Geozoic). This trend can be estimated from the fossil record (see **Figure 2**). (*b*) Clade-level macroevolution of body size of a given monophyletic group of organisms. Trends in body size may be produced by Cope-style within-lineage trends, species sorting across subclades, or size-selective background and mass extinctions. (*c*) Species size distributions of a given clade. Species size distributions have been estimated for many clades in the present time (Smith & Lyons 2013) and for some fossil groups. (*d*) Size-frequency distribution of individual organisms (locally or globally) for a population of a single species. A right-skewed distribution is common in taxa from bacteria to insects and mammals (Stanley 1973, May 1978, Bonner 1988, Dial & Marzluff 1988, Brown & Maurer 1989, Brown 1995). (*e*) Ontogeny of an individual organism. Rate of growth, maximum size, and age at death all reflect the individual's genetic heritage with an ecophenotypic overprint. Body size tends to be highly heritable for many taxa (Falconer 1973, Rutledge et al. 1973, Leamy 1988) and even for species within genera or higher taxonomic levels (Jablonski 1987, Smith et al. 2004, Smith & Lyons 2013).

gravity and interactions with substances such as water are influenced by the size of an organism. Snakes and lizards can crawl up tree trunks, and spiders and insects can walk upside-down on horizontal surfaces. And, while many insects can even walk on water, a mouse or elephant sinks because its weight is too great to be supported by surface tension.

Moreover, the body mass of a species tightly constrains the rates of all biological reactions within the organism. Factors such as energy use and productivity scale tightly with mass in all living taxa from bacteria to vertebrates and plants (Kleiber 1932, Ernest et al. 2003). Such allometric scaling of metabolism has profound ecological and evolutionary consequences. For example, it means that the mass-specific energy demand of an animal the size of a deer mouse is ∼20 times greater than that of a giraffe, resulting in differences in the types of food that can be acquired and assimilated. It also results in a negative relationship between the population density of taxa and mass (Damuth 1981, Enquist et al. 1998, Ernest et al. 2003), which can have implications for community structure and evolutionary processes such as extinction and origination (Harnik et al. 2012).

The medium in which an organism lives also interacts with both size and physiology over both ecological and evolutionary timescales. For example, in mammals, the much higher rate of convective heat loss in aquatic habitats (as much as 90 times greater than in most terrestrial environments) effectively sets a lower boundary of ∼5 kg on the viable size of newborns because of the high cost of maintaining homeothermy in water (Downhower & Blumer 1988). Likewise, the relative environmental stability of seafloor sediments has led to the evolution of giant size in *Thiomargarita namibiensis*, a species of sulfide-oxidizing bacteria. Because of its limited mobility, it has evolved large nitrate-storing vacuoles, which allow survival during periods of nitrate starvation while still maintaining the surface-to-volume ratio required for osmotrophic metabolism. This adaptation for existence in seafloor sediments has thus led to a cell volume about three million times greater than the average for bacteria (Schulz & Jørgensen 2001) (**Table 1**).

For all these reasons, the body size of organisms is often under selection pressure because it provides a direct way to adapt to a number of different environmental regimes (Smith et al.

1995, Atkinson & Sibly 1997, Huey et al. 2000, Angilletta et al. 2004, Hunt & Roy 2006, Kingsolver & Huey 2008); indeed, it may be one of the first responses of species to climate change (Barnosky et al. 2003). Expansion into a new environment because of dispersal, vicariant events, or abrupt environmental alterations can radically alter the pattern of energy allocation among the essential activities of survival, reproduction, and growth, leading to new optimal body sizes. Accordingly, characterizing first-order patterns is important for understanding the potential underlying causes that have shaped the body size of taxa over evolutionary time.

Here, we review what is known about the patterns of body size evolution for all taxa over the Geozoic. We first focus on the patterns at the broadest scale, and then examine separately evolution in aquatic and terrestrial realms and individually in major clades. Finally, we synthesize what we know about potential underlying causes for the variation in size over ecological and evolutionary scales and explore consequences of this variation in terms of both organisms and their influence on the Earth system. For definitions of key terms used throughout this review, see the sidebar Glossary of Terms.

2. PATTERNS OF BODY SIZE OVER TIME

The evolutionary context of organismal body size can be explored over a wide range of temporal, spatial, and phylogenetic scales: from biosphere-scale trends over the entire history of life to genotypic constraints that limit growth and size of individual organisms (**Figure 1**). Theoretical frameworks, research questions, data collection strategies, analytical methodologies, and terminology vary depending on the scale of analysis. Moreover, not all observational scales are equally accessible, with quality and quantity of data generally improving at finer taxonomic and temporal scales. Here, our focus is on temporal scales and broadly applicable clade-level patterns (e.g., **Figure 1a,b**).

2.1. The Geozoic

The when and why of how life evolved are still open questions; there remains a lively debate about the validity of the oldest fossils (Schopf 1993, Brasier et al. 2002, Marshall et al. 2011). Because the earliest life forms were very small, differentiating putative fossils from abiotic look-alikes involves determining whether they were biogenic and whether they are clearly indigenous to rocks of known provenance and well-defined Archean age. Regardless of the ultimate status of these fossils, microscopic cyanobacteria-like organisms had likely evolved by ∼3.5 to 3.4 Ga (Schopf 2006). These were very small, with biovolumes of only ∼3.4×10^{-6} mm^3 (Payne et al. 2009). Over the next 3.5 Ga, the range of body size occupied by life on the planet increased by another ∼18 orders of magnitude (**Figure 2**), to include not only these simple microscopic cells but also giant sauropods, blue whales, and sequoia trees (**Table 1**). Interestingly, these increases in size occurred in a stepwise fashion, with most change occurring during two jumps of about eight orders of magnitude each, one in the mid-Paleoproterozoic (∼1.9 Ga) and another during the late Neoproterozoic–early Paleozoic (600–450 Ma) (Payne et al. 2009). There appears to have been a long period of relative stasis in between. The two jumps in maximum size (**Figure 2**) co-occurred with major innovations in organismal complexity—first, the evolution of the eukaryotic cell, and later, multicellularity—and also in association with substantial increases in the atmospheric oxygen concentration (Payne et al. 2009). However, the early fossil record is not well enough resolved to distinguish cause from effect; although it is possible that changes in oxygen facilitated the evolutionary innovations that led to larger size, it is also possible that evolutionary innovations
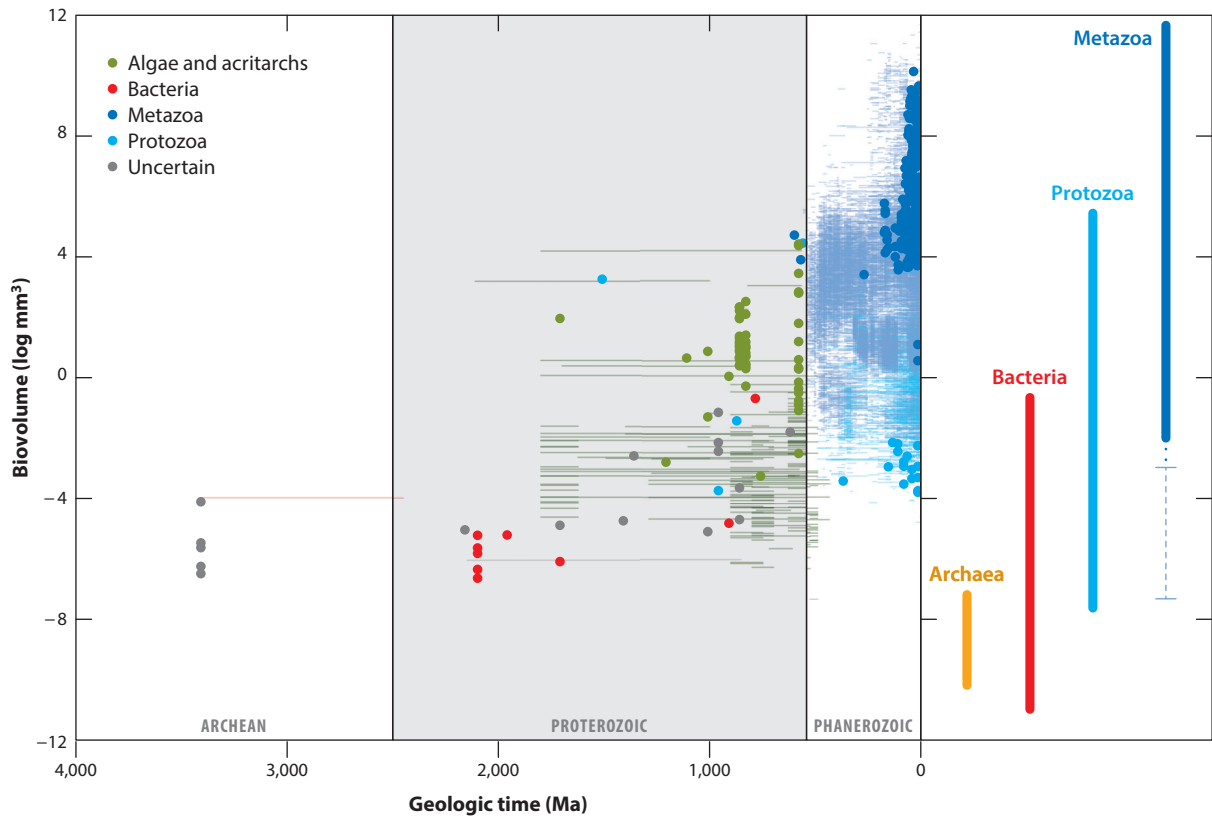
Figure 2

