RESEARCH ARTICLE

Diversity and Evolution of Body Size in Fishes

James S. Albert · Derek M. Johnson

Abstract The diversity of body sizes observed among species of a clade is a combined result of microevolutionary processes (i.e. natural selection and genetic drift) that cause size changes within phylogenetic lineages, and macroevolutionary processes (i.e. speciation and extinction) that affect net rates of diversification among lineages. Here we assess trends of size diversity and evolution in fishes (non-tetrapod craniates), employing paleontological, macroecological, and phylogenetic information. Fishes are well suited to studies of size diversity and evolution, as they are highly diverse, representing more than 50% of all living vertebrate species, and many fish taxa are well represented in the fossil record from throughout the Phanerozoic. Further, the frequency distributions of sizes among fish lineages resemble those of most other animal taxa, in being right-skewed, even on a log scale. Using an approach that measures rates of size evolution (in *darwins*) within a formal phylogenetic framework, we interpret the shape of size distributions as a balance between the competing forces of diversification, pushing taxa away from ancestral values, and of conservation, drawing taxa closer to a central tendency. Within this context we show how non-directional mechanisms of evolution (i.e. passive diffusion processes) can produce an hitherto unperceived bias to larger size, when size is measured on the conventional log scale. These results demonstrate how the interpretation of macroecological datasets can be enriched from an historical perspective, and document the ways in which macroevolutionary and microevolutionary processes may be decoupled in the production of size diversity.

Keywords Allometry · Cope's rule · Darwins · Character evolution · Evolutionary rates · Macroecology · Macroevolution · Metabolic theory · Paleontology · Skewness

Introduction

Large-scale patterns in body size diversity have been studied extensively from both the paleontological and macroecological perspectives. One widely cited trend in the fossil literature is an increase in body size within lineages over time known as Cope's rule (Cope 1877; Newell 1949; Damuth 1993). A net increase in average size over macroevolutionary time scales has been observed in many, although not all, animal taxa (Polly 1998; Jablonski 1997a; Knoll and Bambach 2000; Hone and Benton 2005). Stanley (1973) noted that an evolutionary expansion into an ecologically or physiologically bounded size space from a relatively small ancestral size would result in a passive trend (*sensu* McShea 1994) towards larger average size within lineages (hereafter referred to as the 'Stanley effect'). Indeed many vertebrate taxa are thought to have originated at a relatively small size as compared with the range of sizes into which they eventually diversified (Alroy 1998; Shu et al. 2003; Laurin 2004). May (1988) argued from theory that a simple size diffusion model with an absorbing (i.e. not reflecting) lower boundary, with size change resulting from many multiplicative anagenetic events, will produce log-normal rather than log-skewed

J. S. Albert (✉)
Department of Biology, University of Louisiana at Lafayette,
Lafayette, LA 70504-2451, USA
e-mail: jalbert@louisiana.edu

D. M. Johnson
Department of Biology, Virginia Commonwealth University,
Richmond, VA 23284, USA
e-mail: dmjohnson@vcu.edu

distributions, and (Maurer et al. 1992) confirmed this result using simulation studies.

Yet in most taxonomic groups, the majority of species have relatively small body sizes, as compared with the full range of sizes for that group (Hutchinson and Macarthur 1959). From a macroecological perspective, the size-frequency distribution of most clades is right-skewed, even on a log scale, with more scatter to the right of the median than to the left (Brown and Maurer 1986; Gaston and Blackburn 2000; Maurer et al. 2004). In a right-skewed distribution (i.e. with positive skewness) the tail on the left side of the probability density function is longer than the right side, and the bulk of the values (possibly including the median) lie to the right of the mean (e.g. Fig. 1). Right-skewed size distributions have been interpreted variously as evidence for the selective advantages of small size (e.g. Damuth 1993; Blanckenhorn 2000; Maurer et al. 2004), increased rates of diversification (more speciation and/or less extinction) at small size (Jablonski 1997b; Maurer 1998; Gardezi and da Silva 1999; Knouft and Page 2003), or the long-term survival risks of large size (Maurer et al. 1992; Purvis et al. 2003; Clauset and Erwin 2008; Clauset et al. 2009).

Why are the size-frequency distributions of most higher taxa right-skewed, even on a log scale? Should a right-skewed size distribution be viewed as representing a transient state, i.e. the expansion of species to larger sizes, or as a leftward shift in the mass of the distribution (with more species at smaller sizes)? Does a skewed distribution indicate the operation of different evolutionary processes (i.e. anagenesis, speciation, extinction) at extreme (large and small) sizes (Stanley 1990; Arnold et al. 1995;

Jablonski et al. 2006)? Or does skewness indicate an asymmetrical response to the influence of the same processes among taxa at either end of the size spectrum (Gaston 1998; Clauset and Erwin 2008; Clauset et al. 2009)?

Here we use an integrative approach to assess trends of size evolution, employing paleontological, macroecological, and phylogenetic information in fishes (datasets in Albert et al. 2009). Fishes (non-tetrapod craniates) are an excellent taxonomic group for testing theories on the evolution of continuous traits such as size. Fish clades are phenotypically and ecologically diverse, representing more than 50% of all living vertebrate species (Haussler et al. 2009), and exhibit body size diversity approximating that of all vertebrates combined (Gillman 2007) (Table 1). Fishes also have a rich fossil record from throughout the Phanerozoic (Long 1995; Janvier 1996). We introduce a new use of a method for measuring rates of evolution in *darwins* (Haldane 1949) of continuous traits in an explicitly phylogenetic context (i.e. on a tree), and demonstrate how non-directional mechanisms of evolution (i.e. passive diffusion processes) can produce an hitherto unperceived bias to larger size, when size is measured on the conventional log scale. This approach interprets the shape of a size distribution as a balance between the competing forces of diversification, allowing taxa to evolve away from ancestral values, and of conservation, drawing taxa closer to a central tendency (Fig. 1a). Our goal is to describe the major patterns of size evolution in fishes, and to use these patterns to evaluate particular evolutionary models of size evolution (e.g. Cope's rule).
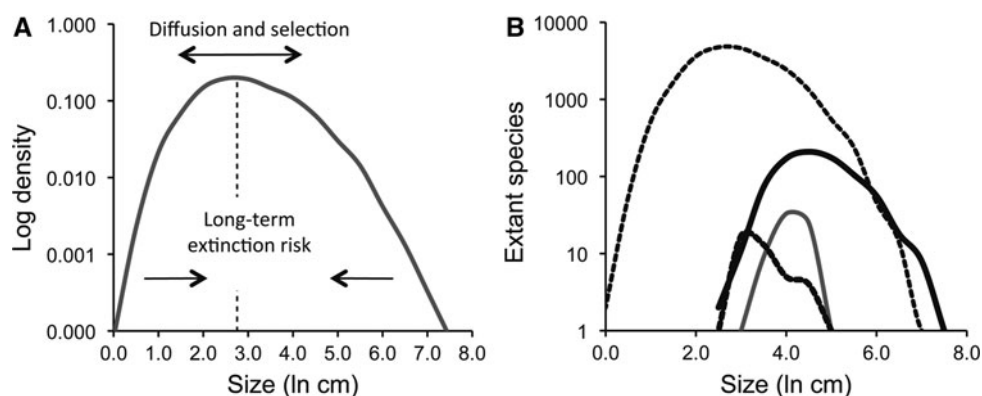

Fig. 1 Smoothed body-size distributions of extant fish species. **a** Size data for 24,260 species pooled. Note this distribution is right skewed ($P < 0.001$) such that the median (*vertical dashed line* at 14.8 cm) is less than the average (not shown at 27.3 cm). Note also the tails have similar rarity values indicating approximately symmetrical boundary effects. **b**. Size-frequency distributions of four extant post-Ordovician fish clades; Myxinoidei (*thin line*), Petromyzontiformes (*thick* *dashes*), Chondrichthyes (*thick line*), Actinopterygii (*thin dashes*). Data for non-tetrapod sarcopterygians (11 species) not shown. Note these hump-shaped size distributions are maintained as a balance between the short-term (microevolutionary) effects of neutral diffusion and selection away from an ancestral condition, and the long-term macroevolutionary risks of extinction in taxa with extreme sizes. Note also the absence of a lower boundary effect in fishes

Table 1 Summary of statistics for the extant fish species dataset

Clade	N	Avg cm	Avg ln cm	Min	Max	Range	Skew
Myxinoidei	69	51.2	3.87	2.91	4.75	1.85	−0.27
Petromyzontiformes	39	29.7	3.24	2.56	4.79	2.23	1.11
Chondrichthyes	829	117.0	4.43	2.36	7.14	4.78	0.43
Sarcopterygii[a]	11	123.9	4.75	3.79	5.30	1.51	−1.09
Actinopterygii	23,312	23.9	2.68	0.00	7.00	7.00	0.31
Total	24,260	27.2	2.75	0.00	7.14	7.14	0.37

Clades are the five (of 14) surviving craniate radiations that emerged from the Ordovician c. 444 Ma (Long 1995; Janvier 1996)

[a] Sarcopterygii excluding tetrapods

Materials and Methods

Size and Stratigraphic Data

Size and stratigraphic data are for 465 fish species are reported in Albert et al. (2009), and a taxonomic summary of this dataset is provided in Table 2. Size was assessed as maximum recorded total length (TL) in cm as measured from the tip of the snout to the posterior margin of the caudal fin. Total length was measured directly from specimens, published photographs or reconstructions of articulated specimens in primary sources, or published lengths (e.g. Frickhinger 1995). Total length is highly correlated with body mass (in grams), where mass may be estimated from TL from the empirical equation: $y = 0.0217x^{2.861}$ (Albert et al. 2009). Importantly, the skewness of log transformed size distributions are identical, regardless of whether size is measured as length or mass.

All analyses were conducted using log transformed total length data and the geometric average was used as a measure of central tendency. Because fishes exhibit indeterminate growth, taxa for which morphologically mature specimens are not known were excluded, as were taxa for which adult body size cannot be reliably estimated from known fossilized fragments (e.g. †*Polymerolepis margaritifera,* †*Lophosteus sp.*). Many macroevolutionary studies of size in organisms with indeterminate growth use maximum rather than average size, despite the statistical difficulties presented by extreme values (Jablonski 1997b; Roy et al. 2000). Mature specimens are recognized by osteological criteria when available; i.e. the shape of bones in the sphenoid and palatoquadrate regions of the skull, and the scapulocoracoid region of the pectoral girdle (Arratia 1997). Size of some Paleozoic forms was estimated from large body fragments (e.g. †*Andinaspis suarezorum,* †*Pituriaspis doylei*). Fossil species were dated to one of 24 geological epochs or series (e.g. Upper Devonian, Paleocene) with geological dates from (Gradstein et al. 2004). These time intervals range from 5 MY (Upper Silurian) to 46 MY (Upper Cretaceous), with an average of 23.6 ± 12.5 MY.

Taxon Sampling

We used a clade-based approach to taxon sampling designed to represent all higher craniate taxa for which reliable size estimates are available. The taxon sampling strategy was to include whenever possible, for each node (branching point) in the tree, at least one species in each of the two daughter taxa. Such a clade-based approach to taxon sampling maximizes representation of phylogenetic diversity among major lineages, and has been shown to be less sensitive to preservational biases than stratigraphically based taxon-counting methods (Griswold et al. 1998; Prendini 2001, Lane et al. 2005). This taxon sampling strategy produced a dataset of sufficiently broad temporal (10^7–10^8 MY) and taxonomic (10^2–10^4 species) scope to avoid nonrandom sampling errors arising from community assembly processes, convergent evolution, or investigator bias (Ackerly 2000).

