

Evolutionary diversification of clades of squamate reptiles

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Keywords:

alethinophidian snakes;
extinction;
key innovation;
lineage-through-time plot;
mass extinction;
passerine birds;
phylogenetic independence;
speciation;
squamate reptiles.

Abstract

We analysed the diversification of squamate reptiles (7488 species) based on a new molecular phylogeny, and compared the results to similar estimates for passerine birds (5712 species). The number of species in each of 36 squamate lineages showed no evidence of phylogenetic conservatism. Compared with a random speciation–extinction process with parameters estimated from the size distribution of clades, the alethinophidian snakes (2600 species) were larger than expected and 13 clades, each having fewer than 20 species, were smaller than expected, indicating rate heterogeneity. From a lineage-through-time plot, we estimated that a provisional rate of lineage extinction (0.66 per Myr) was 94% of the rate of lineage splitting (0.70 per Myr). Diversification in squamate lineages was independent of their stem age, but strongly related to the area of the region within which they occur. Tropical vs. temperate latitude exerted a marginally significant influence on species richness. In comparison with passerine birds, squamates share several clade features, including: (1) independence of species richness and age; (2) lack of phylogenetic signal with respect to clade size; (3) general absence of exceptionally large clades; (4) over-representation of small clades; (5) influence of region size on clade size; and (6) similar rates of speciation and extinction. The evidence for both groups suggests that clade size has achieved long-term equilibrium, suggesting negative feedback of species richness on the rate of diversification.

Introduction

Evolutionary biologists have sought to determine whether particular attributes of organisms or populations contribute to variation in rates of diversification within and between clades (Slowinski & Guyer, 1993). This search has focused on the so-called ‘key innovations’ (Farrell *et al.*, 1991; Heard & Hauser, 1995), but the evidence for traits that promote or retard diversification is mixed (Ricklefs, 2003; Sims & McConway, 2003; Davies *et al.*, 2004; Gianoli, 2004; Gavrillets & Vose, 2005; Ree, 2005; Hulsey, 2006; Phillimore *et al.*, 2006). Phylogenetic reconstructions of large clades allow one to

identify heterogeneity in diversification rate by comparing species richness between sister clades (Barraclough *et al.*, 1998a) and over entire phylogenetic trees (Barraclough *et al.*, 1998b; Pybus & Harvey, 2000). With more complete taxon sampling, one can use lineage-through-time (LTT) plots (Nee *et al.*, 1992; Harvey *et al.*, 1994) and intervals between nodes (Nee, 2001; Pybus *et al.*, 2002) to estimate relative rates of speciation and extinction, and absolute rates when phylogenetic distance can be calibrated with respect to time.

The first reasonably complete phylogeny of a large clade based on genetic data and with relatively dense species sampling was the DNA hybridization phylogeny for birds assembled by Sibley & Ahlquist (1990). This phylogeny has been updated using DNA sequences (e.g. Barker *et al.*, 2004; Beresford *et al.*, 2005). A recent phylogenetic reconstruction (Townsend *et al.*, 2004) of the major squamate (Reptilia: Squamata) lineages

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(snakes, lizards and their allies) invites a comparison of diversification between these two large vertebrate groups, which have both similarities and differences. Here, we compare the squamates with passerine birds (Order Passeriformes). Passerines and squamates resemble each other in being small- to medium-sized terrestrial vertebrates with generally active, mostly visually oriented foraging behaviour, which are distributed globally over a wide range of habitats. The groups differ on average with respect to body temperature and metabolic rate (Ruben, 1995; Hillenius & Ruben, 2004), as well as the predominance of flight in passerines. These differences might accelerate rates of speciation in birds compared with squamates if species formation were accelerated by temperature (Allen *et al.*, 2006), or they might retard speciation if high mobility suppressed population differentiation (e.g. Belliure *et al.*, 2000). In addition, squamates are more diverse than passerines in morphology (e.g. limbless forms have evolved repeatedly, Wiens *et al.*, 2006) and ecological relationships (including burrowing and marine species, but relatively few at high latitudes), and this might affect the heterogeneity of diversification within the clade. In addition, modern squamates appeared much earlier in geological time than passerine birds.

The squamate and passerine clades contain approximately the same number of species (7488 and 5712 respectively). Moreover, like passerines, squamates exhibit great variation in clade species richness, ranging from as few as one (Shinisauridae) or two (Helodermatidae) to more than 900 species of geckos and skinks and approximately 2600 species of alethinophidian snakes.