Body size across the Geozoic. The left panel shows the stratigraphic ranges and biovolume (in log mm^3) for animal, protist, algal, and prokaryote genera known from the fossil record. The points represent Precambrian fossil taxa that are known only from single specimens. The acritarchs, which are a polyphyletic group of organic microfossils that likely represent algal, protistan, and animal forms, are lumped with the "algal" fossils (*green*). All the fossils designated as "algal" in our data set are from Precambrian rocks and have algal-like morphologies, but some may be nonalgal protists. Protists (*light blue*) consist of genera from the kingdom Rhizaria and here include the Foraminifera and Radiolaria. Animals, including Ediacaran forms, are in dark blue, and Bacteria are in red. Note that it is not possible to distinguish Archaea from Bacteria based on the morphotypes preserved in the fossil record. The right panel shows the range in sizes occupied in the modern by Bacteria, Archaea, Protozoa, and Metazoa. The dotted blue line extending below the solid Metazoa line connects the smallest animal in our data set, an ostracode, with *Caenorhabditis elegans*, a typical member of the soft-bodied meiofauna. The dashed blue line further extends the minimum size of animals to that of *Myxosoma chuatsi*, a tiny parasitic cnidarian. Size ranges of living Archaea and Bacteria were extracted from Rosenberg (2014); modern protist sizes were supplemented with data from Lee et al. (2000).

led to larger size, which led to changes in atmospheric oxygen. Recent work suggests that these evolutionary transitions also involved innovations in metabolic design (DeLong et al. 2010), which may have changed the allometric scaling of important life history characteristics.

Interestingly, since the early Paleozoic, even when considering the evolution of giant sauropods and baleen whales, the size of living things has increased by only a few more orders of magnitude to a current maximum of $\sim 10^{12}$ mm^3 (**Table 1**; **Figures 2** and **3**). Further, over time, many diverse groups have been the largest organisms on Earth, including cephalopods, reptiles, fishes, and mammals (see the sidebar Measuring Time). It is likely that terrestrial vertebrates and trees have approached the maximum size possible given structural and physical constraints (McMahon 1973,

MEASURING TIME

A potential complication when comparing evolutionary rates among diverse taxa is standardizing for time. Because evolution is a result of ancestor-descendant selection, the generation time of an organism is relevant. Ten years may represent >20,000 bacterial generations, but only 10 for a woodrat and much less than 1 for an elephant. Characterizing evolution over a biologically relevant timescale is important for evaluating how species may adapt to environmental perturbations, such as climate change. For this reason, scientists have often turned to generation time when making comparisons among diverse taxa (Haldane 1949, Gingerich 1993, Evans et al. 2012), although recent work suggests that productivity and lifestyle also influence evolutionary rates. Traditionally, evolutionary rates were measured in darwins (d) (Haldane 1949), which represent the logarithmic change in a morphological trait (x) over two time periods standardized over 1 Ma:

$$d = \frac{\ln\frac{x_2}{x_1}}{\Delta T}$$

However, when comparing taxa that differ in proportion or generation time, the haldane (h) is preferable because it is independent of the dimensions of the underlying measurements and accounts for differences in life span (Gingerich 1993). Haldanes are computed as the difference in the means of the natural logged measurements divided by the pooled standard deviation of the samples, S_p, again divided by time, but in generational rather than chronological time:

$$h = \frac{\left(\ln\frac{x_2}{x_1}\right)/S_p}{\Delta T_g}$$

Alexander 1982). However, whether aquatic organisms have similarly attained their maximum possible size is unclear. For example, the trajectory of size evolution in whales has not yet plateaued (M.D. Uhen et al., manuscript in review).

In contrast, the minimum size of life on Earth has remained nearly constant over the Geozoic, with Archaea and Bacteria consistently occupying the smallest size classes (**Figure 2**). Recent detailed microscopy has revealed the existence of ultrasmall bacteria that reach what is currently believed to be the theoretical minimum of how small life can get (Luef et al. 2015). These organisms are about 0.008 μm^3, too small to be easily detectable in the fossil record. After the initial jumps in body size during the mid-Paleoproterozoic and late Neoproterozoic–early Paleozoic, the range occupied by each major clade (e.g., Archaea, Bacteria, Protozoa, and Metazoa) has also remained relatively constant (**Figure 2**). Moreover, with the exception of Archaea, which appear to have been restricted to about four orders of magnitude (**Table 1**), most clades occupy about the same range of body size ($\sim$12–14 orders of magnitude), although minimum and maximum limits vary (**Figure 2**).

Figure 3

Phanerozoic body size of multicellular animals and Rhizaria. Each horizontal line depicts the duration of a genus plotted at its biovolume (log mm^3). (*a*) Marine animals and foraminiferans over the entire Phanerozoic, from N.A. Heim (manuscript in preparation). Body masses of more than 19,000 genera are plotted, representing the Foraminifera and the major solitary bilaterian phyla with good fossil records: Arthropoda, Brachiopoda, Chordata, Echinodermata, and Mollusca. (*b*) Terrestrial vertebrates over the Mesozoic and Cenozoic, from Lyons et al. (2015). Body masses of dinosaurs, birds, pterosaurs, and mammals are plotted.
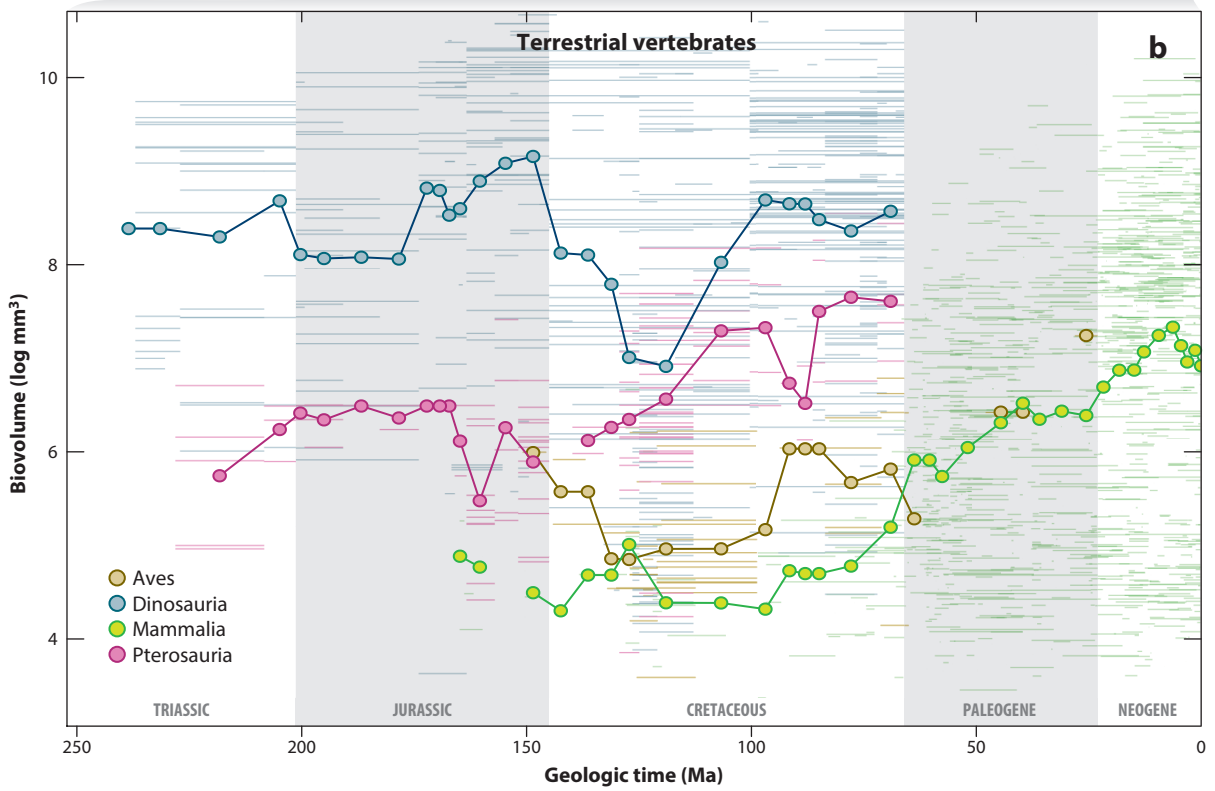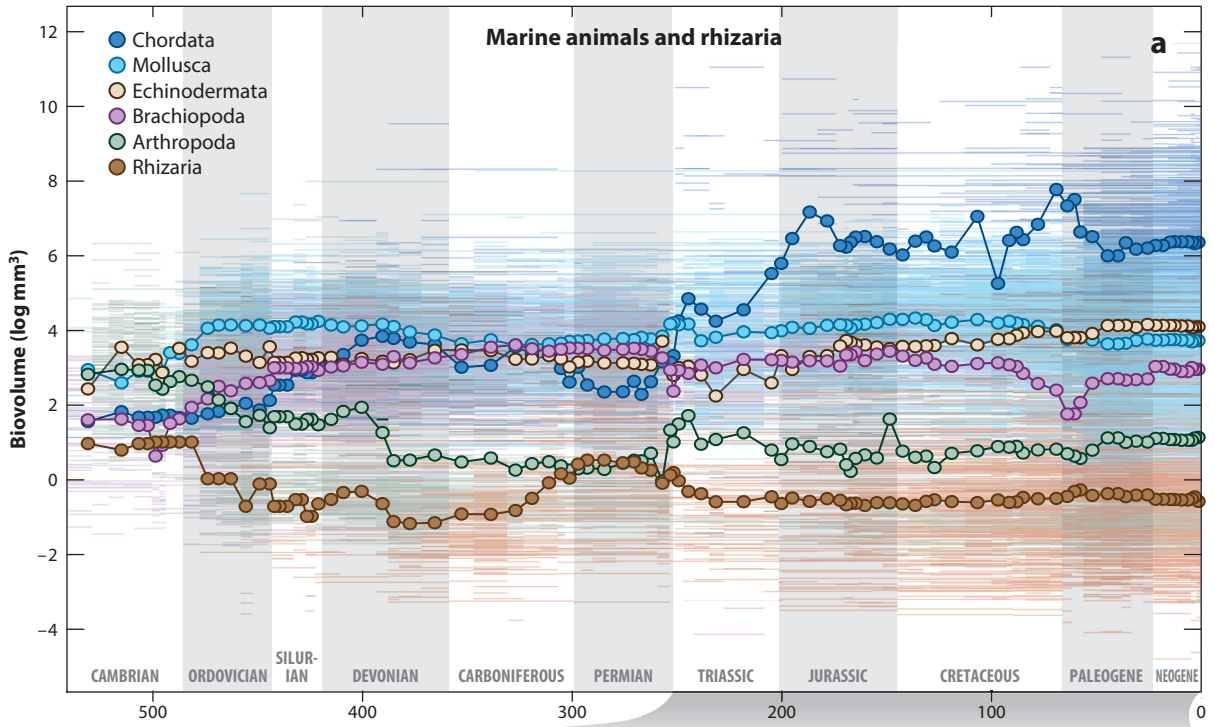
2.2. Life in Water