This taxon-sampling scheme resulted in a dataset with 465 fossil species, of which 425 are known only as fossils. The fossil dataset includes representatives of 26% (164 of 622) of all fish families for which fossils are known, 51% of the 324 fish families known only as fossils (Benton 1993), and 68% (71 of 105) of non-teleost actinopterygian genera known only as fossils (Benton 1993; 106 non-teleost actinopterygian genera in Sepkoski (2002). Conodonts were excluded from analysis due to uncertainties in body size and detailed phylogenetic information (Donoghue and Sansom 2002; Janvier 2003; Dong et al. 2005; Northcutt 2005; Blieck et al. 2005). Triassic neoselachians are known only from teeth (Underwood 2006) and were also excluded from analysis.

In order to more completely sample certain clades that are poorly represented as fossils (Hurley et al. 2007) (Albert et al. 2009), size data for 13 terminal taxa are presented as geometric averages of the log maximum total lengths of the extant species, using data from Froese and Pauly (2005). These clades include the seven extant myxiniform (hagfish) genera, two of the extant petromyzontiform (lamprey) genera, one extant dipnoan genus (*Protopterus*), and five extant actinopterygian genera

Table 2 Taxonomic summary of the fossil fish dataset

Clade	Fossil[a]	Extant[b]	Total	%Total
Cephalochordata	3	1	4	0.86
†Yunnanozoa	2	0	2	0.43
Hyperotreti	3	7	10	2.15
†Myllokunmingiida	2	0	2	0.43
Hyperoartia	5	5	10	2.15
†Pteraspidomorphi	25	0	25	5.38
†Thelodonti	8	0	8	1.72
†Anaspida	6	0	6	1.29
†Galeaspida	7	0	7	1.51
†Pituriaspida	1	0	1	0.22
†Osteostraci	15	0	15	3.23
†Furcacaudiformes	2	0	2	0.43
†Placodermi	39	0	39	8.39
Chondricthyes	91	5	96	20.65
†Acanthodii	17	0	17	3.66
Sarcopterygii	38	4	42	9.03
Actinopterygii	161	18	179	38.49
Total	425	40	465	100.00

Clades are the Ordovician craniate radiations (Blieck and Turner 2003) and first two outgroups. †, extinct taxa. Data are maximum recorded total length (cm), geological age (epoch or series), and phylogenetic position, from multiple sources (see complete dataset in Albert et al. (2009)

[a] Taxa known only as fossils

[b] Extant taxa for clades lacking fossils that have reliable size data (e.g. *Myxine*; *Huso*)

(*Polypterus*, *Acipenser*, *Scaphyrinchus*, *Psuedoscaphyrinchus*, *Clupea*). The addition of these living terminal taxa can potentially affect the analysis of size trends because extant fishes often exhibit larger sizes than fossil representatives of their respective higher taxa (Albert et al. 2009). However excluding these extant taxa resulted in large gaps in the taxon sampling of the major craniate lineages, and so they were retained in the analysis.

Phylogeny

Size-change was traced on a composite tree topology constructed from literature sources (Fig. 2; see Albert et al. 2009 and references therein). The phylogeny of Paleozoic vertebrates (i.e. Ordovician Radiations *sensu* Blieck and Turner 2003) follows Long (1995), Janvier (1996), and Janvier (2003), and references in these papers, with emendations as noted by taxon in Albert et al. (2009). These sources were used to construct a tree topology with 843 branches and 86 polytomies, or a tree that is about 91% resolved. Two chordate outgroup taxa were used to root the size optimizations: Cephalochordata and Yunnanozoa (Mallatt and Chen 2003). The phylogenetic positions of

†*Haikouichthys* as a non-craniate deuterostome follows (Shu 2003). Data for Hyperoartia are from Janvier and Lund (1983), Gess et al. (2006) and Janvier et al. (2006), for post-Paleozoic chondrichthyans from Cappetta (1987), Underwood (2006), for sarcopterygians from Clouthier (1996), Clouthier (1997), Clouthier and Forey (1991), and Clouthier and Ahlberg (1996), for basal actinopterygians from Arratia (1997), Coates (1998), Arratia (1999), Dietze (2000), Arratia and Cloutier (2002), Arratia and Cloutier (2004), Lund (2000), and Friedman and Blom (2006), and for teleost from de Pinna (1996), Johnson and Patterson (1996), Arratia (1997, 2004) and Santini et al. (2009).

Branch lengths were estimated from stratigraphic data from fossils (Benton 1993, 2005; Benton and Donoghue 2007) in millions of years (MY) as the absolute age difference between nodes. Minimum branch lengths were set at 1.0 MY so that all branch lengths were non-zero. Increasing the minimum branch length reduces absolute estimates of size evolution for short branches but does not affect the skew of the size-change frequency distribution (data not shown).

Ancestral Trait Reconstruction

Linear Parsimony (LP) and Least-Squared Parsimony (LSP) optimization methods were employed to estimate total length values at interior tree nodes using the Mesquite v.1.06 software package (Maddison and Maddison 2006). LP minimizes the total amount of trait change along tree branches such that the cost of a change from state x to y is $|x - y|$. LSP, also referred to as Squared-Change Parsimony, follows a Brownian motion model of evolutionary change in which the cost of a change from state x to state y is $(x - y)^2$ (Maddison 1991). LP differs from LSP, and also from model-based (i.e. Bayesian and Likelihood) approaches to character state optimization, in that LP permits the reconstruction of discontinuous events, or of large changes in trait values (Butler and Losos 1997; Pagel 1999; Albert 2006). Although evolutionary change is often thought of as gradual, large differences in trait values between internal tree nodes may result from a variety of real biological processes, including punctuated evolution (Pagel et al. 2006; Monroe and Bokma 2009) or extinction of taxa with intermediate trait values (Butler and Losos 1997). LP also permits the reconstruction of ambiguous ancestral state values when data are insufficient to provide an unambiguous resolution. Nevertheless, estimates of average size among fossil fishes per epoch using LP and LSP are significantly correlated (Albert et al. 2009). All ancestral reconstruction methods assume that trait evolution is conservative enough for node reconstruction techniques to be useful, even in the face of large standard errors (Polly 2001). LP optimization was performed using 10
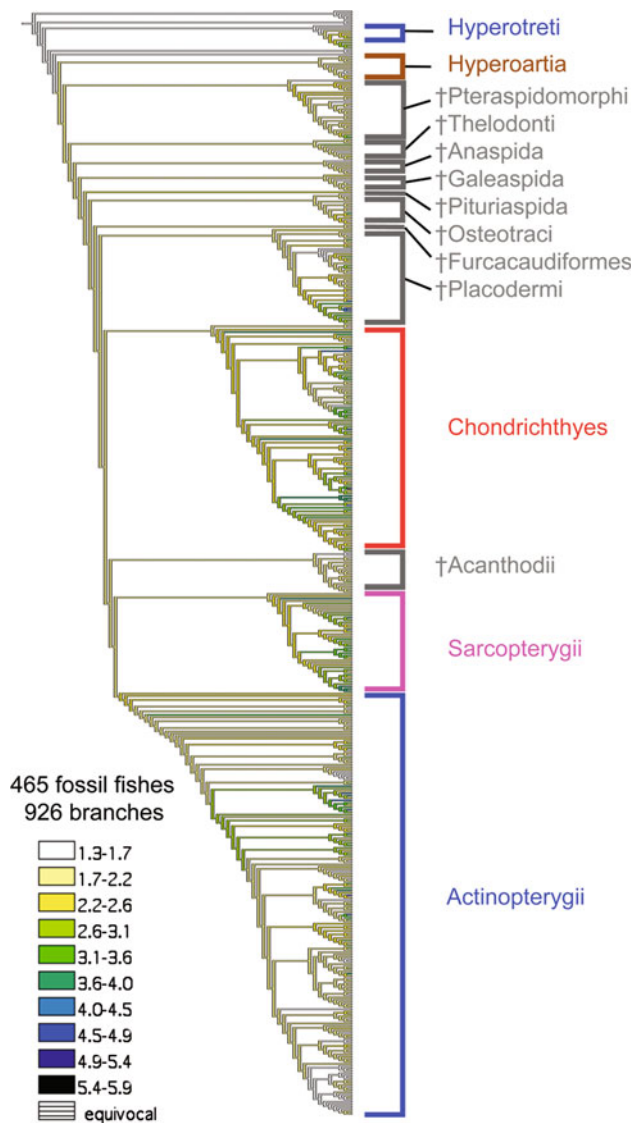
Fig. 2 Phylogeny of 465 fossil fish species with rates of size evolution (in *darwins*) estimated at 928 branches. Tree topology from Albert et al. (2009) and references therein. Extinct clades in gray font; extant clades in *colored fonts*. Size data as ln(cm). Branch lengths in MY (not to scale) estimated from stratigraphic data (see text for methods) (Color figure online)

replicates on arbitrarily fully resolved trees and the qualitative results of the size-change analysis were similar in all replicates (data not shown).

Rates of Evolution

As a direct test of Cope's rule we assessed the proportion and magnitude (per unit time) of changes to larger and smaller sizes, over the internal branches (inter-nodes) of the well-resolved phylogenetic tree of fossil fishes (Fig. 2). All size data were log transformed prior to analysis. Evolutionary rates were expressed in *darwins* (Haldane 1949)

as the difference in size per unit time along internal branches of a phylogenetic tree:

$$d = [\ln S_2 - \ln S_1]/t_2 - t_t \qquad (1)$$

where S_n is the inferred size at node n, and t_n is the estimated geological age of node n in Ma. Equation 1 can be expressed more simply as:

$$d = dS/dt \qquad (2)$$

where dS is the difference in size between nodes per million year of branch length (dt). In this metric scheme one *darwin* is a change in the value of the trait by a factor of e in one million years.

Measuring evolutionary rates in *darwins* has been criticized on the grounds that rates are expected to diminish when measured over larger time intervals due to averaging of higher-order frequency fluctuations in the direction of trait change (Gingerich 1983; Pérez-Claros and Aledo 2007), and should be corrected by plotting rates against time intervals (Gould 1984; Sheets and Mitchell 2001). However, branch lengths used in this study showed low variance (21.8 ± 3.3 MY), and we found no correlation between rate values (in *darwins*) and branch length ($R^2 = 0.0004$; directional $P = 0.30$). Rates were not expressed in *haldanes* (phenotypic standard deviations per generation (Gingerich 1993) due to uncertainties of estimating generation times.

Results

Macroecological Patterns

Extant fish species range in size over about three orders of magnitude as measured on an arithmetic scale (1.0–1,265 cm), or about seven orders of magnitude as measured on a log scale (Table 1; Figs. 1 and 3a). Extant fish families also exhibit a broad range of skewness values, from −2.16 ($n = 7$ species) in the sawfishes (Pristidae, Chondrichthyes) to 2.19 ($n = 173$ species) in the perches and darters (Percidae, Actinopterygii). Although species richness and average body size *per se* do not predict skewness values in extant fish families, most species-rich families have skewness values near zero (median skewness 0.04), and most families with extreme skewness values ($\geq |2|$) have few (<10) species (Percidae being an exception to both these trends) (Fig. 3b). There is a correlation in the relationship between skewness and size (Fig. 3c).

