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E-Article

Clade Age and Not Diversification Rate Explains Species Richness among Animal Taxa

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abstract: Animal taxa show remarkable variability in species richness across phylogenetic groups. Most explanations for this disparity postulate that taxa with more species have phenotypes or ecologies that cause higher diversification rates (i.e., higher speciation rates or lower extinction rates). Here we show that clade longevity, and not diversification rate, has primarily shaped patterns of species richness across major animal clades: more diverse taxa are older and thus have had more time to accumulate species. Diversification rates calculated from 163 species-level molecular phylogenies were highly consistent within and among three major animal phyla (Arthropoda, Chordata, Mollusca) and did not correlate with species richness. Clades with higher estimated diversification rates were younger, but species numbers increased with increasing clade age. A fossil-based data set also revealed a strong, positive relationship between total extant species richness and crown group age across the orders of insects and vertebrates. These findings do not negate the importance of ecology or phenotype in influencing diversification rates, but they do show that clade longevity is the dominant signal in major animal biodiversity patterns. Thus, some key innovations may have acted through fostering clade longevity and not by heightening diversification rate.

Keywords: biodiversity patterns, clade age, diversification rate, metazoa, species richness.

Some groups of organisms are fantastically diverse (e.g., beetles, passerine birds, rodents), and others (e.g., zorapterans, loons, sloths) are not. While many factors have been hypothesized to underlie the disparities in species richness among taxa, general explanations for these differences remain elusive. For example, species richness had long been presumed to scale inversely with body size (Hutchinson and MacArthur 1959; Stanley 1973; Van Valen 1973; May 1986). Empirical studies testing this idea have shown that species richness is inversely related to body size within the carnivores (Gittleman and Purvis 1998) but not in other mammals or birds or across all animals (Dial and Marzluff 1988; Nee et al. 1992; Gardezi and da Silva 1999; Owens et al. 1999; Orme et al. 2002). Similarly, indicators of sexual selection such as different breeding systems or sexual dimorphism sometimes are and sometimes are not associated with increased species richness (Barraclough et al. 1995; Hodges and Arnold 1995; Mitra et al. 1996; Møller and Cuervo 1998; Owens et al. 1999; Arnqvist et al. 2000; Gage et al. 2002; Morrow et al. 2003; Stuart-Fox and Owens 2003). In insects, phytophagous clades are generally more species rich than their nonphytophagous sister clades (Mitter et al. 1988), but clades that adopted carnivorous, parasitic life histories are no more or less diverse than their sister clades (Wiegmann et al. 1993). Colonizing ability and the degree of ecological specialization have also been postulated to increase species richness (MacArthur et al. 1966), but these conjectures are largely untested.

Diversification rate—the balance between speciation and extinction rates—over a given time period determines a clade's species richness. The implicit assumption of all the hypotheses and analyses described above is that phenotypic or ecological differences among clades cause differences in their speciation or extinction rates, which in turn generate patterns of species richness across taxa. However, this simple statement about diversification rate suggests two more fundamental hypotheses that should be true regardless of whether speciation and extinction rates have been influenced by ecology or phenotype: (1) species-level diversification rates have been higher in clades with more species, and (2) older clades have more species, simply because they have had more time to accumulate species. Obviously, the mechanisms implied by these two hypotheses are not mutually exclusive and may sometimes work in opposition.

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These two hypotheses can be tested in various ways. Statistical techniques are now available to estimate diversification rates and clade ages directly from molecular phylogenies (Baldwin and Sanderson 1998; Nee 2001). Estimates of these parameters derived from a wide diversity of clades can be compared to identify whether general patterns consistent with these hypotheses emerge without regard to taxonomic affiliation (e.g., examine whether estimates of diversification rate are positively correlated with number of species in a clade across all animals) or comparisons of these parameters can be made between taxonomic groups that differ in species richness (e.g., evaluate whether average diversification rates vary consistently with species richness among the insect orders). Alternatively, estimates of these same parameters can be developed for clades by matching their extant species richnesses with age estimates derived from their fossil records (Sepkoski 1979; Magallón and Sanderson 2001).

We evaluated these two hypotheses in analyses of two such data sets for animal clades. One data set was based on 163 published species-level molecular phylogenies of arthropods, chordates, and mollusks. For each phylogeny, we used time-calibrated branch lengths to estimate the age of each clade in millions of years (MY), and we calculated λ, a standard measure of diversification rate (Baldwin and Sanderson 1998; Nee 2001). The other data set consisted of fossil-based estimates of crown group ages and estimates of extant species richness for all orders of insects, teleost fishes, amphibians, reptiles, birds, and mammals; from these data we also calculated estimates of diversification rates (Sepkoski 1979; Magallón and Sanderson 2001). Analyses of both data sets showed no consistent relationships between diversification rate and species richness, but species richness increased with clade age in both.