The sizes of oceanic organisms span 23 orders of magnitude in biovolume, from the tiny thermophilic Archaea *Thermodiscus* to the blue whale, *Rorqualus musculus* (**Table 1**). A complete survey of size distributions within the ocean has yet to be attempted. Indeed, even sampling the diversity of microbial and macroscopic life in the oceans is difficult. However, a good deal is known about the maximum sizes of marine animals (McClain et al. 2015), in part because of the public fascination with the largest organisms and in part from long-term fisheries records. Though the largest species of many modern chordate groups are well known (e.g., blue whale, whale shark), there are many impressively large marine invertebrates, including *Xestospongia muta*, a sponge with a biovolume of more than 7 m³, *Riftia pachyptila*, a tube worm more than 3 m long, and *Nemopilema nomurai*, a jellyfish with a bell more than 3 m across (McClain et al. 2015). Documenting the smallest marine organisms is challenging given the difficulty of comprehensively sampling biodiversity in the oceans and because many of the smallest animals are parasitic.

Sampling the marine fossil record is in many ways much easier than sampling the modern ocean. The majority of Earth's sedimentary cover and its constituent fossil record are marine in origin. Thus, the fossil record of Phanerozoic marine life is rich and offers an excellent window into body size evolution across a wide range of skeletonized taxa. A recent compilation of more than 17,000 fossil marine, solitary, bilaterian animal genera (Heim et al. 2015a) (**Figure 3a**) indicated that maximum size has increased by more than five orders of magnitude since the Cambrian. The largest early Paleozoic animals were arthropods, including anomalocaridids and trilobites. Since the Devonian, the largest marine animals have been chordates: fish in the Paleozoic, reptiles in the Mesozoic, and mammals in the Cenozoic. A trend of increasing maximum size is also accompanied by a two-orders-of-magnitude increase in the mean size of marine animals. At the lower end, the smallest animals decreased by a single order of magnitude over the Phanerozoic. The majority of the decrease occurred by the Devonian. The smallest animals in the Cambrian were phosphatic inarticulated brachiopods, but since then they have been arthropods; more specifically, mainly ostracodes, a class of minute bivalved crustaceans. Interestingly, the ostracodes have a mean size that is smaller than the mean size of fossil foraminiferans (a group of exclusively marine single-celled protists) for most of their Phanerozoic history. It remains an open question how and why the ostracodes, which are anatomically complex animals, achieved such a small body size.

Semiquantitative estimation of marine animal energetics suggests that those with high-energy life modes (e.g., bony fish, ammonites) have been diversifying more than their low-energy counterparts since the end of the Paleozoic and, moreover, that these active animals have on average become larger over time (Bambach 1993). In particular, there is a tendency for fast-moving predators to become very large. Pelagic filter feeding is another life mode for reaching large size (e.g., mysticete whales) (Pyenson et al. 2012). Interestingly, one of the largest early Paleozoic arthropods had clear anatomical features adapted for pelagic filter feeding (Van Roy et al. 2015).

The largest aquatic animals are marine tetrapods, including the largest animal to evolve on Earth, the blue whale (*Rorqualus musculus*). Marine gigantism in tetrapods may be due in part to the lack of mechanical constraints in a near-neutral-buoyancy environment. However, the amelioration of mechanical constraints alone does not explain the pervasive pattern of marine tetrapod gigantism. Shortly after the first reptiles evolved a marine lifestyle in the Permian, they evolved large body size; they remained the largest organisms in the oceans over the entire Mesozoic era (**Figure 3a**). Likewise, cetaceans very rapidly evolved large size after entering the marine environment early in the Cenozoic. If living in a neutrally buoyant environment was the primary factor permitting gigantism, why have fish never reached the size of large mosasaurs, ichthyosaurs, or cetaceans? One likely explanation is the exaptation (Gould & Vrba 1982) of air breathing. Air

contains much more O_2 gas than water, and the diffusion of O_2 across cell membranes from a gaseous medium is much more efficient than it is from a liquid medium (Pauly & Kinne 2010). Though explicit tests have yet to be conducted, the ability of marine tetrapods to breathe O_2 from air has allowed them to reach and maintain very large sizes across large swaths of evolutionary time.

2.3. Life on Land

There has yet to be a complete synthesis of body size evolution in terrestrial environments over the Geozoic. However, there are some interesting patterns in the interactions of several dominant clades since the end of the Permian (Lyons et al. 2015). For example, although mammals and dinosaurs originated at roughly the same time (~230–210 Ma), dinosaurs quickly expanded their body size over the Mesozoic (Benson et al. 2014), filling most ecological roles within terrestrial communities (**Figure 3b**). The "early burst niche-filling pattern" (Benson et al. 2014) was followed by reduced evolutionary rates in most lineages. Others have reported that the trajectory of increase in maximum size closely fits a random walk (Lyons et al. 2015), suggesting stochastic evolution during this period of relatively stable climate. A secondary radiation starting in the Middle Jurassic led to the evolution of birds (Benson et al. 2014). Interestingly, the very large sizes of some dinosaur species (>85 metric tons) (Sander & Clauss 2008, Benson et al. 2014) may have suppressed the overall diversity of the group (Codron et al. 2013). Physiological constraints limit how large an egg can be and still supply oxygen to the embryo (Seymour 1979); the shell must be sufficiently thin to allow gaseous exchange. Because of this constraint on egg size, the largest sauropods were up to three to four orders of magnitude larger than their offspring at birth, a much larger difference than in any other extinct or extant tetrapod clade (Codron et al. 2013). The close correspondence between diet niche and body size (Peters 1983, Calder 1984, Schmidt-Nielsen 1984) suggests that the huge size differential most likely led to the occupation of many different ecological niches by juvenile and subadult sauropods over ontogeny. It also suggests that because each sauropod individual and species occupied many different ecological niches, fewer species could coexist overall relative to other clades (Codron et al. 2013).