Positive skewness is a pervasive feature of body-size distributions in fish taxa. Most large datasets of fish diversity are right-skewed, even when size as assessed as *ln*[cm]. The data sets examined for this study include: all extant fish species (Fig. 1; $n = 24,260$; skewness $= 0.37$;
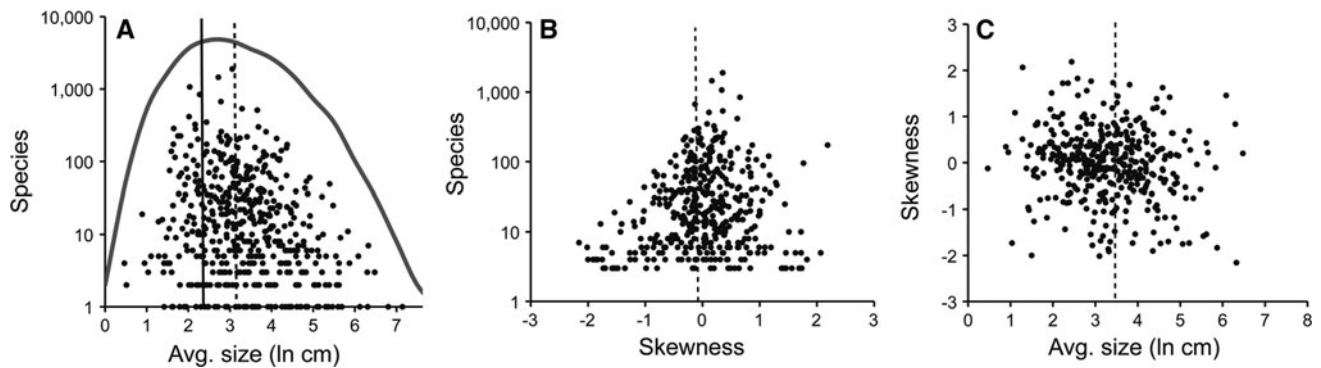
Fig. 3 Relationships between species richness and measures of size diversity (average and skewness of size distributions) among extant fish families. Data for 24,260 species in 515 families from (Froese and Pauly 2005). In all panels each data point represents a single fish family, and *dashed vertical lines* represent average (skewness) or median (size) values of all fish families. *Solid vertical line* in **a** represents average size of all fish species (*solid curve*). **a** Right-skew size distribution of all extant fish species and families. **b** The skewness values of most fish families are close to zero, and few (1% or 5/515) fish families exhibit extreme skewness values >|2|. The median skewness value of all fish families is 0.04, and of all fish species is 0.37. **c** Body size is not correlated with skewness among extant fish families

$P < 0.001$), four of the five extant post-Ordovician fish clades (Table 1, Sarcopterygii excluded), the fossil species dataset of Table 2 ($n = 465$; skewness = 0.09; $P \leq 0.001$), and the distribution of size-change events along the branches of the fossil fish phylogeny in Fig. 2 (see also Table 3; $n = 929$; skewness = 0.29; $P = < 0.001$).

Macroevolutionary Patterns

Diversification of fishes into size space through the Phanerozoic occurred in two readily distinguishable phases (Figs. 4a, b). The first was a relatively rapid Expansion Phase from the Lower Cambrian to the Upper Silurian (542–417 Ma), a duration of about 23% of the Phanerozoic. During this Expansion Phase average arithmetic size (in cm) increased about 10-fold, from about 2.7 cm in the Lower Cambrian ($n = 5$) to 28.7 cm ($n = 59$), and the range of sizes increased from 0.5 cm to about 200 cm. By the Upper Devonian (c. 375 Ma.) giant species like the arthrodire placoderm †*Dunkleosteus terrelli* at about 800 cm had evolved, approaching the upper size limit of fishes as a whole. Further, the size distribution of fossil fishes during the Expansion Phase has a negative skewness (Table 3). Fishes achieved approximately modern dimensions of size diversity (i.e. average size in cm and size range as ± SEM) by the Lower Devonian (c. 416 Ma; 28.7 ± 4.5 cm, compared to the extant 27.2 ± 2.6 cm; Fig. 4c, d). The size range of Devonian fishes spans about three orders of magnitude in metric units, from miniaturized yunnanolepid antiarchs (c. 5 cm) to giant brachythoracid arthrodires (c. 800 cm). The range of sizes for fishes in the Devonian and Recent are therefore very similar, especially considering the limited taxon sampling and

taphonomic filters that obscure understanding the full range of diversity in paleofaunas (Albert et al. 2009).

The second phase of diversification into size space was a much longer time interval, extending from the Lower Devonian to the Recent (416–0 Ma.), or over about 77% of the Phanerozoic. During this interval the average size and size diversity of fishes fluctuated non-directionally in a state of quasi-equilibrium. Size estimates of fossil fishes during this Quasi-equilibrium Phase have an arithmetic average (or mean) value of 51.7 cm (SEM = 4.7 cm; Fig. 3b), as compared with an average of 27.3 cm for all extant fish species (Fig. 1), or 56.7 cm for all extant fish families (Fig. 3d). These data show that the major features of body size diversity in living fishes, especially measures of central tendency (average and mode) and spread (range and standard deviation) had all become established relatively early, when vertebrates had achieved about 23% of their current age. Indeed the limits of size diversity in fishes were largely established within a few tens of millions of years after the origin of Gnathostomata during the Silurian (444–416 Ma).

Patterns of size evolution (as measured in *darwins*) in fossil fishes through the Phanerozoic are similar to those of absolute size itself. The range of size-change values (d) along branches of the fossil fish phylogeny increased rapidly during the early Paleozoic, and then exhibited no directional change for the remainder of the Phanerozoic (Table 3; Fig. 5). Such a rapid size expansion during the early Paleozoic is observed in many metazoan taxa (e.g. Sepkoski 1981; Miller 1997, 1998; Stanley 1998; Novack-Gottshall and Lanier 2008; Alroy 2010). As with the frequency distribution of absolute body size in fossil fishes, the distribution of size-changes (in *darwins*) is also right-skewed (Fig. 5b; skewness = 0.61; $P < 0.001$). The right-skewed distribution of evolutionary rates reported here in a phylogenetic context for fossil fishes

Table 3 Summary of statistics for rates of size evolution (in *darwins*) for fossil fishes during the Phanerozoic

Statistic	Phanerozoic	Expansion phase	Quasi-equilibrium phase
Age (Ma.)	542–0	542–417	416–0
N	928	280	648
Min	−2.43	−2.43	−2.31
Max	3.00	2.04	3.00
Mean	0.01	0.00	0.01
Range	5.43	4.47	5.31
SEM	0.02	0.02	0.02
Skew	0.43	−0.32	0.49

Expansion phase from lower Cambrian to upper Silurian; Quasi-equilibrium phase from lower Devonian to recent. Rates assessed on the log-only ($b = 1.0$) scale. *N*, number of branches in dataset partition, *SEM* standard error of the average

closely resembles those of other fossil and extant vertebrate clades examined to date with comparable taxonomic and temporal resolution (Gingerich 1993; Millien 2006). The values of evolutionary rates in fishes have a median of $d = 0.00$, and range from $d = −1.79$ to 1.90. These are similar to values reported for other fossil (Clyde and Gingerich 1994) (Guthrie 2003) and some (Koch 1986) but not all (Reznick et al. 1997) extant vertebrate groups.

Discussion

Size-Biased Extinction Risks

The most extensive macroecological analyses of size-frequency distributions to date have focused on extant mammals

(including late Quaternary fossils) and extant birds (Clauset and Erwin 2008; Glazier 2008; Clauset et al. 2009; Monroe and Bokma 2009; Olson et al. 2009; Capellini et al. 2010). In both these clades, the shape of the size distribution was shown to closely match a three-parameter simulation model of cladogenetic diffusion (Clauset and Erwin 2008; Clauset et al. 2009). The parameters of this model are: (1) biased rates of anagenesis to larger sizes (Cope's rule), (2) higher extinction risk at larger sizes, and (3) taxon-specific ecophysiological limits at lower sizes. However, the generality of studies on mammals and birds for understanding body size evolution in other animal groups remains unclear. For example, the distribution of body size in fish clades is qualitatively different from that of terrestrial mammals and birds in the apparent absence of a lower boundary effect (Fig. 1). Whereas there are fewer species of terrestrial mammals and birds at the smallest sizes, the proportions of fish species in the two tails (smallest and largest size categories) are similar.

Unlike the situation in mammals and birds, there does not appear to be a size-biased extinction risk for fish taxa with small adult body sizes (Olden et al. 2007). For example, minimum body size has not been correlated with geographic range size (Reynolds et al. 2005; Griffiths 2006; Albert et al. 2011a, b), elevation (Matthews 1998; Fu et al. 2004), hypoxia tolerance (Nilsson and Östlund-Nilsson 2008), or oceanic depth (Smith and Brown 2002). Further, miniaturization is a widespread life-history strategy in many fish groups, both freshwater (Weitzman and Vari 1988a) (Knouft and Page 2003) and marine (Munday 1998). However, large body size is associated with elevated extinction risk in many living fish taxa, due to commercial fishing and anthropogenic habitat degradation (Olden et al. 2007). Although the relative roles of
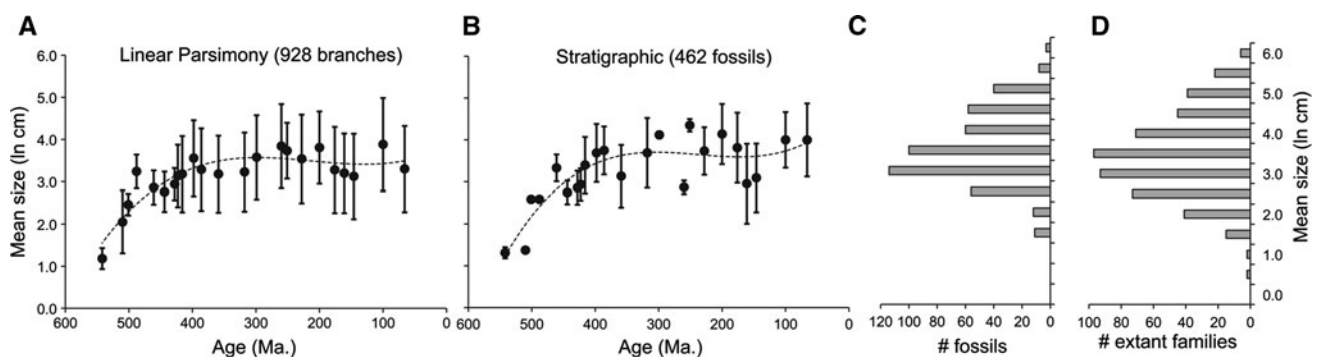

Fig. 4 Average body size of fossil fishes through the Phanerozoic. **a** LP estimates for all branches on the phylogeny of Fig. 2. **b** Average size of fossils for each stratigraphic interval (epoch). *Error bars ±* one standard deviation of the average of branches or fossils per epoch. Data fit to 3rd order polynomials with adjusted R^2 values. See text for methods. **c** Right-skewed size distribution of species in the fossil fish dataset (skewness = 0.09; *P* < 0.01; Kuiper test). **d** Right-skewed distribution of average size in extant fish families (*n* = 515; skewness = 0.46; *P* < 0.0001; Kuiper test). The right tail of the extant fish family distribution is truncated to facilitate comparison with the size range of fossil fishes; the top four size bins are not plotted, containing 8/515 (1.5%) families (with 22 species), each with an average maximum length >4.0 m. By comparison, the smallest size bin contains four families (with 29 species), each family with an average total length <2.7 cm. Note the mode and spread of the size distribution for fishes have been maintained in a state of quasi-equilibrium over the last c. 400 Ma

speciation, extinction and adaptive evolution (anagenesis) have been parsed in an explicitly phylogenetic context in some fish taxa (Knouft 2003; Near et al. 2005; Hardman and Hardman 2008), the generality of these processes among fishes as a whole remain poorly understood (see e.g. Smith 1981; Smith et al. 2010).