Because speciation and extinction are stochastic processes, clades will vary in their species richness by chance alone. The resulting broad distribution of species richness among clades of similar age can be used as a 'null' hypothesis against which observed distributions of present-day clade sizes can be compared. However, failure to reject the null hypothesis might conceal significant effects of extrinsic and intrinsic factors on diversification rate, because the independent influence of many factors can give the appearance of randomness.

We apply the same analytical approaches to studying species diversification in squamates as previously taken with tribe-level clades of passerine birds (Ricklefs, 2003, 2006a). Among passerines, no single clade is larger than one would expect from a random process. Moreover, clade size does not appear to be heritable phylogenetically, i.e. the number of species is no more similar among closely related clades than among distantly related clades (Ricklefs, 2003). Passerines include many small clades of five or fewer species, and these tend to be geographically or ecologically marginal compared with larger passerine clades (Ricklefs, 2005b). A LTT plot for the South American suboscines, based on the phylogeny of Sibley & Ahlquist (1990), was reasonably consistent with time homogeneous diversification, with

an extinction rate estimated to be about 82% of the speciation rate (Ricklefs, 2006c). Clade richness also increased with the size of the region occupied and was larger in tropical compared with that in temperate areas (Ricklefs, 2006a).

In comparing patterns of diversification between squamates and passerines, we address the following three questions specifically concerning squamate diversification: (1) do some squamate clades have more or less species than would be expected under a null model and can such deviations, if they exist, be related to clade attributes? (2) Is species richness more similar among more closely related clades, i.e. is the rate of diversification evolutionarily conservative, that is, heritable? (3) Has the rate of species diversification been constant through time?

Materials and methods

Phylogenetic relationships among squamates

We based our analyses on the molecular phylogeny of Townsend *et al.* (2004), which included approximately 4600 bp of DNA sequence data from two nuclear genes, *RAG-1* and *c-mos*, and the mitochondrial *ND2* region. Although Townsend *et al.*'s phylogeny is at odds in several important ways with the earlier, widely held views of squamate relationships (e.g. Estes *et al.*, 1988; Lee, 1998), similar results were obtained in subsequent studies that included fewer taxa, but data from additional genes (Vidal & Hedges, 2005).

The Townsend *et al.* (2004) analysis included all of the major clades of squamates. For this reason, sampling is complete in the older portion of the phylogeny, but becomes incomplete toward the present. Accordingly, we restrict our analysis to older clades within the Squamata; specifically, we use all taxa that we infer to have evolved by 56 million years ago (Ma), although the clades are not identical in rank. The 36 taxa are recognized at least as subfamilies, and their monophyly is mostly well established (exceptions are the possible paraphyly of the skink subfamily Scincinae with respect to the other skink subfamilies (Brandley *et al.*, 2005) and the possible paraphyly of the Gymnophthalmidae (= microteiids) with respect to the Teiidae (= macroteiids) (see Wiens *et al.*, 2006). The phylogeny included 69 species that were chosen to represent most of the major branches occurring within the older clades. Thus, the sampling of lineages, including those within the clades identified in this analysis, is nearly complete to an age of about 56 Ma. This is important with respect to interpretation of the LTT plot for the squamates (see below).

We used penalized likelihood (Sanderson, 2002) to scale branch lengths proportional to time using the *RAG-1* data. To convert branch lengths into time, we set divergence between squamates and their sister group Rhynchocephalia at 225 Ma, which corresponds to the

earliest fossil rhynchocephalians (note, however, that these fossils are not basal within the Rhynchocephalia, which implies that the divergence between Squamata and Rhynchocephalia might have occurred even earlier (Evans *et al.*, 2001; Evans, 2003). We set clade ages at the ancestral node, that is, the node uniting each clade with its sister. This is commonly referred to as the stem age. Although branches might have been pruned from the stem, diversification within a clade can begin at the time of splitting from its sister, and so the stem age is appropriate for analyses of diversification (Bokma, 2003; Ricklefs, 2006b).

Recently, Wiens *et al.* (2006) created a supertree for squamates by modifying the *RAG-1* data set of Townsend *et al.* (2004) to form the phylogenetic backbone and then adding information from phylogenetic studies of relationships within particular clades. Time was calibrated using several fossil dates. Because Wiens *et al.* (2006) focused on the evolution of limblessness, they did not include all major clades of limbed squamates (e.g. chameleons and some other iguanians were not represented). We note, however, that the phylogenetic structures of the present study and that of Wiens *et al.* (2006) are similar, differing only in the relationships of clades within the Iguania and Scincidae. These rearrangements do not substantially alter the inferred age of the terminal clades we use in our analysis, and the overall correlation (r) between clade ages in the two studies is 0.95 (analysis conducted on all 23 clades that appear in both studies).