Methods

Diversification Rates Estimated from Molecular Phylogenies

This research is the beginning of a process to amass a large database of molecular phylogenies with estimates of branch lengths scaled to time. This process is ongoing, and so the results presented here are the product of our initial analyses. We systematically searched journals that routinely publish molecular phylogenies for articles that presented species-level phylogenies. To be included in this study, the article had to meet several criteria. (1) We established an arbitrary limit that ~50% or more of the species thought to be members of the clade had to be included in the analysis. (2) A phylogeny showing branch lengths calibrated to time or proportional to molecular (nucleotide or amino acid) substitution rate and a scale translating branch lengths into time or substitution rate must have been presented. (3) If only a phylogram of substitution rates was presented, the tree must have been based on molecular data for which a calibration is available in the literature. A PDF format file of each article was obtained, and a digital snapshot of the figure was taken in Adobe Acrobat 7.0. This image was transferred to a PowerPoint (Microsoft) file and printed on a laser printer. The phylogenies included in this study are listed in the appendix.

All branch lengths were measured by hand from these printed sheets using dial calipers. Final trees included in the database included one branch for each putative species. (Subspecies were combined into a single species.) Because many trees present multiple sequences from the same putative species and these are frequently not reciprocally monophyletic with respect to species identity, we established a series of criteria for placing species and determining branch lengths in the final tree. Briefly, when sequences from ≥ 2 species were not reciprocally monophyletic, we took the branch point for each species to be the highest branch point of each species from the rest, and we selected the longest external branch for that species from that point as the representative. Also, when sequences from a putative species appeared in disparate clades within the tree, we assumed that these sequences represented cryptic species and were identified as such in the resulting trees. Calculations on resulting trees using alternative resolutions of these issues to those described here show that these decisions have no appreciable effect on the results. Each tree was entered into the database in Newick format, with the calibration units to convert measured branch lengths into time or substitution rates.

A computer program written by M. A. McPeek in Java 1.5 (Sun Microsystems) was used to process and analyze all resulting trees (available on request from M. A. McPeek). First, the mean path length technique was used to make each tree ultrametric (Britton et al. 2002). For trees with branch lengths given in units of substitutions/site, appropriate molecular clock calibrations taken from the literature were then applied to convert branch lengths into units of time expressed in millions of years (MY). All included phylogenies were based on mtDNA data, and so we used the standard calibration of 2.3% MY^{-1} as the molecular clock estimate (Brower 1994). Because parameters derived from phylogenies calibrated by the authors of the original studies were indistinguishable from parameters derived from phylogenies that we calibrated, we believe that no bias exists because of inconsistencies in the way genetic distances were converted to time estimates.

We used the time-calibrated distance from the root to the tips of the phylogeny as the estimate for clade age. We estimated diversification rate for each phylogeny by calculating λ according to equation (7) of Nee (2001); λ is

a standard measure of diversification rate for molecular phylogenies (Baldwin and Sanderson 1998; Nee 2001) and has units of MY^{-1}. We also estimated separate speciation and extinction rates for each phylogeny by maximum-likelihood methods (Nee et al. 1994) and implementing a truncated Newton search algorithm in Java by translating the original source code written by S. G. Nash in FORTRAN (original source code at http://iris.gmu.edu/~snash/nash/software/software.html). We present results only for λ in this article because conclusions based on analyses using λ and those from estimates of separate speciation and extinction rates were identical.

Fossil-Based Diversification Rate Estimates

We also compiled a comparable fossil-based data set from the literature. The data were compiled at the level of taxonomic order. We used crown group age as the estimate for the age of each order in this data set. Crown group age was taken as the oldest first occurrence in the fossil record of an extant family in the order: this is therefore a minimum estimate of the last common ancestor of the extant species in the order. All data for 25 insect orders were compiled from Grimaldi and Engel (2005). Species richness values were compiled from standard sources for the 29 orders of teleost fishes (Nelson 2006), the three amphibian orders (Duellman and Trueb 1986), the four reptile orders (Parker 1982), the 33 bird orders (Dickinson 2003), and the 21 mammal orders (Nowak 1999). Crown group ages for the vertebrate orders were compiled from Benton (1993). Geologic intervals were converted to time using the International Geologic Time Scale 2004 (Gradstein et al. 2004).

From these data, we also calculated an estimate of diversification rate for each order assuming exponential growth of the clade. For this, we used the estimator (r) given in equation (7) of Magallón and Sanderson (2001) for crown group age. To apply this estimator, we assumed that extinction rate was 90% of the speciation rate (i.e., $\varepsilon = 0.9$ in eq. [7] of Magallón and Sanderson [2001]); calculations assuming other values of ε gave qualitatively similar results. Obviously, most taxa have not accumulated lineages at a constant exponential rate over their evolutionary histories. Although the overall diversification rate may slow over time, many taxa do continue to accumulate taxa (see, e.g., Miller and Sepkoski 1988; Wagner 1995; Alroy 1996; Sepkoski 1998). However, more sophisticated models of diversification cannot be evaluated with this type of data. Note that these data are not equivalent to fossil data, since the dynamics of species richness over time cannot be evaluated. Also, crown group age is the estimate of the date of the last common ancestor for the extant taxa and thus changes as species become extinct within a lineage. Therefore, we use this estimate only as a first approximation to compare with diversification rate estimates derived from the molecular phylogenies.