In contrast to nonavian dinosaurs, mammals occupied a fairly narrow range of body masses until after the Cretaceous–Paleocene (K–Pg) mass extinction (Lillegraven et al. 1979, Smith et al. 2010a) (**Figure 3b**). Indeed, during the Mesozoic, the mammalian body size niche was relatively constant at ~3–5 g to ~10–15 kg, encompassing only about three orders of magnitude. This relatively restricted size range strongly limited the ecological niches occupied by early mammals (Smith et al. 2010a). Following the mass extinction, there was a rapid and driven trend (Alroy 1998, 1999; Smith et al. 2010a; Lyons et al. 2015) of morphological, ecological, and phylogenetic diversification in terrestrial mammals. Within 20 Ma, mammals had expanded their upper body size threshold by more than four orders of magnitude and occupied a full range of ecological roles (Smith et al. 2010a, Smith & Lyons 2011). Although ecological release was clearly important, the maximum body mass mammals attained over the Cenozoic appears to be strongly constrained by temperature (Smith et al. 2010a, Saarinen et al. 2014). Further, the body size patterns are replicated on all continents, at both the class and ordinal level (Smith et al. 2010a, Smith & Lyons 2011), with mammalian orders reaching their maximum size at the same times on the various continents despite dissimilar taxonomic compositions (Saarinen et al. 2014). Mammalian orders reached their maximum sizes in the middle Eocene, the Oligocene, or the Pleistocene.

The relationship between the various clades of flying organisms is more complicated. Pterosaurs evolved during the Mesozoic and for ~100 Ma occupied about the same range of body mass, averaging about 1.4 kg. Shortly after birds evolved, however, there was a rapid and statistically

robust driven increase in pterosaur body size (Benson et al. 2014, Lyons et al. 2015) to a mean of ∼52 kg (**Figure 3b**) (Lyons et al. 2015), with birds replacing pterosaurs at the lower end of the size range. Anatomical studies of morphology and wing-loading ratios for pterosaurs suggest that they were predominantly gliders (Templin 2000), which may have allowed evolution of large size. However, it is likely that pterosaurs were at a competitive disadvantage compared to birds that had evolved powered flight (Smith et al. 2013). After the extinction of nonavian dinosaurs and pterosaurs, the maximum size of birds increased further (**Figure 3b**), perhaps because of a lack of competition. Intriguingly, the largest volant birds (e.g., the giant teratorn, of the late Miocene) have generally been largely gliders with only limited use of powered flight (Campbell & Tonni 1980, Marden 1994, Vizcaíno & Fariña 1999).

Other clades too evolved fantastically large size over Earth history. Perhaps the most famous are the giant dragonflies and griffinflies of the middle to late Paleozoic. These taxa evolved during the Permo-Carboniferous, amid a marked increase in atmospheric oxygen partial pressure (Berner et al. 2007). *Meganeura* and other genera of similarly sized flying insects were about three times the size of the largest flying insects today, with wingspans exceeding 65–71 cm (Shear & Kukalová-Peck 1990). Their evolution has been tied to the absence of other aerial predators (Bechly 2004) coupled with the much higher oxygen content/density of the atmosphere at this time, which may have facilitated breathing and flight (Graham et al. 1995, Chapelle & Peck 1999, Harrison et al. 2006, Clapham & Karr 2012). Recent laboratory studies confirm that increasing atmospheric oxygen partial pressure can lead to the evolution of significantly larger insect body mass in less than a dozen generations (Harrison et al. 2006, Kaiser et al. 2007).

3. TRENDS, CAUSES, AND LIMITS

Why are organisms the size they are? In his essay "On Being the Right Size," the noted evolutionary biologist J.B.S. Haldane speculated on the relationship between body structure and function and body size (Haldane 1928). He noted that various trade-offs led to most taxa having a "most convenient size." Here, we review what we know about the trends, causes, and constraints that act collectively to produce the characteristic sizes of organisms (see the sidebar Why Large Size?).

WHY LARGE SIZE?

Cope's rule, or the trend over time for many groups to get larger, has led to considerable debate (e.g., Bonner 1988, Jablonski 1997, Blankenhorn 2000). Why is large size advantageous? For some taxa, increased size may be correlated with higher reproductive output, decreased predation, increased longevity, greater intelligence, or enhanced competitive abilities, all or some of which can lead to differential survival (Peters 1983, Calder 1984, Schmidt-Nielsen 1984, Smith 1992, Kingsolver & Huey 2008). However, body size is also correlated with reduced reproductive output and/or population density, longer generation times, and greater overall resource requirements (Peters 1983, Calder 1984, Schmidt-Nielsen 1984, Blankenhorn 2000), which may lead to higher extinction and lower origination probabilities (Brown 1995, Finnegan et al. 2009, Dirzo et al. 2014, McCauley et al. 2015). Large mammals on islands often show a dramatic reduction in body size, presumably because of the trade-offs of these factors with the lack of competition common in insular habitats; this phenomenon has occurred often enough over evolutionary history to be called the island rule (Foster 1964).
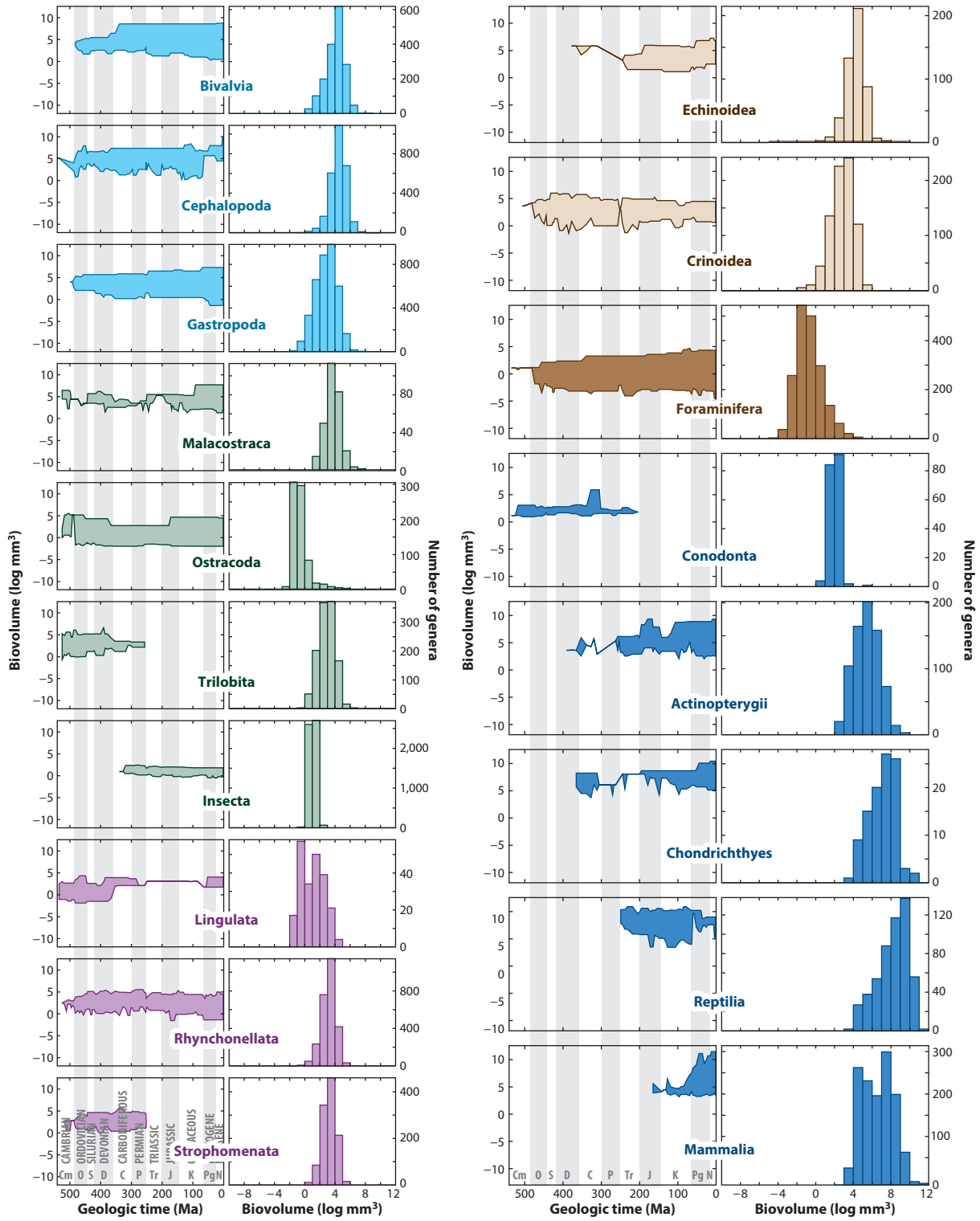
3.1. Trends in Minimum and Maximum Size

All extant animal groups except insects, reptiles, and ostracodes have achieved larger sizes today than earlier in Earth history (**Figure 4**). This pattern, known as Cope's rule (Cope 1887, Bonner 1988, Jablonski 1997, Alroy 1998, Heim et al. 2015a), is perhaps the best-known example of a large-scale trend—one encompassing higher taxa and occurring over macroevolutionary timescales. Although attributed to E.D. Cope, it is not clear whether he formulated the rule himself, and thus there is no single precise definition. In the broadest sense, Cope's rule refers to the tendency of groups to increase in body size over time. However, such an increase could result from within-lineage trends, among-lineage sorting, or some combination of both. In a stricter sense, Cope's rule refers to a within-lineage increase in size, resulting from a tendency of descendants to be larger than their ancestors. This stricter sense excludes many possible mechanisms that would be included in the broader definition, such as size-biased extinction and origination, bounded random drift, and species selection (or clade sorting) of larger taxa. Although most groups appear to increase in size over evolutionary time—substantial evidence exists that marine animals as a whole have increased in mean and maximum size over the Phanerozoic (Novack-Gottshall 2008a; Heim et al. 2015a,b), and the pattern is especially clear for mammals, nonavian dinosaurs, and birds (Alroy 1998, Alroy 1999, Hone et al. 2005)—attributing an evolutionary mechanism to the pattern is less straightforward.