The generality of the Clauset and Erwin (2008) model may be further limited by the different ways in which homeothermic and poikilothermic species respond to metabolic constraints on size evolution. As compared with other vertebrates, mammals and birds have an elevated and relatively constant basal metabolic rate, and they also exhibit determinate growth in which somatic development slows abruptly at sexual maturity. By contrast the great majority (∼74%, Haussler et al. 2009) of vertebrate species, including all fishes, are poikilotherms, in which mass-specific metabolic rate increases with ambient temperature (Makarieva et al. 2005), and in which the aerobic capacity (power density) of mitochondria is about one order of magnitude lower than homeotherms (Wieser 1995). Poikilotherms also exhibit indeterminate growth, in which growth rate and maximum adult body size are more plastic (less constrained by genetics), and in which lifetime reproductive output has a higher variance (Stebens 1987) than in homeotherms. Because fishes exhibit indeterminate growth, size is a better parameter than chronological age to use as an independent variable in the study of metabolic rates (Kaufmann 1981). Also in contrast to homeotherms, the upper limit to body size in poikilotherms is constrained by a minimum mass-specific metabolic rate, below which biological performance is impaired (Makarieva et al. 2005). Thus the maximum body size of a poikilothermic species inhabiting warmer environments should be larger than that of a closely related species inhabiting cooler environments. Such physiological constraints due to size

do not apply to homeothermic animals that have metabolic control of body temperature.

Evolution Near Extreme Sizes

Examination of the total extant fish size distribution (Figs. 1 and 5), and of fish species near the limits of the total size distribution (Table 4), indicate little or no asymmetry in upper and lower boundaries to body size. In other words these data do not support the hypothesis that it is harder to scale the left side of the size distribution than the right (contra Clauset and Erwin 2008; Clauset et al. 2009). If extreme body size is defined as a total length greater than three standard deviations from the average value of all fishes, then 33 extant fish species may be regarded as extreme giants (>825 cm TL), and 32 extant species as extreme miniatures (<1.4 cm TL). A total of 21 genera include species that are extreme giants and another 24 genera include extreme miniatures. Thus, assuming the monophyly of these genera, we can infer that living fish species with extreme body sizes, both giants and miniatures, have evolved multiple times, and also that fishes have minimally evolved about the same numbers of times to either size extreme.

Does the transition to very smallest mature body sizes require more adaptive (ecophysiological) modifications than change to the largest sizes? Species at both ends of the size spectrum in fishes exhibit phenotypic specializations associated with extreme size. One of the main constraints to maturation at extremely small size is the energetic demand of securing sufficient energy to allocate to eggs in a small animal with high tissue specific metabolic rates (Weitzman and Vari 1988b; Ruber et al. 2007). Ecological and physiological limits to extremely large size in fishes may be associated with demographic factors (e.g. small
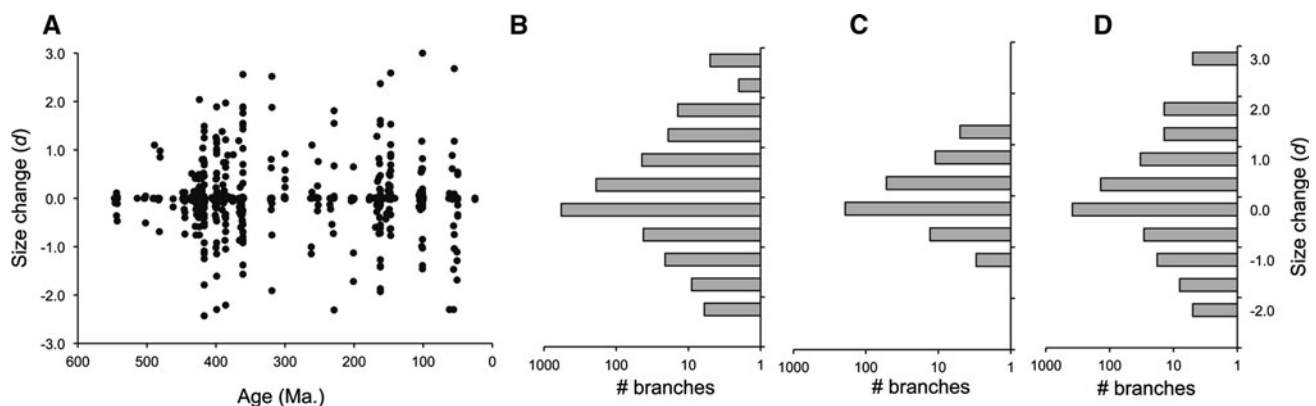

Fig. 5 Patterns of size-evolution in fossil fishes through the Phanerozoic. a Rates of size-change in *darwins* (d) estimated along 928 branches on the phylogeny of fossil fishes in Fig. 2. b–d Frequency distributions of size-change events for the: b Phanerozoic (542–0 Ma; n = 928; skewness = 0.37), c Expansion Phase (542–417 Ma; n = 280; skewness = −0.32), and d Quasi-equilibrium Phase (416–0 Ma.; n = 648; skewness = 0.49). Note skewness is negative during the Expansion Phase and positive in the Quasi-equilibrium Phase. Additional summary statistics for these phases are provided in Table 2

Table 4 Summary of data for fish species with extreme body size; i.e. those beyond three standard deviations from the average

Tail	Families	Genera	Species	Range	
				ln(cm)	ln(cm)^0.75
Largest	18	21	33	1.06	0.49
Smallest	12	24	32	0.41	0.51
Largest/ smallest	1.50	0.88	1.03	2.60	0.97
Total	30	45	65		

Data for 65 species representing 0.27% of the extant species dataset. Extreme giants grow to more than 825 cm TL, and extreme miniatures do not exceed 1.4 cm TL

effective population sizes, long generation times) that may ultimately confer elevated extinction risk (Knouft 2003; Knouft and Page 2003; Hardman and Hardman 2008).

It is interesting to note that the pool of higher taxa (18 families) from which extreme giants are recruited is (1.5 times) larger than the pool of taxa (12 families) from which the extreme miniatures evolved. Considered within the context of all fish families from which species of extreme size could potentially be drawn, the difference between 18/515 (3.5%) and 12/515 (2.3%) is not significant (two tail Chi Square test $P = 0.34$ when Yates corrected), and such a difference could easily have arisen by chance alone. Yet body size diversity has a strong phylogenetic component (e.g. Ramirez et al. 2008), and species with extreme size are not distributed randomly among all fish families (Table 4). Further, clades within certain fish families (i.e. Characidae, Cyprinidae, Gobiidae, Poeciliidae) do appear ecophysiologically or ontogenetically predisposed to produce extreme miniatures (Weitzman and Vari 1988b; Ruber et al. 2007). However, the family-level clades from which fish species that have extreme sizes are recruited do not have a predictable bias in their skewness; 8/18 (44%) of families with extreme giants have positive skewness (longer right tail), and 5/18 (28%) have negative skewness. The numbers for extreme miniatures are 8/12 (67%) families with positive skewness and 3/12 (25%) with negative skewness (numbers do not total to 100% because skewness values for families with few species cannot be calculated). Thus, although the proportion of clades with positive skewness is slightly greater in the pool of families that gave rise to extreme miniatures than to extreme giants, both pools exhibit similar proportions of clades with negative skewness.

The range of sizes exhibited by species with extreme sizes could also provide information on the symmetry of evolution near the limits of size space. Extreme giants range in size 2.60 times more (on a log scale) than do the extreme miniatures (Table 4). One interpretation of this

asymmetry in size ranges near the limits of size space is that the lower limit is a more difficult barrier to approach closely. It is also interesting to note the size range of species near the two limits are almost precisely the same when size measured on a power-log scale (see below). To summarize, data on fishes with extreme sizes indicate that the ecophysiological or ontogenetic barriers to achieving the largest and smallest body sizes do not appear to differ quantitatively. This means that the total amount of phenotypic modification (adaptation) required to achieve very large or very small body sizes is similar.

Lower Boundary Effect

The lower boundary effect observed in the body size distributions of homeothermic vertebrate clades (birds and mammals) is qualitatively different from that of poikilothermic fishes. Phenomenologically it appears that the special constraints on evolving to the very smallest sizes observed in homeotherms, are not present in fish clades. In other words, although the overall frequency distribution of fishes is right skewed, both tails of the distribution (at largest and smallest sizes) similarly taper to the lowest values gradually. By contrast the tails of size distributions for homeotherms are highly uneven, with what appears to be veil-line (*sensu* Preston 1948)) over the smallest size values. Why are there no bird or mammals species below this apparent veil line?

One possible explanation is the different physiological responses of poikilothermic and homeothermic animals to temperature changes. Whereas metabolic rate in poikilotherms is largely monotonic response to ambient temperatures, most homeotherms exhibit a thermoneutral zone of non-stressful metabolic activity within a range of temperatures to which they are adapted, and thermostress zones at lower and higher temperatures (Lindstedt and Boyce 1985; Ruel and Ayres 1999). The idea is that homeotherms with very small adult sizes reach their maximum tolerable metabolic rate at both low and high temperatures, whereas stressfully high metabolic rates are never achieved by poikilotherms at low temperatures. Therefore, homeotherms experience metabolic constraints on the evolution of small sizes not imposed on poikilotherms.

A possible complication to this argument is that most (or all) homeothermic vertebrates employ a range of behavioral responses to thermoregulation that buffer them from experiencing very low temperatures, whereas fish taxa in an aquatic medium are almost always strict thermoconformers (McNab 2002). However, the consequences of behavioral thermoregulation in shaping the size-frequency distribution of a large clade is probably very limited. Most extant vertebrate species (both poikilotherms and homeotherms) inhabit tropical environments, and most of the

clades to which they belong (e.g. families) originated in relatively warm and thermally stable environments (Wiens and Donoghue 2004; Wiens and Graham 2005; Wiens 2007). The differential macroevolutionary responses of poikilothermic and homeothermic taxa to low temperatures may therefore be regarded as negligible.

Power Scaling in Ecology

Studies on body size diversity have generally assessed the parameter 'size' in units of mass or length on the natural log scale: $\log_e(S)$, where S is a measure of size in cm or g, and the natural logarithm is the inverse function of the exponential function: $S = \ln[e^S]$ (if $S > 0$). The natural log is an intuitive scale for the study size diversity, in part because the exponential function (e^S) is a common feature of growth and other dynamic processes (Haldane 1949; Hayami 1978; Kaufmann 1981; Demetrius 1997, 2000; Glazier 2005), and perhaps also because the log function is (or closely matches) the native scale of human mensural perception (Dehaene et al. 2008; Dehaene 2011). Nevertheless, the natural log differs only in scale from that of logarithms in other fixed bases, and many historically important investigations have successfully analyzed size diversity on a $\log_{10}$ scale (Schmidt-Nielsen 1984; McNab 2002).

In addition, a lengthy history of physiological studies has shown how many important ecophysiological and evolutionary variables, such as metabolic rate, generation time, and mutation rate, do not scale with size as an isometric log function, but rather according to allometric power functions of the form: $y = aS^b$, or $\ln[y] = \ln[a] + b \ln[S]$, where a and b are empirically derived constants (Rubner 1883; Kleiber 1932, 1947; McNab 1990, 2002). In this relationship the y-intercept (a) is a proportionality coefficient, and the scaling exponent (b) expresses the (negatively allometric) relationship between the values of phenotypic traits S (e.g. size) and y (e.g. mass specific metabolic rate at a given size; Rolfe and Brown 1997; Darveau et al. 2002).

Power scaling theory posits that changes in adult body size are constrained by the hierarchical, fractal-like design of resource distribution networks within organisms (Gillooly et al. 2001; West et al. 2003). Body size directly influences many of the demographic factors involved in adaptation and phenotypic diversification, including rates of reproduction, population growth, population density, organismal vagility, and gene flow (Brown et al. 2004). Individual size and metabolic rate have been correlated with species-specific rates of development (Reiss 1989; Gillooly et al. 2008) and molecular evolution (Allen et al. 2005; Gillooly et al. 2005), and with energy use and tropic level (Brown et al. 2007; Romanuk et al. 2011). It is important to note that the relationships between metabolic rate, temperature and body mass differ substantially among taxa (Glazier 2005, 2006, 2009; Capellini et al. 2010; Cassemiro and Diniz 2010; Glazier 2010; Isaac and Carbone 2010; Lima-Ribeiro et al. 2010; McCain and Sanders 2010).