Results

Diversification Rates Estimated from Molecular Phylogenies

Of the 163 phylogenies in the data set, 56% reported including all species in the clade, and 83% reported sampling >75% of all species. Also, the percentage of sampled clade members was uncorrelated with the number of included species ($r = -0.08$, $df = 161$, $P > .25$) and with λ ($r = 0.08$, $df = 161$, $P > .25$). Thus, we believe that incomplete taxonomic sampling does not affect any of our conclusions. Phylogenies included from three to 116 species (median 14, and 5% and 95% quantiles of 5 and 49, respectively), and the estimated clade ages (i.e., distance from tree root to tips) ranged from 0.2 to 89 MY (median 7.5, and 5% and 95% quantiles of 1.7 and 30.3, respectively). For the three animal phyla included in the data set, mollusk phylogenies included on average the most species per clade, arthropods were intermediate, and chordates included the fewest ($F = 6.48$, $df = 2, 160$, $P < .002$).

Overall, diversification rate, as measured by λ, was uncorrelated with the number of species in the clade ($r = 0.13$, $df = 161$, $P > .05$; fig. 1*A*) but was strongly negatively correlated with estimated clade age ($r = -0.90$, $df = 161$, $P < .001$; fig. 1*B*). Because λ is a function of the number of species and the summed total branch lengths in the phylogeny (Nee 2001), this correlation structure indicates that variation in λ is primarily due to variation in clade age, while species richness contributes little. Also, when compared directly, λ values were statistically indistinguishable among the three animal phyla (ANOVA: $F = 0.24$, $df = 2, 160$, $P > .75$; figs. 1*A*, 2*A*). Because λ and clade age were strongly correlated, we also compared λ values with clade age as a covariate. When standardized by clade age, λ values were different among the three phyla, with mollusks having the largest and chordates having the smallest (ANCOVA: $F = 9.61$, $df = 2, 159$, $P < .001$; fig. 1*B*); these differences reflect the differences in species numbers per clade after standardizing by clade age (see above).

We also had adequate sample sizes within the arthropods and chordates to compare λ values at lower taxonomic levels. The results of comparisons when clade age was and was not included in analyses as a covariate led to identical conclusions; for brevity, we therefore present only results of analyses without this covariate. We also analyzed nested taxonomic subsets of the data to maintain statistical independence of the tests. Within the arthropods, the crus-

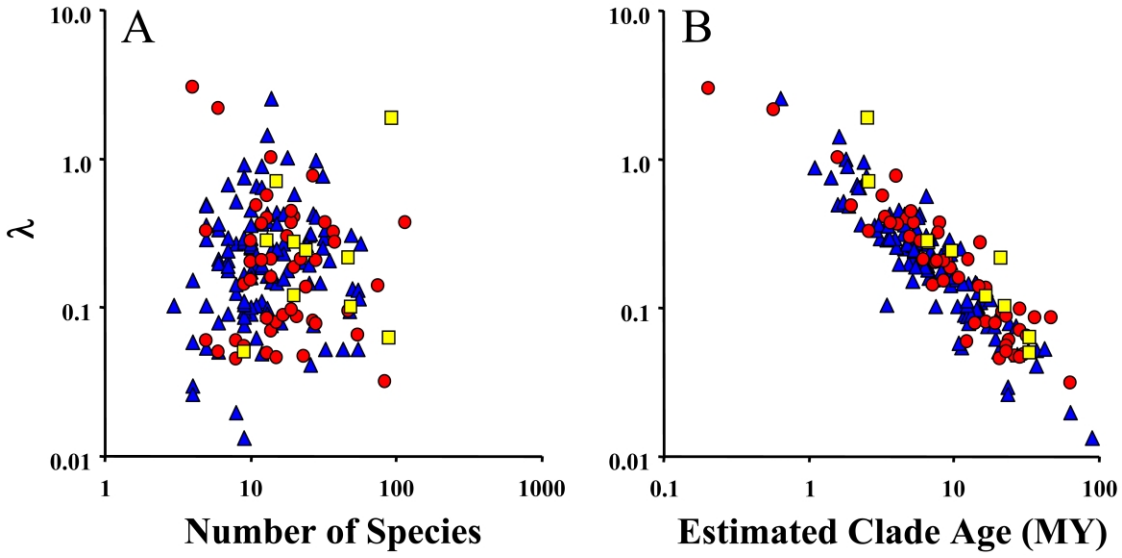

Figure 1: Relationships between diversification rate (λ) and (*A*) the number of species included in the phylogeny and (*B*) the estimated clade age derived from species-level molecular phylogenies. Each point represents one phylogeny. Symbols for the three major animal phyla are Chordata (*blue triangles*), Arthropoda (*red circles*), and Mollusca (*yellow squares*).