Moreover, there is considerable heterogeneity in terms of how many times in a clade's evolutionary trajectory large size is achieved. Further, there appears to be no consistent pattern between when a clade originates and when it achieves maximum size (**Figure 4**), even when accounting for generational versus chronological time (Saarinen et al. 2014). For many clades, the largest sizes were achieved fairly early in their evolutionary history, and body size has remained smaller since (e.g., crinoids); others show a more heterogeneous trajectory (e.g., ostracodes). A few clades are almost invariant in terms of the body size niche occupied over time. For example, despite an evolutionary history that spans more than 300 Ma, insects have varied very little in the range of body size they occupy (**Figure 4**). There may be underlying environmental processes that influence the evolution of maximum size among taxa, but for most clades, we still lack an appreciation for the actual constraints that operate over time (Saarinen et al. 2014).

Similarly, there has been considerable heterogeneity in the minimum body size of groups over Earth history (**Figure 4**), with some clades exhibiting a relatively consistent minimum (e.g., Rhynchonellata, Ostracoda, Bivalvia, Mammalia, Foraminifera, Insecta) and others being quite variable (e.g., Cephalopoda, Malacostraca, Chondrichthyes, Lingulata). Some of the heterogeneity in minimum size may result from poor preservation of smaller-bodied forms.

3.2. Null Trends

Evolutionary mechanisms responsible for observed size trends in a clade can be divided broadly into two categories: those driven by pervasive selection acting across all species in the clade, and those resulting from different causes acting independently on each species (McShea 1994, Hunt 2006). In theoretical work on trends, the latter is commonly used as a null model. The null serves as a crucial reference point. That is, the existence of pervasive forces is revealed by comparing the actual record of change with the null expectation—the pattern of change expected when no forces act. Consider **Figure 1b**. The thin lines represent small-scale lineages—say, individual species—and the entire ensemble of thin lines represents the larger clade containing them. The figure illustrates the punctuational case, where change in body size occurs only at speciation events (i.e., the nodes where small-scale lineages branch), giving rise to one species that is larger than

Bivalvia

Cephalopoda

Gastropoda

Malacostraca

Ostracoda

Trilobita

Insecta

Lingulata

Rhynchonellata

Strophomenata

Echinoidea

Crinoidea

Foraminifera

Conodonta

Actinopterygii

Chondrichthyes

Reptilia

Mammalia

Biovolume (log mm³)

Number of genera

Geologic time (Ma)

Biovolume (log mm³)

CAMBRIAN ORDOVICIAN SILURIAN DEVONIAN CARBONIFEROUS PERMIAN TRIASSIC JURASSIC CRETACEOUS PALEOGENE NEOGENE

Cm O S D C P Tr J K PgN

the ancestor and another that is smaller. As drawn, there is no upward tendency, as increases and decreases in size are equally frequent. This is the pattern expected in the null case with no evolutionary forces acting at the scale of the lineage. Notice, however, that there is nevertheless a trend—a trend in the maximum. The distinction is that "tendency" refers to the pattern of change at the lower level, in this case the species level, whereas "trend" refers to a change in a summary statistic at the clade level, in this case an increase in the clade maximum. Other summary statistics of interest include the mean, median, and minimum. Thus, there is not necessarily a connection between tendency and trend: One can have a trend without a tendency. For body size evolution in particular, the most commonly observed and documentable kind of trend—a rise in the maximum—does not by itself tell us much about underlying tendencies. Maxima are expected to increase even if no tendencies, no evolutionary forces, are present. Thus, we cannot infer the existence of a selective advantage of large size merely from an increase in the maximum.

The situation is actually more complex than this simple case. Trends can be caused not just by underlying tendencies but also by differences in speciation and extinction rate; indeed, close inspection of **Figure 1***b* suggests a trend in the mean, as well as the maximum, which may result from a greater number of speciation events (branchings) among large species relative to small ones. Trends can also be the result of boundaries, such as a lower size limit. For example, an increasing trend in the mean can result when diversity is increasing in the presence of a lower limit on body size, even when there is no increasing tendency at the lineage level (Stanley 1973). If a clade first evolves at a size close to the minimum size possible for a particular body plan or ecology and subsequent speciation events are random with respect to size (i.e., descendants are equally likely to be larger or smaller than their ancestors), then mean size will increase, because the lower bound prevents the variance from increasing in the direction of smaller sizes. This is an example of a passive trend, one with no increasing tendency. By contrast, trends resulting from biased lineage-level tendencies are known as driven trends. Trends can also be produced by biases in the magnitude of change upward versus downward, that is, if the magnitude of increases in body size is typically greater than the magnitude of decreases, and by other more complex lineage-level mechanisms. All of these represent departures from the null model, and their detection and documentation require small-scale lineage-level data.

Various statistical tests have been devised to detect underlying tendencies, most requiring data at a finer scale than gross clade statistics. A definitive test is the ancestor-descendant test (McShea 1994), which looks for an excess of increases or decreases in ancestor-descendant pairs. This test, however, requires a lineage-level phylogeny, which is not available for most clades in most time periods. Other tests have been developed that do not require detailed phylogenetic information. One example is the minimum test (McShea 1994). As described above, the maximum is expected to increase even if there is no tendency toward larger size. By symmetry, the minimum is expected to decrease in such a situation, or remain the same if there is a lower size boundary. Thus, an increase in the minimum contradicts the null expectation and indicates a tendency toward larger size. Another test that does not require a detailed phylogeny is the subclade test (McShea 1994) and its related variant, the analysis of skewness (Wang 2001). These tests are based on the direction of skew in the size distribution of subgroups of the clade in question; a full explanation is beyond the

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Figure 4

Size distributions of Linnaean classes through time. The left panels show the range in size (*colored fills*) and the maximum and minimum sizes (*dark colored lines*) through the Phanerozoic; the right panels show the size-frequency distributions of all Phanerozoic genera within each class, including extant and extinct genera. Birds are included with reptiles, and no distinction is made between marine and nonmarine genera.

Table 2   Summary statistics and evolutionary trends for selected phyla

Phylum	N	log median	log mean	log variance	Skewness	Kurtosis	Evolutionary trend[a]
Arthropoda	8,754	1.15	1.33	1.84	0.59	4.14	Stasis
Brachiopoda	4,552	3.18	3.04	1.23	−0.97	4.72	Unbiased random walk
Chordata	3,153	6.22	6.25	4.28	−0.10	2.53	Unbiased random walk
Echinodermata	1,805	3.47	3.37	1.65	−0.55	3.41	Unbiased random walk
Foraminifera	1,976	−0.83	−0.65	1.90	0.65	3.49	Unbiased random walk
Mollusca	11,373	3.71	3.52	2.14	−0.43	2.85	Unbiased random walk

[a]Evolutionary trends were calculated using *R* package *paleoTS* (Hunt 2008).

scope of this review. More recently, Hunt (2006, 2008) has developed methods based on explicit likelihood-based models of evolution, which are able to distinguish stasis, biased sequences, and unbiased sequences of trait data in evolving lineages.

Analysis of the trend in mean size across all Phanerozoic marine animals (**Figure 3a**) suggests that the observed increase from the Cambrian to the Recent is most consistent with the existence of an upward tendency, a driven trend (Heim et al. 2015a). Furthermore, a simple branching model (Raup et al. 1973) reveals that the observed increase in the maximum size is inconsistent with the null expectation. However, when patterns of size increase are examined within lower-level taxa (e.g., phyla, classes), the trends found there are generally more consistent with the null (**Table 2**). Often the increases in means are due largely to species selection (Vrba & Gould 1986) whereby clades with a larger overall body size diversify more than clades with smaller-sized genera. The underlying factors promoting this differential diversification have not been positively identified, but innovations related to ecology or life mode (Bush et al. 2007) in the emergence of novel clades are likely to have played an important role (Bush et al. 2007, Novack-Gottshall & Lanier 2008, Klompmaker et al. 2015). Similar analyses suggest the trends among terrestrial organisms are driven by an upward tendency (**Figure 3b**; **Table 2**).