The scaling exponent (b) between size and metabolic rate exhibits a range of empirical values among vertebrate clades, from 0.67 to 1.06, with an average value for teleost fishes of 0.80 (Clarke and Johnson 1999; McNab 2002; Julian et al. 2003). Further, empirically derived allometric relationships between size and metabolic rate are not always log-linear (Glazier 2005, 2006). Thus, despite the well-characterized macroecological relationships between size and metabolic rate (Brown et al. 2004; Brown and Sibly 2006; Allen and Gillooly 2007; Gaston et al. 2009), the macroevolutionary consequences of allometric constraints on body size diversification remain incompletely understood.

Interestingly, positive skewness in log size and size change data can be removed by applying a power term to the logged size data:

$$y = a[\ln S]^b \qquad (3)$$

where $b = 1.0$ represents the special case where size (or size change) is measured on the conventional log-only scale. Could power laws act on the log scale for size change evolution rather than the traditional linear scale? If so, then this would provide an alternative explanation for the widespread occurrence of right-skewed size distributions. Or is this just a phenomenological relationship with no mechanistic basis? While our current knowledge of power law relationships occur at the linear scale, we encourage more thought into the relevance of power laws at alternative scales.

During the Quasi-equilibrium Phase of size evolution, the skewness of the size-change distribution was positive when size is measured on the log-only scale (Fig. 5d; $n = 392$; skewness = 0.50; $P = 0.11$; Kuiper test). However, the skewness of the size-change distribution does not differ significantly from zero when size-change is measured on the power-log scale (Fig. 6b; $0.36 < b < 0.67$; $P < 0.05$; Kuiper test). The best fit to these data are at $b = 0.50$ ($P < 0.0001$ that the power function equals 1.0). In other words, the size-change distribution converges to normal below the theoretically expected exponent value of three-quarters (McNab 2002).

Such an unexpectedly low value of b may reflect real differences in the physiological scaling of the fishes that constitute the fossil versus extant fishes datasets, or it may reflect a history of selection within multiple taxa for larger body sizes; i.e. Cope's rule. In principle, right-skewed body size distributions could arise from directional trends in size evolution, as a result of differential rates of anagenesis
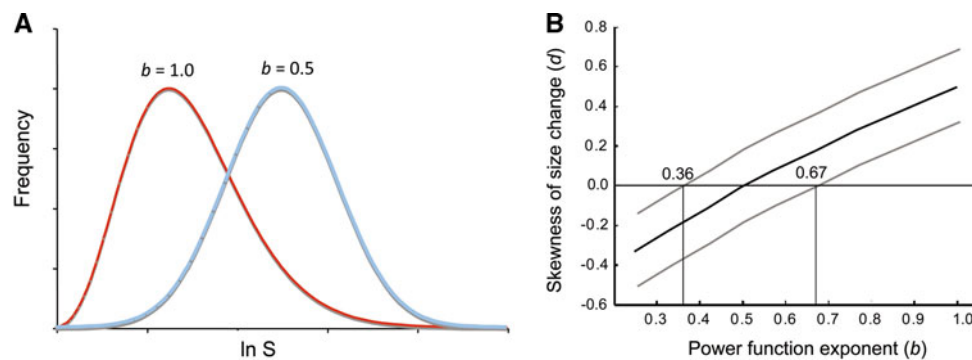
Fig. 6 A new hypothesis for the origin of right-skewed size distributions. **a**. Size distributions expected from a passive diffusion (non-directional) model of trait evolution; i.e. no size-biased rates of anagenesis, cladogenesis or extinction. Note both *curves* represent the same data, plotted alternatively on a conventional log-only (*red*) and power-log (*blue*) mensural scales, where b is the allometric scaling exponent. The *red curve* is right-skewed (at $b = 1.0$), with more scatter to the right of the median than to the left, whereas the *blue* curve is symmetrical or non-skewed (at $b = 0.5$). **b** Relationship between the power function exponent (b) and the empirical skewness values of size-change (d) data for fossil fishes. *Black line* traces skewness (with 95% CI in *grey lines*) of the size-change (d) distribution for all branches during Quasi-equilibrium Phase from the Lower Devonian to Recent ($n = 648$ branches). Note the empirical distribution does not deviate from that of a standard normal distribution in the range: $0.36 < b < 0.67$ (Color figure online)

(selection and drift), speciation (cladogenesis), or extinction (Tables 5 and 6, models 1–5). For example, a right-skewed size distribution could be seen to represent an excess of small-bodied species (Gaston and Blackburn 2000). In such as case the mass of the distribution (e.g. mode) would have shifted historically towards the smaller end of the size spectrum, in comparison to the mode of a normal distribution (i.e. with the same range of sizes and with a skewness of zero). However, this explanation does not apply to the fish datasets because the mode, skewness and range values of size distributions have not shifted substantially since the Lower Devonian. The Stanley effect (Tables 5 and 6, model 6) can also contribute to the production of right-skewed size distributions by affecting rates of anagenesis towards larger versus smaller sizes in the non-equilibrium Expansion Phase (Fig. 4c). Comparing the qualitative expectations of these alternative models with empirical patterns observed in the fossil fish datasets shows partial although incomplete matches (Table 6).

Another possibility is suggested by the empirical distribution of size-change data in Fig. 6, namely that the right-skewed body size distribution arose from symmetrical diffusion on a metabolically relevent power-log scale (Brown et al. 1993); i.e. the scaling exponent b was significantly less than 1.0 (Table 5, model 7). In this case, skewness arises from excesses in the magnitude (as opposed to the number or frequency) of changes to larger sizes. Empirical patterns in the skewness of body sizes, and of size-change events, in fossil fishes are largely consistent with the hypothesis of symmetrical diffusion of size on a power-log scale, with the exception of the sign of the skewness of the size-change distribution during the Expansion Phase (Table 6). Among the models outlined in

Tables 5 and 6, only model 1 (Cope's rule) successfully predicts the later.

Power Scaling and the Metabolic Theory of Ecology

From an ecophysiological perspective, species can and do respond adaptively to different environments by allometric changes in body size (Damuth 1993; Demetrius 2000). Biological rate processes that constrain changes in adult size, including cardiac and respiratory cycles, circulation of blood volume, growth rate and generation time, all scale with body size as a power function with exponent values below unity: $b < 1$ (Glazier 2009). From this ecophysiological perspective therefore, a power-log mensural scale $[\ln \text{cm}]^b$ may be a more relevent scale than the conventional log-only scale, on which to assess directional hypotheses of size evolution like Cope's rule. Passive diffusion of a continuous trait like body size on a power-log scale (where $b < 1$) into a bounded size space is expected to produce a symmetrical (non-skewed) distribution when assessed on that same power-log scale. However, this passive diffusion produces a right-skewed distribution when size assessed on a log-only scale (where $b = 1$). The biological mechanisms by which metabolic scaling at the organismal level translate into asymmetries in the evolutionary responses of populations (due to selection, drift, and the probabilities of speciation and extinction) are as yet poorly understood (Brown et al. 1993, 2004; West et al. 1997). Although skewness in the logged data can be accounted for by a power-log transformation, our current knowledge suggests that power laws act on the linear sizes, not logged sizes. The fit between the expectations of the power-log model and empirical data must therefore be regarded at this point as phenomenological.

Table 5 Alternative models of size-evolution proposed to generate right-skewed size distributions, based on differential rates of anagenesis (selection and drift), speciation (cladogenesis) and/or extinction

#	Model	Evolutionary process				
		Anagenesis	Speciation	Extinction	Fossil fish dataset	References
1	Selection for larger sizes within lineages	Yes	No	No	NA	(1 – 2)
2	Selection for smaller sizes within lineages	Yes	No	No	NA	(3)
3	Higher speciation rates at small sizes	No	Yes	No	NA	(4 – 6)
4	Higher extinction rates at large sizes	No	No	Yes	NA	(7 – 9)
5	Higher extinction rates at extreme sizes	No	No	Yes	NA	(10 –12)
6	Asymmetric diffusion within a bounded size space	Yes	No	No	Yes in EP No in QP	(13 – 14)
7	Symmetrical diffusion on a power-log scale	No	No	No	Yes	(15 – 16)

Note the fossil fish dataset compiled for this study does not have sufficient taxon sampling to evaluate models positing differential rates of speciation or extinction (models 1–5). References: 1. Newell (1949). 2. Kingsolver and Pfennig (2004). 3. Brown and Sibly (2006). 4. Kochmer and Wagner (1988). 5. Poulin and Morand (1997). 6. Munday and Jones (1998). 7. Maurer et al. (1992). 8. Gaston and Blackburn (1995). 9. Clauset and Erwin (2008). 10. Fenchel (1993). 11. Brown et al. (1993). 12. Webster et al. (2004). 13. Stanley (1973). 14. Purvis et al. (2003). 15. Brown et al. (1993). 16. Albert and Johnson (herein)

EP expansion phase, *QP* quasi-equilibrium phase

Table 6 Qualitative patterns of size evolution in fossil fishes and expectations of alternative models of size evolution

#	Model	Scale	Skew (size)		Skew (size change)	
			Expansion	Quasi-equilibrium	Expansion	Quasi-equilibrium
1	Selective advantage of larger size	Micro	−	−	−	−
2	Selective advantage of smaller size	Micro	+	+	+	+
3	Greater speciation in smaller species	Macro	+	+	0	0
4	Greater extinction of larger species	Macro	+	+	0	0
5	Higher extinction rates at extreme sizes	Macro	+	+	0	0
6	Physiological lower and upper bounds only	Micro	+	0	+	0
7	Symmetrical diffusion on a power-log scale	Micro	+	+	+	+
	Empirical					
	Fossil fish data	Macro	+	+	−	+

Signs indicate positive or negative skewness values. Expansion and quasi-equilibrium phases of the phanerozoic as in Table 5. Size as ln[cm], size change as *darwins* (dS/dt)

Micro microevolutionary (intraspecific), *Macro* macroevolutionary (interspecific)

Statistical and Sampling Considerations

The major patterns of size evolution recovered in this analysis do not appear to be statistical or taphonomic artifacts (Albert et al. 2009). If, as predicted by Cope's rule for example, there were persistent and general tendencies to increase body sizes within lineages, ancestral size estimates obtained from analysis of terminal (fossil or extant) taxa would be systematically overestimated (Stanley 1998; Polly 1998; Hone and Benton 2005). This is because methods for optimizing ancestral-trait values are not capable of estimating values outside the range of the terminal taxa. As a result sizes at internal tree nodes may be overestimated regardless of optimization method used (i.e. LP vs. LSP). However, the principal qualitative results of

this study do not seems to be artifacts of parsimony-based optimization methods; among the 23 Phanerozoic Epochs for size data are evaluated, estimates of internal node values from LP and LSP approaches are significantly correlated (at $P < 0.001$) with each other, and with that of the direct stratigraphic approach that does not use phylogenetic methods (Albert et al. 2009).

Estimates of body size taken from the taxonomic literature have been found to be slightly larger than the average of bulk samples, which is expected since type materials are generally selected from mature and more well preserved specimens. This effect has been shown in marine brachiopods and bivalves, where whole body size is well preserved in the size of the fossil shells (Krausse et al. 2007). However, this study also concluded that the average

size of the monograph sample, though biased, closely approximates that of the bulk sample, and that relative changes in size through time should be detected equally well by both data types.