taceans had lower λ values than the chelicerates and insects, with the chelicerates and insects not different from each other ($F = 3.36$, df $= 2, 40$, $P < .05$; fig. 2*B*). The eight insect orders represented in the data set all had very similar λ values ($F = 0.20$, df $= 7, 21$, $P > .95$; fig. 2*C*). Within the chordates, λ values were not different among the teleost fishes, amphibians, and amniotes ($F = 2.55$, df $= 2, 108$, $P > .05$; fig. 2*D*). However, within the amniotes, bird clades has significantly higher diversification rates than reptile or mammal clades, with reptiles and mammals not different from each other ($F = 14.33$, df $= 2, 75$, $P < .001$; fig. 2*E*). Although we found no overall relationship between diversification rate and number of species (fig. 1) and few differences among clades (fig. 2), the range of diversification rates among the 163 phylogenies was quite large—from 0.013 to 3.000 MY^{-1}, with an average of 0.200 MY^{-1} (95% confidence interval [CI] [0.173, 0.230]; fig. 5*A*).

Although few consistent differences in λ were apparent among the various taxonomic groups, this data set of molecular phylogenies did reveal a positive relationship between the number of species included in the phylogeny and estimated clade age (fig. 3). For the entire data set the correlation between log (number of species) and clade age was significant ($r = 0.16$, df $= 161$, $P < .05$; fig. 3). Residual analyses indicated that the chordate point at 89 MY in figure 3 is an outlier that imposes undue influence on the relationship (Cook's *D* statistic 0.631). When this point was removed from the analysis, the relationship was substantially stronger ($r = 0.21$, df $= 160$, $P < .01$), and the major axis regression equation was number of species $= 11.65 \exp(0.014 \times$ clade age) (fig. 3).

Fossil-Based Diversification Rate Estimates

In the fossil-based data set of extant species richness and crown group ages for the orders of insects, teleost fishes, amphibians, reptiles, birds, and mammals, only one order was identified as an outlier (the reptile order Sphenodontida—the green diamond at 228 MY on the crown group age axis in fig. 4) and was excluded from these analyses. These data showed a strong positive relationship between $\log_e$(species richness) and crown group age ($r = 0.65$, df $= 111$, $P < .001$; fig. 4), with a major axis regression equation of species richness $= 19.55 \exp(0.031 \times$ crown group age). The variances in residuals around this regression line did not differ among the six taxa (Levene test for homogeneity of variances: $F = 0.47$, df $= 5, 107$, $P > .75$).

The six major taxa did not differ in *r*, the estimate of diversification rate for these data ($F = 0.61$, df $= 5, 107$, $P > .65$). Values of *r* averaged 0.066 MY^{-1} (95% CI [0.063, 0.069]) across the entire data set and assuming that extinction rate was 90% of speciation rate (for comparison, assuming no extinction [i.e., $\varepsilon = 0.0$], *r* averaged 0.100), which was less than that estimated from the molecular phylogenies (i.e., λ; fig. 5*B*). As with λ, the correlation structure among *r*, species richness, and crown group age