3.3. Fundamental Physical and Physiological Limits

Because genome size scales positively with cell size (DeLong et al. 2010), there is a feedback between the size of an organism and its complexity. As the genome becomes larger, more enzymes and more complicated biochemical networks can arise (DeLong et al. 2010). Certainly, one of the most important modifications required for the achievement of large body size over evolutionary time is the development of active transport mechanisms. At small sizes, microbes are able to carry out their metabolic activities largely via diffusion of substrates and products, both within and outside the cell. However, the time required for diffusive transport becomes prohibitively long over greater distances, such that even millimeter-scale cells require active transport of materials to carry out metabolism (Payne et al. 2012). Similarly, large, multicellular organisms typically depend upon internal networks for active transport of materials, such as xylem and phloem in a tree or respiratory and circulatory systems in a vertebrate. In many cases, large organisms not only transport materials actively within their bodies but also move materials in the external environment, for example, by fracturing rocks via the growth of roots or stirring the soil or sediment in the case of burrowing animals. There is also a feedback between the environment and the mode of transport within the organism; for instance, higher atmospheric oxygen levels have been implicated in the rise of giant Paleozoic animals in a diverse array of organisms ranging from insects and millipedes to amphibians (Graham et al. 1995, Berner 2006, Harrison et al. 2006).

ECTOTHERMY, MESOTHERMY, AND ENDOTHERMY

Body temperature is a fundamental regulator of both metabolic rate and activity levels. Vertebrates are typically placed into one of two thermoregulatory categories: mammals and birds, with their high, stable body temperatures, are classified as endotherms, while reptiles, amphibians, and fish, whose body temperature varies with the environment, are termed ectotherms. Endothermic metabolic rates are typically one to two orders of magnitude higher than ectothermic rates for a given body size. This high rate of heat production, when coupled with insulatory fur, feathers, or fat, enables endothermic mammals and birds to elevate their bodies to temperatures between 35°C and 42°C. Some organisms, however, do not easily slot into this classification scheme. Warm-blooded tuna and lamnid sharks, for instance, rely on metabolic heat to elevate their body temperature, as do endotherms, but like ectotherms, they do not metabolically defend a thermal set point. For instance, if a tuna dives to colder depths, no shivering occurs, and its metabolic rate and body temperature decline. This intermediate strategy of elevating body temperature internally but not defending a set point has been termed mesothermy (Grady et al. 2014). Scientists have recently argued that many Mesozoic dinosaurs, with their intermediate growth and calculated metabolic rates, were likely mesothermic (Grady et al. 2014).

3.4. Role of Temperature and the Environment

Environmental temperature influences the body mass of organisms over both space and time (Mayr 1956, Smith et al. 1995, Atkinson & Sibly 1997, Millien et al. 2006, Kingsolver & Huey 2008, Forster et al. 2012). This is not surprising given that temperature directly influences metabolism and the physiology of taxa, especially in ectotherms, whose body temperature largely reflects ambient conditions (Peters 1983, Calder 1984, Schmidt-Nielsen 1984) (see the sidebar Ectothermy, Mesothermy, and Endothermy). There are many studies demonstrating a link over ecological timescales between physiology and the environment. For example, adult body size in many invertebrates is dependent on ambient temperature (Atkinson & Sibly 1997, Angilletta et al. 2004), with cooler temperatures selecting for slower development but larger size at maturity. This pattern is so pervasive it is called the temperature-size rule (Angilletta et al. 2004). Indeed, changes in body size are how many animals—both vertebrates and invertebrates—adapt to environmental variation (e.g., Mayr 1956, Smith et al. 1995, Huey et al. 2000, Barnosky et al. 2003, Smith & Betancourt 2003, Angilletta et al. 2004, Millien et al. 2006). The spatial relationship between body mass and temperature is so predictable it is called Bergmann's rule: the principle that within a broadly distributed genus, species of larger size are found in colder environments and smaller ones in warmer areas (Bergmann 1847, Rensch 1938, Mayr 1956). The majority (>70%) of modern endotherms follow this pattern (Millien et al. 2006). Interestingly, many but not all ectothermic clades, such as bacteria, protists, insects, reptiles, and plants, also demonstrate larger body size with cooler environments, although the proximal cause is likely to be different. Further, the temperature-size response of aquatic organisms is stronger than that of terrestrial ones, which may be related to the greater difficulty of oxygen uptake in aqueous environments (Forster et al. 2012). There remains considerable debate about whether there are universal factors underlying the temperature-size rule and Bergmann's rule and the extent to which they represent adaptive responses to environmental temperature (Angilletta et al. 2004, Millien et al. 2006, Kingsolver & Huey 2008).

A growing number of studies have demonstrated that temperature influences the evolutionary body size trajectory for some groups, most notably mammals (Davis 1981, Smith et al. 1995,

Smith & Betancourt 2003, Millien et al. 2006, Smith et al. 2010a, Secord et al. 2012) and deep-sea ostracodes (Hunt & Roy 2006). How universal this pattern is remains unclear. Temperature has been demonstrated to drive some trends over evolutionary time (Hunt et al. 2015). Nonetheless, Bergmann's rule underscores the strong selection imposed on the body size of an organism by its environment and the potential ability of species to adapt to fluctuating abiotic conditions.

3.5. Role of Ecology

Ultimately, the body size of an organism results from trade-offs between energy acquisition (as influenced by life history characteristics and the physical environment) and allocation to various activities, including reproduction (Brown et al. 1993, Brown 1995). But interactions between organisms also influence the process of energy acquisition and allocation. These can include intra- or interspecific competition, predation, and/or resource limitations (Thompson 1942, Alexander 1982, Peters 1983, Calder 1984, Schmidt-Nielsen 1984, Brown & Maurer 1989, Smith 1992, Bambach 1993, Brown et al. 1993, Brown 1995). How these ecological factors interact is most evident in insular habitats, where reduced species diversity leads to the alleviation of continental selective pressures. Indeed, body size changes on islands are so pervasive over evolutionary time that the term island rule has been coined to describe the pattern (Van Valen 1973). Body size anomalies include dwarfism in larger-bodied lineages (e.g., mammoths, deer, rhinos, dinosaurs), gigantism in small-bodied forms (e.g., rodents, insects, birds), and changes in shape or form (e.g., insular woodiness in trees, loss of flight in insects and birds) (Foster 1964, Carlquist 1965, Van Valen 1973, Lomolino 1985, Smith 1992, Benson et al. 2014). Many of these authors ultimately attribute evolutionary trends in body size to reduced resource availability peculiar to insular habitats; when predation is of lesser concern (Smith 1992), larger size in small animals can enhance access to resources, while smaller size in larger animals can reduce overall resource use. But resources may also influence body size in continental or aquatic habitats. For example, there is a highly significant relationship between the maximum body size of mammals and the size of the island, continent, or ocean basin occupied (Smith et al. 2010a, figure S5). The authors suggested available resources limit the biomass that can be supported in a habitat, which in turn may limit the maximum size possible because of the allometric scaling of population density with body mass (Damuth 1981). It is intriguing that nonavian dinosaurs achieved a body mass about an order of magnitude greater than terrestrial mammals over their evolutionary history; this corresponds well with the roughly 10× difference in energy requirements between ectotherms and endotherms, suggesting that resource availability may also have limited dinosaur maximum size (Smith et al. 2010a). Resource limitations are also thought to underlie the well-known pattern between body size and species richness (e.g., **Figure 1c**), where across taxa there are many more species of small-bodied organisms than larger ones (Hutchinson & MacArthur 1959, Dial & Marzluff 1988, Brown & Maurer 1989, Brown & Nicoletto 1991, Brown 1995).

4. CONSEQUENCES

The body size of an organism has both short- and long-term biotic and abiotic consequences. Moreover, these become disproportionately more important with increased size.

4.1. Biotic Consequences: Evolutionary Rates

Body size plays a critical role in determining rates of evolution within species and higher taxa (Evans et al. 2012). The most obvious reason for this connection is the allometric scaling of generation

time with body size (Brown 1995), which should lead to faster rates of evolution in small-bodied versus larger-bodied organisms. Consequently, even early workers such as Haldane (1949) considered measurements of evolutionary rates in terms of change per generation as a complement to measurements of rates per unit time. This intuition is supported by more recent studies of rates of molecular evolution. Smaller-bodied animals tend to have faster rates of molecular substitution per unit time, potentially reflecting a combination of effects from shorter generation times and higher mass-specific metabolic rates (Martin & Palumbi 1993, Liow et al. 2008, Bromham 2009).