In general, large scale trends of size evolution in vertebrates through the Phanerozoic have not been reported to reflect variation in the nature of the fossil record or of fossil bearing sediments (Alroy et al. 2001). Average body size has not been correlated with the amount of sedimentary rock volume (Peters and Foote 2001), or the average size of top predators (Janvier 1996; Twitchett et al. 2005). Madin et al. (2006) found that ecological interactions such as predation and bioturbation did not drive Phanerozoic macroevolutionary patterns in a large dataset of fossil benthic marine invertebrates.

One of the limitations of the macroevolutionary approach to studying size diversity its heavy use of statistical associations among taxa selected at an equivalent taxonomic rank (e.g. species, families). This approach makes several necessary assumptions, with varying degree of veracity, including the assertion that all the ranked taxa are monophyletic, and that the evolution of the quantitative trait under consideration (e.g. size) is not structured phylogenetically within or between the ranked taxa (Garland et al. 1992; Blomberg et al. 2003; Albert 2006). Regarding the former assumption, fish systematics of the past several decades has made exceptional progress towards generating an entirely phylogenetic classification, and most family-level taxa are now well supported monophyletic groups (Wiley and Johnson 2010). Regarding later assumption however, many aspects of size diversity have been shown to evolve within (Knouft 2003; Knouft and Page 2003; Hardman and Hardman 2008) and between (Albert et al. 2009) nominal fish families. A formal analysis using modern comparative methods will therefore be required to test the macroecological correlations presented here.

References

Ackerly, D. D. (2000). Taxon sampling, correlated evolution, and independent contrasts. *Evolution, 54*(5), 1480–1492.

Albert, J. S. (2006). Phylogenetic character reconstruction. In J. H. Kaas (Ed.), *Evolution of nervous systems volume 1: History of ideas, basic concepts, and developmental mechanisms* (pp. p41–p54). Oxford: Academic Press.

Albert, J. S., Bart, H. J., & Reis, R. E. (2011a). Species richness and cladal diversity. In J. S. Albert & R. E. Reis (Eds.), *Historical biogeography of neotropical freshwater fishes* (pp. 89–104). Berkeley: University of California Press.

Albert, J. S., Knouft, J. H., & Johnson, D. M. (2009). Fossils provide better estimates of ancestral body size than do extant taxa in fishes. *Acta Zoologica, 90*(Suppl. 1), 308–335.

Albert, J. S., Petry, P., & Reis, R. E. (2011b). Major biogeographic and phylogenetic patterns. In J. S. Albert & R. E. Reis (Eds.), *Historical biogeography of neotropical freshwater fishes* (pp. p21–p57). Berkeley: University of California Press.

Allen, A. P., & Gillooly, J. F. (2007). The mechanistic basis of the metabolic theory of ecology. *Oikos, 116*(6), 1073–1077.

Allen, A. P., Gillooly, J. F., & Brown, J. H. (2005). Linking the global carbon cycle to individual metabolism. *Functional Ecology, 19*(2), 202–213.

Alroy, J. (1998). Cope's rule and the dynamics of body mass evolution in North American fossil mammals. *Science, 280*(5364), 731–734.

Alroy, J. (2010). Geographical, environmental and intrinsic biotic controls on Phanerozoic marine diversification. *Palaeontology, 53*, 1211–1235.

Alroy, J., Marshall, C. R., Bambach, R. K., Bezusko, K., Foote, M., Fursich, F. T., et al. (2001). Effects of sampling standardization on estimates of Phanerozoic marine diversification. *Proceedings of the National Academy of Sciences of the United States of America, 98*(11), 6261–6266.

Arnold, A. J., Kelly, D. C., & Parker, W. C. (1995). Causality and cope rule—evidence from the planktonic- foraminifera. *Journal of Paleontology, 69*(2), 203–210.

Arratia, G. (1997). Basal teleosts and teleostean phylogeny. *Palaeo Ichthyologica, 7*, 1–168.

Arratia, G. (1999). The monophyly of the Teleostei and stem-group teleosts. In G. Arratia & H.-P. Schultz (Eds.), *Mesozoic fishes 2—Systematics and fossil record* (pp. 265–334). Munchen: Verlag Dr. Friedrich Pfeil.

Arratia, G. (2004). Mesozoic halecostomes and the early radiation of teleosts. In G. Arratia & A. Tintori (Eds.), *Mesozoic fishes 3–systematics, paleoenvironments and biodiversity* (pp. 279–315). München: Verlag Dr. Friedrich Pfeil.

Arratia, G., & Cloutier, R. (2002). Cheirolepiform fish from the Devonian of Red Hill, Nevada. *Journal of Vertebrate Paleontology, 22*(3), 33A.

Arratia, G., & Cloutier, R. (2004). A new cheirolepidid fish from the middle-upper Devonian of Red Hill, Nevada, USA. In G. Arratia, M. V. H. Wilson, & R. Cloutier (Eds.), *Recent advances in the origin and early radiation of vertebrates* (pp. 583–598). München: Verlag Dr. Friedrich Pfeil.

Benton, M. J. (1993). *The fossil record 2* (845 p). London: Chapman and Hall.

Benton, M. J. (2005). *Vertebrate palaeontology* (472 p). Oxford: Blackwell.

Benton, M. J., & Donoghue, P. C. J. (2007). Paleontological evidence to date the tree of life. *Molecular Biology and Evolution, 24*(1), 26–53.

Blanckenhorn, W. U. (2000). The evolution of body size: what keeps organisms small? *Quarterly Review of Biology, 75*, 385–407.

Blieck, A., & Turner, S. (2003). Global Ordovician vertebrate biogeography. *Paleogeography, Paleoclimatology, and Paleoecology, 195*, 37–54.

Blieck, A., Turner, S., Burrow, C. J., Schultze, H.-P., Rexroad, C. B., Bultynck, P., & Nowlan, G. S. (2010). Fossils, histology, and phylogeny: Why conodonts are not vertebrates. *Episodes, 33*, 234–241.

Blomberg, S. P., Garland, T., & Ives, A. R. (2003). Testing for phylogenetic signal in comparative data: Behavioral traits are more labile. *Evolution, 57*(4), 717–745.

Brown, J. H., Allen, A. P., & Gillooly, J. F. (2007). The metabolic theory of ecology and the role of body size in marine and freshwater ecosystems. In A. Hildrew, D. Raffaelli, & R. Edmonds-Brown (Eds.), *Body size: The structure and function of aquatic ecosystems* (pp. 1–15). Cambridge: Cambridge University Press.

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., & West, G. B. (2004). Toward a metabolic theory of ecology. *Ecology, 85*(7), 1771–1789.

Brown, J. H., Marquet, P. A., & Taper, M. L. (1993). Evolution of body-size—Consequences of an energetic definition of fitness. *American Naturalist, 142*(4), 573–584.

Brown, J. H., & Maurer, B. A. (1986). Body size, ecological dominance and Cope's rule. *Nature, 324*(6094), 248–250.

Brown, J. H., & Sibly, R. M. (2006). Metabolic rate constrains the scaling of production with body mass. *Proceedings of the National Academy of Sciences of the United States of America, 103*(47), 17595–17599.

Butler, M. A., & Losos, J. B. (1997). Testing for unequal amounts of evolution in a continuous character on different branches of a phylogenetic tree using linear and squared-change parsimony: An example using lesser antillean Anolis lizards. *Evolution, 51*(5), 1623–1635.

Capellini, I., Venditti, C., & Barton, R. A. (2010). Phylogeny and metabolic scaling in mammals. *Ecology, 91*(9), 2783–2793.

Cappetta, H. (1987). *Chondrichthyes II: Mesozoic and Cenozoic elasmobranchii* (193 p). Stuttgart and New York: Gustav Fischer Verlag.

Cassemiro, F. A. S., & Diniz, J. A. F. (2010). Deviations from predictions of the metabolic theory of ecology can be explained by violations of assumptions. *Ecology, 91*(12), 3729–3738.

Clarke, A., & Johnson, N. M. (1999). Scaling of metabolic rate with body mass and temperature in teleost fish. *Journal Animal Ecology, 68*, 893–905.

Clauset, A., & Erwin, D. H. (2008). The evolution and distribution of species body size. *Science, 321*(5887), 399–401.

Clauset, A., Schwab, D. J., & Redner, S. (2009). How many species have mass M? *American Naturalist, 173*, 256–263.

Clouthier, R. (1996). The primitive actinistian *Miguashaia bureaui* Schultze (Sarcopterygii). In H. P. Schultze & R. Clouthier (Eds.), *Devonian fishes and plants of miguasha, Quebec, Canada* (pp. 227–247). München: Verlag Dr. Friedrich Pfeil.

Clouthier, R. (1997). Morphologie et variations du toit crânien du Dipneuste *Scaumenacia curta* (Whiteaves) (Sarcopterygii), du Dévonien supérieur du Québec. *Geodiversitas, 19*, 59–105.

Clouthier, R., & Ahlberg, P. E. (1996). Morphology, characters, and the interrelationships of basal sarcopterygians. In M. L. Stiassny, L. R. Parenti, & G. D. Johnson (Eds.), *Interrelationships of Fishes* (pp. 445–479). San Diego: Academic Press.

Clouthier, R., & Forey, P. L. (1991). Diversity of extinct and living actinistian fishes (Sarcopterygii). *Environmental Biology of Fishes, 32*, 59–74.

Clyde, W. C., & Gingerich, P. D. (1994). Rates of evolution in the dentition of early eocene *Cantius*—Comparison of size and shape. *Paleobiology, 20*(4), 506–522.

Coates, M. I. (1998). Actinopterygians from the Namurian of Bearsden, Scotland, with comments on early actinopterygian neurocrania. *Zoological Journal of Linnean Society, 122*(1), 27–59.

Cope, E. D. (1877). A contribution to the knowledge of the ichthyological fauna of the Green River shales. *Bulletin of United States Geological and Geographical Survey, 3*(34), 807–819.

Damuth, J. (1993). Copes rule, the Island rule and the scaling of mammalian population-density. *Nature, 365*(6448), 748–750.

Darveau, C. A., Suarez, R. K., Andrews, R. D., & Hochachka, P. W. (2002). Allometric cascade as a unifying principle of body mass effects on metabolism. *Nature, 417*(6885), 166–170.

de Pinna, M. C. C. (1996). Teleostean monophyly. In M. L. J. Stiassny, L. R. Parenti, & G. D. Johnson (Eds.), *Interrelationships of Fishes* (pp. 147–162). New York: Academic Press.

Dehaene, S. (2011). *The number sense: How the mind creates mathematics*. New York: Oxford University Press.

Dehaene, S., Izard, V., Spelke, E., & Pica, P. (2008). Log or linear? Distinct intuitions of the number scale in Western and amazonian indigene cultures. *Science, 320*, 1217–1220.

Demetrius, L. (1997). Directionality principles in thermodynamics and evolution. *Proceedings of the National Academy of Sciences of the United States of America, 94*(8), 3491–3498.

Demetrius, L. (2000). Directionality theory and the evolution of body size. *Proceedings of the Royal Society of London Series B-Biological Sciences, 267*(1460), 2385–2391.

Dietze, K. (2000). A revision of paramblypterid and amplypterid actinopterygians from upper carboniferous-lower permian lacustrine deposits of central Europe. *Palaeontology, 43*(5), 927–966.

Dong, X. P., Donoghue, P. C. J., & Repetski, J. E. (2005). Basal tissue structure in the earliest euconodonts: Testing hypotheses of developmental plasticity in euconodont phylogeny. *Palaeontology, 48*, 411–421.

Donoghue, P. C. J., & Sansom, I. J. (2002). Origin and early evolution of vertebrate skeletonization. *Microscopy Research and Technique, 59*(5), 352–372.

Fenchel, T. (1993). There are more small than large species? *Oikos, 68*, 375–378.

Frickhinger, K. A. (1995). Fossil atlas fishes. Jeffies RPS, translator. Melle: Hans A Baensch. 1088 p.