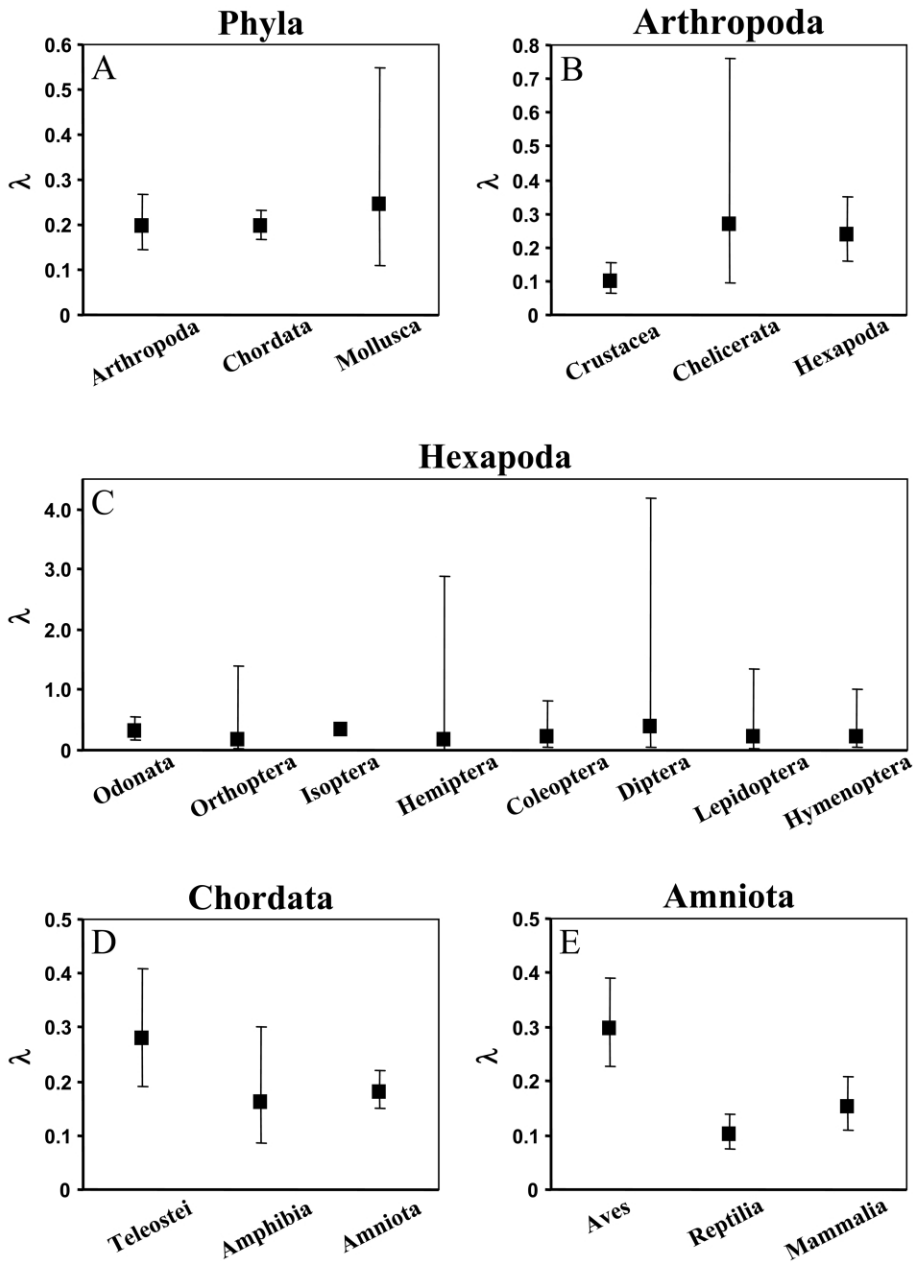

Figure 2: Diversification rates (λ) calculated from the species-level molecular phylogenies subdivided into various taxonomic levels. Means ± 95% confidence intervals are shown for each taxonomic group. Because λ was lognormally distributed, confidence intervals were calculated on a log scale and back-transformed for presentation here. Sample sizes for *A* are as follows: Arthropoda, 43; Chordata, 111; Mollusca, 9. Sample sizes for *B* are as follows: Crustacea, 10; Chelicerata, 4; Hexapoda, 29. Sample sizes for *C* are as follows: Odonata, 5; Orthoptera, 3; Isoptera, 1; Hemiptera, 2; Coleoptera, 7; Diptera, 3; Lepidoptera, 3; Hymenoptera, 5. Sample sizes for *D* are as follows: Teleostei, 24; Amphibia, 9; Amniota, 78. Sample sizes for *E* are as follows: Aves, 33; Reptilia, 22; Mammalia, 23.

showed that variation in r was primarily due to variation in crown group age ($r = -0.19$, df = 113, $P < .05$), with species richness contributing much less ($r = 0.10$, df = 113, $P > .25$).

Discussion

Data from both molecular phylogenies and fossils provided little support for the hypothesis that differences in species

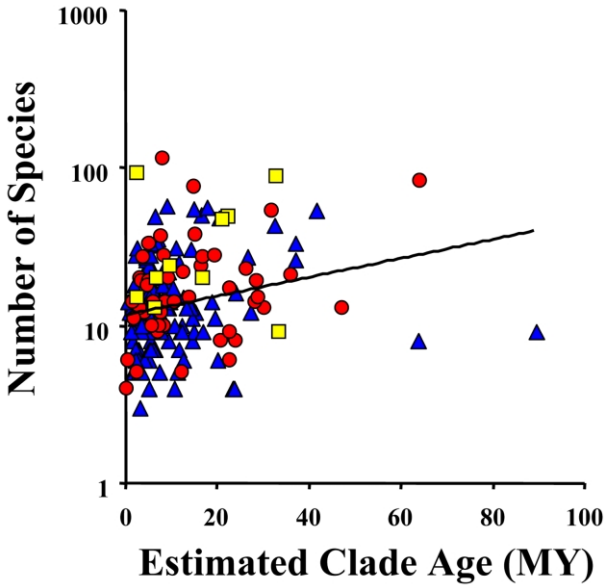

Figure 3: Relationship between number of species and estimated clade age in the species-level molecular phylogenies. Each point represents one phylogeny. Symbols are as given in the legend of figure 1. The major axis regression line is given in black and was calculated excluding the chordate point at 89 MY on the clade age axis as an outlier.