In contrast to rates of molecular evolution, taxonomic rates of extinction and origination tend to be inversely correlated with body size. Most previous studies on this topic have focused on extinction. A positive association between body size and extinction risk has been demonstrated for Pleistocene and living mammals (Lyons et al. 2004, Davidson et al. 2009), marine and freshwater fishes (Olden et al. 2007), and birds (Boyer 2010). The association between body size and extinction risk is widely interpreted to result from the inverse association of body size with ecologically important traits such as population size, fecundity, and total resource requirements (Brown 1995).

However, the relationship between size and extinction risk appears to be more complex. Although the end-Cretaceous mass extinction was size selective for terrestrial vertebrates (Archibald 1996) and fishes (Friedman 2009), the end-Cretaceous, Triassic, and Permian extinctions were not size selective within gastropods and bivalves (Jablonski & Raup 1995, McRoberts & Newton 1995, Lockwood 2005, Payne 2005), although the end-Permian extinction was size biased within brachiopods (E.K. Schaal, M.E. Chapham, B.L. Rego, S.C. Wang & J.L Payne, manuscript in review). Because nearly all attention focuses on charismatic mass extinctions, it is difficult to assess whether background extinctions, which constitute the vast majority of species- and genus-level extinction in the geological record, are biased with respect to size. In a general survey of body size and extinction risk in marine animals and protists, Finnegan et al. (2009) found no evidence for a consistent difference in size between victims and survivors of extinction events in the fossil record. Overall, fossil data suggest that size selectivity in extinction is an exception rather than a rule, making it a potentially useful biological indicator of specific extinction processes. Intriguingly, size bias appears to be more common in vertebrates than in invertebrates, suggesting that the biological underpinnings to size-biased extinction may be more common in this group.

The relationship between body size and rates of taxonomic origination has received far less attention. That said, the long-term trends toward larger size in diverse higher taxa such as mammals (Alroy 1998) and marine bilaterians (Novack-Gottshall 2008a, Heim et al. 2015a) require that if there is a bias toward extinction of larger-bodied species and genera, this bias is counteracted by an even stronger bias toward the origination of larger-bodied species and genera. Consistent with this supposition, higher rates of origination appear to be typical of larger-bodied mammals (Liow et al. 2008). In the marine realm, the early Paleozoic trend toward larger size in brachiopods is best explained by the preferential origination of larger-bodied families across geological time, rather than by within-lineage evolution or a bias in the extinction process (Novack-Gottshall & Lanier 2008). Similar patterns were reported for Mesozoic decapods; newly originating groups not only were typically larger but also inhabited novel life habitats (Klompmaker et al. 2015). Moreover, much of the long-term increase in marine animal body sizes can be explained by the differential diversification of larger-bodied Linnaean classes (Heim et al. 2015a). Although some of the Phanerozoic increase certainly reflects the loss of diversity in brachiopods, which are smaller than the average marine animal, much of it reflects the rapid, largely post-Paleozoic radiations of bivalve molluscs and fishes.

Perhaps the most challenging unsolved problem involving body size and evolutionary rate is the decoupling of molecular and taxonomic measures of evolutionary rate. In the most detailed study of this topic to date, Liow et al. (2008) found that the higher rates of molecular evolution in mammals did not translate to higher rates of taxonomic evolution. Instead, larger mammals exhibit slower rates of molecular evolution but higher rates of origination and extinction of species and genera. The authors proposed behavioral differences as an explanation for this discrepancy, with the preferential ability of small mammals to hide or enter a state of torpor as a mechanism facilitating survival during rapid environmental changes. Because the inverse correlation between body size and taxonomic rates appears to hold in many other groups of animals that do not exhibit the same behavioral correlates of size, it is possible that additional mechanisms are also at play. For example, correlation between body size and population size and/or geographic range may influence the propensity of species and genera to give rise to new taxa or experience extinction. In particular, if most speciation is allopatric and most extinction happens via local or regional habitat change, then rates of molecular evolution may have little influence on long-term taxonomic rates. Although the topic clearly merits much more detailed investigation, we provisionally hypothesize that the evolution of taxa is rarely limited by rates of molecular evolution and that extinction and origination rates largely reflect processes related to biogeography rather than mutation and selection within populations.

4.2. Biotic Consequences: Ecology

Body size not only shapes evolutionary rates within species; it also plays a key role in controlling the assembly of organisms and species into communities and ecosystems. For example, competitive displacement often takes the form of changes in organism size, with closely related species separated in size by some limiting similarity (Brown & Wilson 1956, Hutchinson & MacArthur 1959). To the extent that ecological roles are determined by size, local communities often display body size distributions that differ from those expected under random draws from a regional species pool (Brown & Nicoletto 1991). In addition, food chains are typically structured by organism size, with predators exhibiting larger sizes than prey (Peters 1983, Kerr & Dickie 2001). At least in modern ecosystems, allometric scaling of generation time, home range size, and nutrient requirements also results in fundamental changes in the sizes, response times, and patterns of nutrient flow in ecosystems as a function of the minimum, mean, maximum, and modal sizes (Brown 1995, Woodward et al. 2005). The implications for ancient ecosystems are just beginning to be explored, especially through analyses of metabolic demand based on the evolution of organism size (e.g., Finnegan & Droser 2008, Finnegan et al. 2011, Payne et al. 2014) as a method for testing hypothesized increases in animal energy use across the Phanerozoic (Bambach 1993). Although perhaps not generally thought of as a consequence of body size evolution per se, the evolution of large, multicellular organisms has almost certainly created a positive feedback in the evolution of taxonomic diversity. For example, the large trees in tropical rainforests create complex, three-dimensional, and environmentally heterogeneous habitats that house the most diverse animal ecosystems on the planet (e.g., Erwin 1982). Large colonial corals perform a similar function in tropical reef ecosystems, and large mammals and sauropod dinosaurs host diverse anaerobic prokaryotic communities within their guts to avoid a terrestrial environment that is otherwise completely bathed in oxygen.

4.3. Feedbacks to the Earth System

Life depends upon Earth for the raw materials with which to build organisms and conduct metabolism, and biological activity in turn influences the evolution of the planet. The dramatic

chemical impact of biological evolution on Earth's surface environments has long been appreciated; such impacts range from the oxygenation of the atmosphere (Knoll 2003) to, according to more recent arguments, the production of minerals and mineral assemblages that would not exist without life (Hazen et al. 2008) and even the accelerated growth of continental crust (Rosing et al. 2006). Numerous other effects of biology on the Earth system have also been recognized, from the bioturbation of sediments, to the mixing of the surface ocean by the daily migration of pelagic organisms, to the formation of biogenic sediments such as coal and shell beds, to the modification of regional climate. It is likely that the order and nature of these feedbacks reflect and result from the evolution of organism size. Early in the history of life, most biological activity depended upon chemical potential gradients established through the abiotic advection of Earth materials, such as the movement of rocks due to plate tectonic activity or the convection of water through hydrothermal vent systems (Rosing et al. 2006).

The early feedbacks of life on the Earth system were largely chemical. Life remained entirely prokaryotic for approximately the first half of Earth's history, and neither the fossil record nor comparative phylogenetic analysis indicates that any organism exceeded a cubic millimeter in size prior to ~2.5 Ga (**Figure 2**). Due to the small sizes of early organisms, their interactions with the environment depended almost entirely upon diffusion of materials into and out of their cells. Survival depended upon the maintenance of chemical gradients maintained by the abiotic advection of Earth materials, driven by thermal gradients within Earth and the supply of solar energy to the oceans and atmosphere (Rosing et al. 2006). During this time, biological feedbacks on the Earth system took the form of metabolic innovations that enabled organisms to drive new chemical reactions and accelerate chemical reactions beyond the rates that would have occurred in the absence of biology. The most transformative of these innovations was the evolution of oxygenic photosynthesis, but the list extends to methanogenesis, methanotrophy, iron oxidation, iron reduction, and numerous forms of anoxygenic photosynthesis, among many others (reviewed in Buick 2012). The direct physical manifestations of these early life forms are limited, including only rare fossilized cells and microbially induced sedimentary structures such as stromatolites, thrombolites, and wrinkle structures (Buick 2012).

The evolution of eukaryotes during Paleoproterozoic time (~2 Ga) and the radiation of large animals and plants during the Neoproterozoic and early Paleozoic vastly expanded the range of feedbacks from biology to the Earth system. This occurred not because eukaryotes added any novel metabolisms—they did not—but rather because they are larger than prokaryotes. Larger organisms use chemical energy to drive additional advection both within their bodies and of external materials, enabling them to bring products and reactants together at higher rates, to maintain steeper chemical gradients in the environment, and thereby to fundamentally change the rates of Earth system processes. This advection takes many forms, such as the movement of air within lungs or blood within veins, the pumping of water by clams and oysters as they filter feed, the construction of dams by beavers to create a new habitat, or the sprint of a cheetah to run down its prey. Large size did not simply enable organisms to more effectively drive the advection of Earth materials; large size *required* this ability because metabolism cannot occur at biologically useful rates in large organisms without a capacity to drive at least internal advection. The consequences of these developments are widely apparent in the geological record.