Friedman, M., & Blom, H. (2006). A new actinopterygian from the Famennian of east Greenland and the interrelationships of Devonian ray-finned fishes. *Journal of Paleontology, 80*(6),1186–1204.

Froese, R., & Pauly, D. (2005). *FishBase 2005: Concepts, design and data sources*. Los Banos: ICLARM.

Fu, C., Wu, J., Wang, X., Lei, G., & Chen, J. (2004). Patterns of diversity, altitudinal range and body size among freshwater fishes in the Yangtze River basin, China. *Global Ecology and Biogeography, 13*, 543–552.

Gardezi, T., & da Silva, J. (1999). Diversity in relation to body size in mammals: A comparative study. *American Naturalist, 153*(1), 110–123.

Garland, T., Harvey, P. H., & Ives, A. R. (1992). Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Systematic Biology, 41*(1), 18–32.

Gaston, K. J. (1998). Species-range size distributions: Products of speciation, extinction and transformation. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences, 353*(1366), 219–230.

Gaston, K. J., & Blackburn, T. M. (1995). Birds, body size and the threat of extinction. *Philosophical Transactions: Biological Sciences, 347*(1320), 205–212.

Gaston, K. J., & Blackburn, T. M. (2000). *Pattern and process in macroecology* (377 p). Oxford: Blackwell Science Ltd.

Gaston, K. J., Chown, S. L., Calosi, P., Bernardo, J., Bilton, D. T., Clarke, A., et al. (2009). Macrophysiology: A conceptual reunification. *American Naturalist, 174*(5), 595–612.

Gess, R. W., Coates, M. I., & Rubidge, B. S. (2006). A lamprey from the Devonian period of South Africa. *Nature, 443*(7114), 981–984.

Gillman, M. P. (2007). Evolutionary dynamics of vertebrate body mass range. *Evolution, 61*(3), 685–693.

Gillooly, J. F., Allen, A. P., West, G. B., & Brown, J. H. (2005). The rate of DNA evolution: Effects of body size and temperature on the molecular clock. *Proceedings of the National Academy of Sciences of the United States of America, 102*(11), 140–145.

Gillooly, J. F., Brown, J. H., West, G. B., Savage, V. M., & Charnov, E. L. (2001). Effects of size and temperature on metabolic rate. *Science, 293*(5538), 2248–2251.

Gillooly, J. F., Londono, G. A., & Allen, A. P. (2008). Energetic constraints on an early developmental stage: A comparative view. *Biology Letters, 4*(1), 123–126.

Gingerich, P. D. (1983). Rates of evolution: Effects of time and temporal scaling. *Science, 222*, 159–161.

Gingerich, P. D. (1993). Quantification and comparison of evolutionary rates. *American Journal of Science, 293A*, 453–478.

Glazier, D. S. (2005). Beyond the '3/4-power law': variation in the intra- and interspecific scaling of metabolic rate in animals. *Biological Reviews, 80*(4), 611–662.

Glazier, D. S. (2006). The 3/4-power law is not universal: Evolution of isometric, ontogenetic metabolic scaling in pelagic animals. *BioScience, 56*(4), 325–332.

Glazier, D. S. (2008). Effects of metabolic level on the body size scaling of metabolic rate in birds and mammals. *Proceedings of the Royal Society B-Biological Sciences, 275*(1641), 1405–1410.

Glazier, D. S. (2009). Ontogenetic body-mass scaling of resting metabolic rate covaries with species-specific metabolic level and body size in spiders and snakes. *Comparative Biochemistry and Physiology A-Molecular & Integrative Physiology, 153*(4), 403–407.

Glazier, D. S. (2010). A unifying explanation for diverse metabolic scaling in animals and plants. *Biological Reviews, 85*(1), 111–138.

Gould, S. J. (1984). Smooth curve of evolutionary rate: A psychological and mathematical artifact. *Science, 226*, 984–985.

Gradstein, F. M, Ogg, J. G., Smith, A. G., Agterberg, F. P., Bleeker, W., Cooper, R. A., et al. (2004). *A geologic time scale* (589 p). Cambridge: Cambridge University Press.

Griffiths, D. (2006). Pattern and process in the ecological biogeography of European freshwater fish. *Journal of Animal Ecology, 75*(3), 734–751.

Griswold, C. E., Coddington, J. A., Hormiga, G., & Scharff, N. (1998). Phylogeny of the orb-web building spiders (Araneae, Orbiculariae: Deinopoidea, Araneoidea). *Zoological Journal Linnean Society, 123*, 1–99.

Guthrie, R. D. (2003). Rapid body size decline in Alaskan Pleistocene horses before extinction. *Nature, 426*, 169–171.

Haldane, J. B. S. (1949). Suggestions as to quantitative measurement of rates of evolution. *Evolution, 3*(1), 51–56.

Hardman, M., & Hardman, L. M. (2008). The relative importance of body size and paleoclimatic change as explanatory variables influencing lineage diversification rate: An evolutionary analysis of bullhead catfishes (Siluriformes: Ictaluridae). *Systematic Biology, 57*, 116–130.

Haussler, D., O'Brien, S. J., Ryder, O. A., Barker, F. K., Clamp, M., Crawford, A. J., et al. (2009). Genome 10 K: A proposal to obtain whole-genome sequence for 10,000 vertebrate species. *Journal of Heredity, 100*(6), 659–674.

Hayami, I. (1978). *Notes on the rates and patterns of size change in evolution paleobiology, 4*(3), 252–260.

Hone, D. W. E., & Benton, M. J. (2005). The evolution of large size: how does Cope's Rule work? *Trends in Ecology & Evolution, 20*(1), 4–6.

Hurley, I. A., Mueller, R. L., Dunn, K. A., Schmidt, E. J., Friedman, M., Ho, R. K., et al. (2007). A new time-scale for ray-finned fish evolution. *Proceedings of the Royal Society B, 274*, 489–498.

Hutchinson, G. E., & Macarthur, R. H. (1959). A theoretical ecological model of size distributions among species of animals. *American Naturalist, 93*(869), 117–125.

Isaac, N. J. B., & Carbone, C. (2010). Why are metabolic scaling exponents so controversial? Quantifying variance and testing hypotheses. *Ecology Letters, 13*(6), 728–735.

Jablonski, D. (1997a). Body-size evolution in Cretaceous molluscs and the status of Cope's rule. *Nature, 385*(6613), 250–252.

Jablonski, D. (1997b). Body-size evolution in Cretaceous molluscs and the status of Cope's rule. *Nature, 385*, 250–252.

Jablonski, D., Roy, K., & Valentine, J. W. (2006). Out of the tropics: Evolutionary dynamics of the latitudinal diversity gradient. *Science, 314*(5796), 102–106.

Janvier, P. (1996). *Early vertebrates* (393 p). Oxford: Oxford University Press.

Janvier, P. (2003). Vertebrate characters and the Cambrian vertebrates. *Comptes Rendus Palevol, 2*(6–7), 523–531.

Janvier, P., Desbiens, S., Willett, J. A., & Arsenault, M. (2006). Lamprey-like gills in a gnathostome-related Devonian jawless vertebrate. *Nature, 440*(7088), 1183–1185.

Janvier, P., & Lund, R. (1983). *Hardistiella montanensis* N. Gen. et sp. (Petromyzontida) from the Lower Carboniferous of Montana, with remarks on the affinities of the lampreys. *Journal of Vertebrate Paleontology, 2*, 407–413.

Johnson, G. D., & Patterson, C. (1996). Relationships of lower euteleostean fishes. In M. L. J. Stiassny, L. R. Parenti, & G. D. Johnson (Eds.), *Interrelationships of Fishes* (pp. 251–332). New York: Academic Press.

Julian, D., Crampton, W. G. R., Wohlgemuth, S. E., & Albert, J. S. (2003). Oxygen consumption in weakly electric Neotropical fishes. *Oecologia, 137*(4), 502–511.

Kaufmann, K. W. (1981). Fitting and using growth curves. *Oecologia, 49*(3), 293–299.

Kingsolver, J. G., & Pfennig, D. W. (2004). Individual-level selection as a cause of Cope's rule of phyletic size increase. *Evolution, 58*(7), 1608–1612.

Kleiber, M. (1932). Body size and metabolism. *Hilgardia, 6*, 315–351.

Kleiber, M. (1947). Body size and metabolic rate. *Physiological Reviews, 27*(4), 511–541.

Knoll, A. H., & Bambach, R. K. (2000). Directionality in the history of life: Diffusion from the left wall or repeated scaling of the right? *Paleobiology, 26*(4), 1–14.

Knouft, J. H. (2003). Convergence, divergence, and the effect of congeners on body size ratios in stream fishes. *Evolution, 57*(10), 2374–2382.

Knouft, J. H., & Page, L. M. (2003). The evolution of body size in extant groups of North American freshwater fishes: Speciation, size distributions, and Cope's rule. *American Naturalist, 161*(3), 413–421.

Koch, P. L. (1986). Clinal geographic variation in mammals: Implications for the study of chronoclines. *Paleobiology, 12*, 269–281.

Kochmer, J. P., & Wagner, R. H. (1988). Why are there so many kinds of passerine birds? Because they are small. A reply to Raikow. *Systematic Zoology, 37*, 68–69.

Krausse, R. A. J., Stempien, J. A., Kowalewski, M., & Miller, A. I. (2007). Body size estimates from the literature: Utility and potential for macroevolutionary studies. *Palaios, 22*, 60–73.

Lane, A., Janis, C. M., & Sepkoski, J. J., Jr. (2005). Estimating paleodiversities: A test of the taxic and phylogenetic methods. *Paleobiology, 31*, 21–34.

Laurin, M. (2004). The evolution of body size, Cope's rule and the origin of amniotes. *Systematic Biology, 53*(4), 594–622.

Lima-Ribeiro, M. S., Vale Brito Rangel, T. F. L., Pinto, M. P., Moura I., Melo, T. L., & Terribile, L. C. (2010). Spatial patterns of viperid species richness in South America: Environmental temperature vs. biochemical kinetics. *Acta Scientiarum Biological Sciences, 32*(2), 153–158.

Lindstedt, S. L., & Boyce, M. S. (1985). Seasonality, fasting endurance, and body size in mammals. *The American Naturalist, 125*(6), 873–878.

Long, J. A. (1995). *The rise of fishes: 500 Million Years of Evolution* (223 p). Baltimore & London: Johns Hopkins University Press.

Lund, R. (2000). The new actinopterygian order Guildayichthyiformes from the lower carboniferous of Montana (USA). *Geodiversitas, 22*, 171–206.

Maddison, W. P. (1991). Squared-change parsimony reconstructions of ancestral states for continuous-valued characters on a phylogenetic tree. *Systematic Zoology, 40*(3), 304–314.

Maddison, W. P., & Maddison, D. R. (2006). *Mesquite: A modular system for evolutionary analysis*. Version 1.11. p http://mesquiteproject.org.

Madin, J. S., Alroy, J., Aberhan, M., Fursich, F. T., Kiessling, W., Kosnik, M. A., et al. (2006). Statistical independence of escalatory ecological trends in phanerozoic marine invertebrates. *Science, 312*(5775), 897–900.

Makarieva, A. M., Gorshkov, V. G., & Li, B. L. (2005). Gigantism, temperature and metabolic rate in terrestrial poikilotherms. *Proceedings of the Royal Society B, 272*, 2325–2328.

Mallatt, J., & Chen, J. Y. (2003). Fossil sister group of craniates: predicted and found. *Journal of Morphology, 258*, 1–31.

Matthews, W. J. (1998). *Patterns in freshwater fish ecology* (756 p). London: Chapman and Hall.

Maurer, B. A. (1998). The evolution of body size in birds. I. Evidence for non-random diversification. *Evolutionary Ecology, 12*(8), 925–934.