richness among animal taxa were the result of differences in diversification rates. In fact, both data sets suggest that species-level diversification rates have been rather homogeneous across the animals. In the data derived from molecular phylogenies, λ was uncorrelated with the number of species included in the phylogeny, and comparisons among taxa showed little correspondence between λ and species richness. For example, the three animal phyla represented in the data set did not differ in average λ despite the stark differences in their species richnesses, with the arthropods having ~10 times as many species as chordates and ~8 times as many species as mollusks (Parker 1982). Given that species richness varies over two orders of magnitude among the insect orders represented in this data set (Grimaldi and Engel 2005), their similarity in λ is again inconsistent with higher diversification rates begetting higher species richness. Because bird species richness is approximately double that of reptiles and mammals (Parker 1982; Nowak 1999; Dickinson 2003), the greater average λ values in bird clades, as compared to those of reptile and mammal clades, are the only difference in this data set that is consistent with the hypothesis that higher diversification rates caused higher species richnesses (fig. 2*E*).

In addition, the fossil-based data set yielded no support whatsoever for this hypotheses. Species richness was uncorrelated with *r*, despite the fact that species richness is one of only two parameters used to calculate *r*. Also, the six major taxa of animals were indistinguishable in *r*. Taken together, these two data sets derived from very disparate types of information decidedly do not support the general hypothesis that variation in extant species richness across major animal taxa was generated by differences in species-level diversification rates.

Estimates of diversification rates derived from species-level molecular phylogenies have a broader distribution and are higher on average than those derived from fossil ages (fig. 5). A number of factors may cause the fossil-based diversification estimates to be lower. First, the taxa included in the molecular phylogenetics data set may not be a random sample of animal clades. Because many phylogenetics studies are directed at questions of species diversity, it is understandable that they may be biased toward clades that appear to have rapidly diversified. Also, these two data sets capture macroevolutionary processes operating on very different timescales and at very different levels in the taxonomic hierarchy (i.e., within genera versus within orders). For example, speciation rates appear to decline over the histories of major taxa (Sepkoski 1998), and so the distributional difference between λ and *r* may simply reflect these scale differences. Finally, estimates of overall species richness for orders of animals may greatly

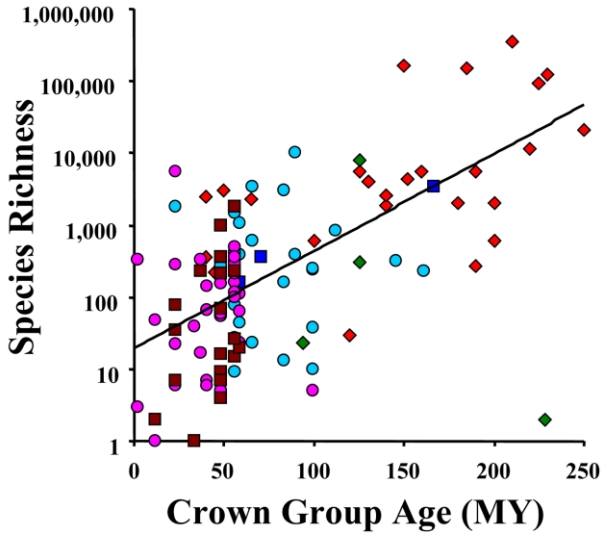

Figure 4: Relationship between extant species richness and crown group age for the orders of insects (*red diamonds*), teleost fishes (*blue circles*), amphibians (*blue squares*), reptiles (*green diamonds*), birds (*pink circles*), and mammals (*red squares*). Each point represents the value for a taxonomic order. The major axis regression line is given in black. The point for the Sphenodontida (green diamond at 228 MY on the crown group age axis) was excluded as an outlier.