Perhaps the most obvious and pervasive effect of body size evolution in the geological record is the development of bioturbation—the physical reworking of sediments through the activities of organisms. Phanerozoic sedimentary rock packages are often easily distinguished from their Precambrian counterparts by the presence of animal burrows. In fact, the base of the Phanerozoic is defined by the first occurrence of a feeding burrow, the trace fossil *Treptichnus pedum*, at the

Mistaken Point stratigraphic section in Newfoundland, Canada (Brasier et al. 1994). The prevalence, depth, and intensity of bioturbation have all increased across Phanerozoic time (Ausich & Bottjer 1982) along with the sizes of organisms. Bioturbation does not simply mix sediments within depositional beds; it also mixes sediments across depositional beds, obscuring original depositional textures and creating sedimentary sequences composed of much thicker sedimentary units (Tarhan & Droser 2014). Biological disturbance of sediments not only affects the physical characteristics of the sediments; it also modifies habitats in ways that influence the structure of local ecosystems. For example, widespread bioturbation of the seafloor has shifted the substrate at the sediment-water interface from firm-grounds to soft-grounds (Bottjer et al. 2000). The greater prevalence of bioturbation in more recent times has made the seafloor largely uninhabitable for unattached, nonmotile suspension feeders such as strophomenid brachiopods and the oyster *Exogyra* that were formerly diverse and abundant because under present intensities of bioturbation they would be overturned and then suffocate due to their inability to right themselves to reestablish their filtering behavior (Thayer 1979). Modern examples include both soil compaction resulting from the movement of large-bodied vertebrates and bioturbation by small burrowing rodents and insects.

The evolution of physically and chemically robust structural elements to support large organisms has also impacted the nature of the sedimentary rock record. In addition to being bioturbated, Phanerozoic sedimentary rock sequences are identifiable by the accumulations of biogenic sediments, including coal, phosphorites, and shell beds in the form of shallow-marine accumulations of animal shells to deeper-marine accumulations of protistan tests of carbonate and silica. The oldest shell beds occur in Neoproterozoic carbonate rocks, comprising shells of *Cloudina* and *Namacalathus*, two genera of calcified metazoans with uncertain phylogenetic affinities (Grotzinger et al. 2000). The thickness of shell beds, like the depth and prevalence of bioturbation, has generally increased across the Phanerozoic along with the sizes of shell-producing animals. Paleozoic shell beds are typically a few centimeters to tens of centimeters thick, whereas post-Paleozoic shell beds commonly exceed one meter in thickness (Kidwell & Brenchley 1994, Li & Droser 1999). Economically important coal seams first appear in the geological record during Devonian time, coincident with the initial evolution of large, woody trees, and have remained an important part of the sedimentary rock record for the past 350 Ma (Cross & Phillips 1990). Interestingly, they became less abundant and substantially thinner for an interval of 5 to 10 Ma following the end-Permian mass extinction (ca. 252 Ma). This coal gap followed the extinction of the large, coal-producing glossopterid trees in the Southern Hemisphere and coincided with an interval during which terrestrial vegetation was temporarily dominated by small shrubs (Retallack et al. 1996). Coal beds are particularly important because they are not only physically distinct but also chemically novel, housing a concentrated supply of reduced carbon that has ultimately enabled the development of industrial civilization.

Although the evolution of macroscopic organisms did not entail the discovery of any new energy metabolisms, the advent of large organisms did enable life to influence the chemical structure of air, water, and sediments in novel ways, with important impacts on global biogeochemical cycles. For example, bioturbation not only mixes sediments but also increases the time over which sedimentary organic matter is exposed to oxidants dissolved in seawater, such as oxygen and sulfate, thus altering rates of organic carbon burial and impacting the geological cycling of carbon and sulfur as well as the accumulation of oxygen in the atmosphere (Canfield & Farquhar 2009, Boyle et al. 2014). Animals are also important for the mixing of seawater. Schooling animals and daily vertical migration provide mixing potentially comparable to that of physical processes such as storms, winds, and tides (Katija & Dabiri 2009). The evolution of large, filter-feeding animals may even have shifted the oceans from a eutrophic to an oligotrophic state. For example, the evolution

of sponges has been hypothesized to have drawn down the concentration of dissolved organic carbon in seawater, perhaps by several orders of magnitude, thereby enhancing the concentration of dissolved oxygen (Butterfield 2009, Sperling et al. 2011). Alternatively, or in addition, the evolution of large pelagic animals may have enhanced the oxygenation of surface waters either through the production of fecal pellets (Logan et al. 1995) that increased the efficiency of organic carbon transport to deeper water or by daily vertical migrations (Bianchi et al. 2013), in either case shifting oxygen demand from surface waters to greater depths in the ocean. In more recent times, the overharvesting of oysters has caused the opposite effect. Whereas oysters formerly filtered the entire volume of the Chesapeake Bay every three days, maintaining clear water, overharvesting has curtailed this biological filtering of bay waters and led to the development of eutrophic conditions (Jackson et al. 2001). Finally, the evolution of large plants with high capacity to transport water has had a large influence on both global and regional climate. At the global scale, the evolution of large plants with extensive root systems has been hypothesized to have increased the efficiency of silicate weathering as a function of atmospheric $p\text{CO}_2$, generally cooling global climate and perhaps helping to explain the timing of the Permo-Carboniferous glacial interval (Berner & Kothavala 2001). Transient nutrient pulses to the oceans associated with the increase in chemical weathering on land during the initial expansion of terrestrial forests have even been linked to the development of ocean anoxia and associated mass extinction during Late Devonian time (Algeo & Scheckler 1998). On a more regional scale, the high water transport capacity of angiosperms has increased the size of the Amazon rainforest approximately fivefold over the extent expected in a world inhabited by plants with lower transpiration capacity (or no plants at all) (Boyce & Lee 2010).

In addition to effects directly related to advection of sediment and water by large-bodied organisms, the evolution of large body size has also influenced atmospheric chemistry through the creation of novel microhabitats within the bodies of large organisms. For example, large herbivores often feed on vegetation with low nutritional quality containing high levels of cellulose, hemicellulose, and lignin. Because these compounds are refractory to enzymatic digestion, herbivores maintain a symbiotic relationship with microorganisms in their stomach or cecum to break down plant matter; methane is a byproduct. Enteric methane production has risen significantly in recent decades along with the global population of cattle (Crutzen et al. 1986), serving as a climate forcing mechanism. Interestingly, the earlier extinction of the Pleistocene megafauna may have reduced enteric methane production enough to account for the decline in atmospheric methane concentrations during the Younger Dryas (Smith et al. 2010b, 2015). Similarly, enteric methane production in sauropod dinosaurs may have approached the magnitude of global methane production from all sources today, potentially helping to account for the overall warmth of the Mesozoic climate (Wilkinson et al. 2012).

Finally, the evolution of large body size has been critical to the development of the geologically most important new group since cyanobacteria—humankind. Humans not only alter the biosphere (Dirzo et al. 2014, McCauley et al. 2015) but are now also modifying many global biogeochemical cycles (Vitousek et al. 1997). Moreover, humans are among the most important forces moving sediment across continents (Wilkinson 2005), with the nutrient runoff from agriculture causing the development of widespread, anoxic dead zones in many coastal marine settings. The capacity of humans to take these actions depends upon body size sufficiently large to support a brain sophisticated enough to develop language, use tools, and ultimately develop a complex, technological society. In particular, a large component of the growth of human population sizes and geological footprint results from our ability to transport or chemically alter large quantities of Earth materials over long distances—highlighting once again the impact of the evolution of large organism

sizes on the movement of geological materials and the ultimate acceleration of geochemical reactions.

SUMMARY POINTS

1. Body size determines energetic demands, regulates the rates of fundamental physiological processes, and influences many vital ecological-, population-, and community-level characteristics.

2. There have been two major jumps in the body size of living things on Earth—in the mid-Paleoproterozoic (∼1.9 Ga) and during the late Neoproterozoic–early Paleozoic (600–450 Ma), leading to the ∼22 orders of magnitude of variation seen across life today.

3. Many animal groups—especially marine animals, terrestrial mammals, and nonavian dinosaurs—show a pattern of size increase over their evolution (Cope's rule). Recent studies point to species selection as the primary driver, especially a tendency for newly originating taxonomic groups to have larger body sizes.

4. Evidence suggests that life originated close to the smallest theoretical size where all cellular machinery could be incorporated. In contrast, there is no clear evidence that life has yet reached a physically imposed maximum size.

5. Organisms tend to move materials, both internally and externally, in order to maintain their energy metabolism. Consequently, they play crucial roles in the biogeochemical cycling of many critical nutrients and elements, including sulfur, nitrogen, and methane.

6. Large organisms create habitat space for smaller species to diversify taxonomically, from rainforests to coral reefs to the guts of large animals.

7. The evolution of larger organisms has increased the influence of life on global geological processes and biogeochemical cycles.

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