Maurer, B. A., Brown, J. H., Dayan, T., Enquist, B. J., Morgan Ernest, S. K., Hadly, E. A. et al. (2004). Similarities in body size distributions of small-bodied flying vertebrates. *Evolutionary Ecology Research 6*(6), 783–797.

Maurer, B. A., Brown, J. H., & Rusler, R. D. (1992). The micro and macro in body size evolution. *Evolution, 46*(4), 939–953.

May, R. M. (1988). How many species are there on earth? *Science, 241*, 1441–1448.

McCain, C. M., & Sanders, N. J. (2010). Metabolic theory and elevational diversity of vertebrate ectotherms. *Ecology, 91*(2), 601–609.

McNab, B. K. (1990). The physiological significance of body size. In J. Damuth & B. J. MacFadden (Eds.), *Body size in mammalian paleobiology* (pp. 11–24). Cambridge: Cambridge University Press.

McNab, B. K. (2002). *Physiological ecology of vertebrates: A view from energetics* (576 p). Ithaca: Cornell University Press.

McShea, D. W. (1994). Mechanisms of large-scale evolutionary trends. *Evolution, 48*(6), 1747–1763.

Miller, A. I. (1997). Dissecting global diversity patterns: Examples from the Ordovician Radiation. *Annual Review of Ecology and Systematics, 28*, 85–104.

Miller, A. I. (1998). Biotic transitions in global marine diversity. *Science, 1157*, 281.

Millien, V. (2006). Morphological evolution is accelerated among island mammals. *PLoS Biology, 4*(10), e321.

Monroe, M. J., & Bokma, F. (2009). Do speciation rates drive rates of body size evolution in mammals? *American Naturalist, 174*, 912–918.

Munday, P. L. (1998). The ecological implications of small body size among coral-reef fishes. *Oceanography and Marine Biology: An Annual Review, 36*, 373–411.

Munday, P. L., & Jones, G. P. (1998). The ecological implications of small body size among coral-reef fishes. *Oceanography and Marine Biology: An Annual Review, 36*, 373–411.

Near, T. J., Bolnick, D. I., & Wainwright, P. C. (2005). Fossil calibrations and molecular divergence time estimates in centrarchid fishes (Teleostei: Centrarchidae). *Evolution, 59*(8), 1768–1782.

Newell, N. D. (1949). Phyletic size increase, an important trend illustrated by fossil invertebrates. *Evolution, 3*(2), 103–124.

Nilsson, G. E., & Östlund-Nilsson, S. (2008). Does size matter for hypoxia tolerance in fish? *Biological Reviews, 83*(2), 173–189.

Northcutt, R. G. (2005). The new head hypothesis revisited. *Journal of Experimental Zoology Part B-Molecular and Developmental Evolution, 304B*(4), 274–297.

Novack-Gottshall, P. M., & Lanier, N. A. (2008). Scale-dependence of Cope's rule in body size evolution of Paleozoic brachiopods. *Proceedings of the National Academy of Sciences of the United States of America, 105*(14), 5430–5434.

Olden, J. D., Hogan, Z. S., & Zanden, M. J. V. (2007). Small fish, big fish, red fish, blue fish: size-biased extinction risk of the world's freshwater and marine fishes. *Global Ecology and Biogeography, 16*(6), 694–701.

Olson, V. A., Davies, R. G., Orme, C. D. L., Thomas, G. H., Meiri, S., Blackburn, T. M., et al. (2009). Global biogeography and ecology of body size in birds. *Ecology Letters, 12*(3), 249–259.

Pagel, M. (1999). The maximum likelihood approach to reconstructing ancestral character states of discrete characters on phylogenies. *Systematic Biology, 48*(3), 612–622.

Pagel, M., Venditti, C., & Meade, A. (2006). Large punctuational contribution of speciation to evolutionary divergence at the molecular level. *Science, 314*(5796), 119–121.

Pérez-Claros, J. A., & Aledo, J. C. (2007). Comment on "Morphological evolution is accelerated among island mammals". *PLoS Biology, 5*(7), 180.

Peters, S. E., & Foote, M. (2001). Biodiversity in the Phanerozoic: A reinterpretation. *Paleobiology, 27*(4), 583–601.

Polly, P. D. (1998). Cope's rule. *Science, 282*(5386), 50–51.

Polly, P. D. (2001). Paleontology and the comparative method: Ancestral node reconstructions versus observed node values. *American Naturalist, 157*(6), 596–609.

Poulin, R., & Morand, S. (1997). Parasite body size distributions: Interpreting patterns of skewness. *International Journal for Parasitology, 27*(8), 959–964.

Prendini, L. (2001). Species or supraspecific taxa as terminals in cladistic analysis? Groundplans versus exemplars revisited. *Systematic Biology, 50*(2), 290–300.

Preston, F. W. (1948). The commonness and the rarity of species. *Ecology, 29*, 254–283.

Purvis, A., Orme, C. D. L., & Dolphin, K. (2003). Why are most species small-bodied? A phylogenetic view. In T. M. Blackburn & K. J. Gaston (Eds.), *Macroecology: Concepts and consequences* (pp. 155–173). Oxford: Blackwell Science.

Ramirez, L., Diniz-Filho, J. A. F., & Hawkins, B. A. (2008). Partitioning phylogenetic and adaptive components of the geographical body-size pattern of New World birds. *Global Ecology and Biogeography, 17*(1), 100–110.

Reiss, J. O. (1989). The meaning of developmental time—A metric for comparative embryology. *American Naturalist, 134*(2), 170–189.

Reynolds, J. D., Webb, T. J., & Hawkins, L. A. (2005). Life history and ecological correlates of extinction risk in European freshwater fishes. *Canadian Journal of Fisheries and Aquatic Sciences, 62*(4), 854–862.

Reznick, D. N., Shaw, F. H., Rodd, F. H., & Shaw, R. G. (1997). Evaluation of the rate of evolution in natural populations of guppies (*Poecilia reticulata*). *Science, 275*(5308), 1934–1937.

Rolfe, D. F., & Brown, G. C. (1997). Cellular energy utilization and molecular origin of standard metabolic rate in mammals. *Physiological Reviews, 77*(3), 731–758.

Romanuk, T. N., Hayward, A., & Hutchings, J. A. (2011). Trophic level scales positively with body size in fishes. *Global Ecology and Biogeography, 20*(2), 231–240.

Roy, K., Jablonski, D., & Martien, K. K. (2000). Invariant size-frequency distributions along a latitudinal gradient in marine bivalves. *Proceedings of the National Academy of Sciences of the United States of America, 97*(24), 13150–13155.

Ruber, L., Kottelat, M., Tan, H., Ng, P., & Britz, R. (2007). Evolution of miniaturization and the phylogenetic position of *Paedocypris*,

comprising the world's smallest vertebrate. *BMC Evolutionary Biology, 7*(1), 38.

Rubner, M. (1883). Über den einfluss der körpergrösse auf stoff- und kraftwechsel. *Zeitschrift fur Biologie, 19*, 536–562.

Ruel, J. J., & Ayres, M. P. (1999). Jensen's inequality predicts effects of environmental variation. *Trends in Ecology & Evolution, 14*(9), 361–366.

Santini, F., Harmon, L. J., Carnevale, G., & Alfaro, M. E. (2009). Did genome duplication drive the origin of teleosts? A comparative study of diversification in ray-finned fishes. *BMC Evolutionary Biology, 9*(194), 1–15.

Schmidt-Nielsen, K. (1984). *Scaling. Why is animal size so important?* Cambridge: Cambridge University Press.

Sepkoski, J. J. (1981). A factor analytic description of the Phanerozoic marine fossil record. *Paleobiology, 7*, 36–53.

Sepkoski, J. J. (2002). A compendium of fossil marine animal genera. *Bulletins of American Paleontology, 363*, 1–560.

Sheets, H. D., & Mitchell, C. E. (2001). Uncorrelated change produces the apparent dependence of evolutionary rate on interval. *Paleobiology, 27*(3), 429–445.

Shu, D. G. (2003). A paleontological perspective of vertebrate origin. *Chinese Science Bulletin, 48*(8), 725–735.

Shu, D. G., Morris, S. C., Han, J., Zhang, Z. F., Yasui, K., Janvier, P., et al. (2003). Head and backbone of the Early Cambrian vertebrate *Haikouichthys*. *Nature, 421*(6922), 526–529.

Smith, G. R. (1981). Late Cenozoic freshwater fishes of North America. *Annual Review Ecology and Systematics, 12*, 163–193.

Smith, G. R., Badgley, C., Eiting, T. P., & Larson, P. S. (2010). Species diversity gradients in relation to geological history in North American freshwater fishes. *Evolutionary Ecology Research, 12*, 693–726.

Smith, K. F., & Brown, J. H. (2002). Patterns of diversity, depth range and body size among pelagic fishes along a gradient of depth. *Global Ecology and Biogeography, 11*(4), 313–322.

Stanley, S. M. (1973). An explanation for Cope's Rule. *Evolution, 27*(1), 1–26.

Stanley, S. M. (1990). The general correlation between rate of speciation and rate of extinction: Fortuitous causal linkages. In: R. M. Ross & W. D. Allmon (Eds.), *Causes of evolution: A paleontological perspective* (p. 494). Chicago: Univesit of Chicago Press.

Stanley, S. M. (1998). *Macroevolution. Pattern and process* (332 p). Baltimore: The Johns Hopkins University Press.

Stebens, K. P. (1987). The ecology of indeterminate growth in animals. *Annual Review of Ecology and Systematics, 18*, 371–407.

Twitchett, R. J., Feinberg, J. M., O'Connor, D. D., Alvarez, W., & McCollum, L. B. (2005). Early Triassic ophiuroids: Their paleoecology, taphonomy, and distribution. *Palaios, 20*, 213–223.

Underwood, C. J. (2006). Diversification of the Neoselachii (Chondrichthyes) during the Jurassic and Cretaceous. *Paleobiology, 32*(2), 215–235.

Webster, A. J., Gittleman, J. L., & Purvis, A. (2004). The life history legacy of evolutionary body size change in carnivores. *Journal of Evolutionary Biology, 17*(2), 396–407.

Weitzman, S., & Vari, R. (1988a). Miniaturization in South American freshwater fishes; an overview and discussion. *Proceedings of the Biological Society of Washington, 101*, 444–465.

Weitzman, S. H., & Vari, R. P. (1988b). Miniaturization in South American freshwater fishes; an overview and discussion. *Proceedings of the Biological Society of Washington, 101*(2), 444–465.

West, G. B., Brown, J. H., & Enquist, B. J. (1997). A general model for the origin of allometric scaling laws in biology. *Science, 276*(5309), 122–126.

West, G. B., Savage, V. M., Gillooly, J., Enquist, B. J., Woodruff, W. H., & Brown, J. H. (2003). Why does metabolic rate scale with body size? *Nature, 421*(6924), 713.

Wiens, J. J. (2007). Global patterns of diversification and species richness in amphibians. *American Naturalist, 170*, S86–S106.

Wiens, J. J., & Donoghue, M. J. (2004). Historical biogeography, ecology and species richness. *Trends in Ecology & Evolution, 19*(12), 639–644.

Wiens, J. J., & Graham, C. H. (2005). Niche conservatism: Integrating evolution, ecology, and conservation biology. *Annual Review of Ecology, Evolution, and Systematics, 36*, 519–539.

Wieser, W. (1995). Energetics of fish larvae, the smallest vertebrates. *Acta Physiologica Scandinavica, 154*(3), 279–290.

Wiley, E. O., & Johnson, G. D. (2010). A teleost classification based on monophyletic groups. In: J. S, Nelson, H.-P. Schultze, & M. V. H. Wilson (Eds.), *Origin and phylogenetic interrelationships of teleosts* (pp. 123–182). München Verlag Dr. Friedrich Pfeil.