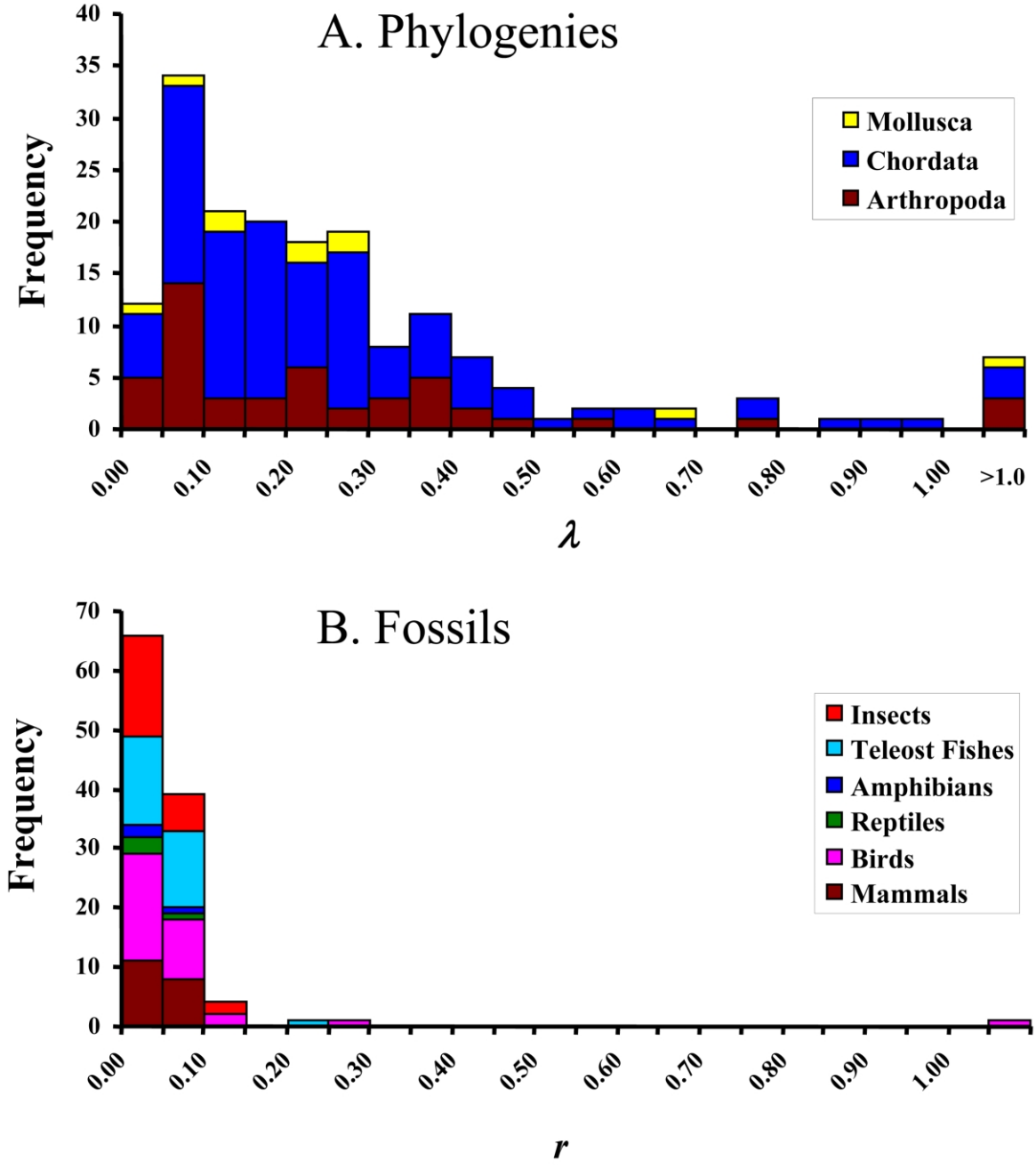

Figure 5: Stacked frequency histograms of diversification rates estimated from (*A*) the molecular phylogenies data set and (*B*) the fossil-based data set. The key in each identifies the contributions of major taxa in the respective data set to the distributions. Each bar represents the frequencies of diversification values in 0.05 increments (e.g., the first bar is the interval [0.00, 0.05], the second is [0.05, 0.10], etc.). The rightmost bar in *A* and *B* identifies the frequency of diversification rate values >1.0 in the data set.

underestimate the true numbers (May 1988; Wilson 1999; Prance et al. 2000), which would also lead to r having a more narrow distribution centered on lower values.

In contrast to these results for diversification rates, both data sets strongly implicate clade age as a primary determinant of major phylogenetic patterns of animal species richness. Species richness was positively correlated with clade age in both data sets (figs. 3, 4). This relationship

was much stronger for the fossil-based data set than for the data derived from molecular phylogenies, and this difference in strength is probably due to the substantially greater range of clade ages represented in the fossil-based data set. Although the oldest clade age represented among the molecular phylogenies was 89 MY, 80% of the clades in this data set were ≤20 MY old. Despite this small range of variation in clade age, the relationship is still apparent in these data. In fact, the slopes of the regressions in figures 3 and 4 are not statistically different from each other ($F = 2.62$, df $= 1, 273$, $P > .10$). The facts that major protostome and deuterostome taxa comprise the relationships and that these groups show homogeneity of residual variation around the regression lines suggest that these results may generally apply to all animals.

Interpretations of species richness patterns must therefore be strongly tempered by knowledge of clade age. The apparently fantastic richness levels in some groups (e.g., beetles) do not appear quite so exceptional when viewed from the perspective of clade age. This same caution also applies to relatively less diverse groups. Modern birds and mammals did not begin to diversify until the dinosaurs' mass extinction at the end of the Cretaceous, and their more recent origins explain why they are much less species rich than many arthropod lineages. The only real discrepancy in these data is the placement of the reptile order Sphenodontida. Its outlier status suggests that the relationship in figure 4 may provide objective criteria for categorizing taxa as "living fossils."

Care must also be taken to distinguish stem groups from crown groups when evaluating diversity, because crown group age will change as lineages become extinct within a clade. Extinction within a lineage will obviously decrease a taxon's position on the species richness axis, but extinction will tend to decrease the crown group age of the lineage as well, since crown group age is the time since the last common ancestor for all extant species. Thus, as major lineages are pruned from the phylogeny of a taxon, the position of that taxon in figure 4 will tend to decrease on both axes. For example, stem group amphibians extend back to the beginning of the Carboniferous, ca. 345 MYA (Benton 1993), but the three modern amphibian orders fall almost exactly on the line of expected species richness levels based on their crown group ages (fig. 4). Likewise, the stem group Odonata (Insecta) extends back into the Carboniferous, ca. 320 MYA (Bechley 1996; Grimaldi and Engel 2005), but the crown group falls very near the major axis regression line at ca. 160 MY (fig. 4). Extinction may peel away lineages from a taxon over time, but the relatively homogeneous species-level diversification rates across animals appear to perpetuate the accumulation of species richness in surviving lineages. Obviously, the definition and identification of crown groups will influence our perception of this relationship.

In contrast to the strong signal of clade age for animal species richness, plant species richness does not appear to correlate with clade age. Magallón and Sanderson (2001) calculated diversification rates for the major angiosperm taxa based on crown group age. The average diversification rate for angiosperm clades in their study was $r = 0.069$ MY^{-1} (based on values presented in their table 2 for $\varepsilon = 0.9$), which is comparable to our average estimate for the animals (i.e., $r = 0.066$ MY^{-1}) included in this study ($F = 0.07$, df $= 1, 162$, $P > .75$). They also present the comparable relationship of log (species richness) versus crown group age for the major taxa of angiosperm plants in their figure 4 (see also Magallón et al. 1999). Despite the similarity in diversification rates, no clear relationship between log (species richness) and crown group age is apparent (see fig. 4 in Magallón and Sanderson 2001). This difference suggests that the factors driving diversification and the patterns of diversification across taxa may be quite different between plants and animals, despite diversification rates being quite similar.

Although time available to accumulate species is the dominant signal among animal taxa, much of the variability around the line in figure 4 may still correlate with ecological and phenotype differences among taxa. Groups at the upper extreme of the points around the line (e.g., perciform fishes; passerine birds; rodents; bats; beetles; ants, bees, and wasps; butterflies and moths) probably have phenotypes or ecologies that have accelerated their diversification. Conversely, lineages at the bottom extreme (e.g., aardvarks; loons; zorapteran insects; alderflies and dobsonflies) probably have phenotypes or ecologies that retard their diversification. Even smaller residual differences among taxa may have ecological causes. Phytophagy appears to promote diversification in some insect lineages and may explain why Lepidoptera are far above the regression line and their sister clade Trichoptera is near the line (fig. 4; Mitter et al. 1988). Differences in diversification rates that correlate with ecological or phenotypic differences may also be more apparent at lower taxonomic levels of comparison. For example, body size appears to correlate with species richness within the Carnivora but not across all mammals or all metazoa (Gittleman and Purvis 1998; Orme et al. 2002). Also, most studies that have identified correlates of species richness have used sister clade comparisons (e.g., Mitter et al. 1988; Wiegmann et al. 1993; Møller and Cuervo 1998), which is necessarily comparing lower taxonomic levels. In addition, recent studies of bird clades suggested latitudinal gradients in diversification rates (Cardillo et al. 2005; Ricklefs 2006). As more molecular phylogenies accumulate, differences in species-level diversification rates may become more apparent (e.g., our

sample sizes may be inadequate to identify more subtle differences, or the phylogenies available now may be a biased sample that focuses on more rapidly diversifying clades in all groups), but at present such signals are obscure.

These results on the whole do, however, demand that we expand our focus for understanding the mechanisms that shape biodiversity patterns to include traits and processes that extend clade longevity, in addition to those that heighten diversification rates. To expand on J. B. S. Haldane's famous quip, God's inordinate fondness for beetles was not expressed by making so many but rather by allowing them to persist for so long. The success of insects has been attributed to low overall extinction rates, which would have increased clade longevity (Labandeira and Sepkoski 1993). While some clades were likely lost because of bad luck (Raup 1991), the persistence of most is probably determined by their ecological abilities to deal with their abiotic environments and to interact with other species. For example, the evolution of phytophagy in many insect clades permitted those lineages to move onto what has been a stable, predictable, and plentiful resource base that itself has expanded and persisted (Wilf et al. 2001; Grimaldi and Engel 2005) but did not necessarily increase diversification rates overall (Labandeira and Sepkoski 1993). The greater vagility of insects may also have permitted them to move and thus track favorable environmental conditions, which would buffer them from the consequences of environmental perturbations (Coope 1995). Species range size and dispersal abilities have also been implicated in lowering extinction rates (Hansen 1978; Jablonski 1989; Jablonski and Hunt 2006). Some key innovations may thus be traits that promote clade longevity but do not heighten diversification rates.

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