Source of clade data

Species richness of clades was taken from Pough (2004).

The speciation–extinction process

In a random-walk diversification model, when rates of speciation (λ) and extinction (μ) are uniform across clades, the number of species in a clade assumes a geometric distribution (Kendall, 1948; Nee *et al.*, 1992, 1996; Magallón & Sanderson, 2001; Bokma, 2003). Accordingly, the average species richness of extant clades at time t is $\bar{N} = (\lambda e^{(\lambda-\mu)t} - \mu) / (\lambda - \mu)$, and the standard deviation of N is $(\bar{N}(\bar{N} - 1))^{1/2}$, which is approximately equal to the mean for large \bar{N} .

Simulating clades by a random speciation–extinction process

To determine whether particular clades were larger or smaller than expected by chance, we simulated speciation and extinction following Ricklefs (2003), using a program written in SAS language (SAS Institute, 1990). The program generated species within a clade by randomly causing each lineage to either split, with probability λ , or terminate, with probability μ , at each

of $t = 1000$ time steps. For most analyses, 36 clades, representing the number of squamate clades recognized in this study, were simulated simultaneously. Each set of simulations over clades was repeated 100 times, providing 100 values for the mean clade size (\bar{N}) and the sizes of clades at all ranks from 1 to 36. We also calculated the standard deviations and the 5–95% distribution intervals of individual clade size. The standard deviation of these values over the 100 sets of simulations provides an estimate of the standard error of the mean. All simulations and statistics were carried out by SAS version 8.12 software.

At each time step, two random uniform variates (R1 and R2, range of 0–1) were generated for each lineage within the clade and an event occurred when $R1 < \lambda$ or $R2 < \mu$. Speciation events were tabulated before extinction events, and so the rare (less than 10^{-4}) cases of double events resulted in no change in species number. For a particular average clade size (\bar{N}), the distribution of clade size is independent of the combination of speciation and extinction rates used in the simulation. Thus, most simulations were run with $\mu = 0$. Hence $\bar{N} = \exp(\lambda t)$ and λt was estimated by $\ln(\bar{N})$. Further details of the simulations are presented in the Results section.

Phylogenetic conservatism

Phylogenetic independence of clade size was tested by using the program Phylogenetic Independence (PI) (Abouheif, 1999; Reeve & Abouheif, 1999), which compares the variance between adjacent clades in a phylogenetic tree to a distribution of values generated by randomization. The test is sensitive to phylogenetic conservatism at all levels within a phylogenetic tree.

Lineage-through-time plot

An LTT plot portrays the increase in number through time of lineages ancestral to extant species. Harvey *et al.* (1994) showed that one can use a LTT plot to estimate speciation and extinction rates within a clade when these rates are constant through time. Further details are provided in the Results section. Confidence limits on estimates of speciation and extinction rates are typically broad (Bokma, 2003) and one must exercise caution against over-interpreting results obtained from LTT plots. In addition, the same pattern of increasing slope of the LTT plot towards the present can be evidence of either a constant rate of extinction in a time homogeneous process or an increase in the rate of speciation (Pybus & Harvey, 2000). Nonetheless, LTT plots can provide first approximations to rates of diversification, which can be instructive in a comparative framework.

We constructed an LTT plot for the squamate phylogeny by rank ordering the relative ages of the nodes from the stem age (1) and the first node (2) to the youngest

node (69) in the Townsend *et al.* (2004) phylogeny, and plotting the logarithm of the rank as a function of relative age from the oldest to the youngest. However, when analysing the squamate LTT plot, we used only clades inferred to have originated more than 56 Ma, the youngest age for which we believe the phylogeny to be reasonably complete. We only have one representative of some clades that existed at this point. For these clades, it is possible that intra-clade divergence occurred before 56 Ma. By contrast, for all clades for which we have multiple species, these taxa represent all the named subclades (often subfamilies) that occur within these clades. Because these subclades are thought to be monophyletic, with the two possible exceptions noted above, we can be confident that these clades did not diversify before 56 Ma. Most clades represented by a single sampled taxon are either only slightly older than 56 Ma, or contain few species; consequently, it is unlikely that these clades diversified to an appreciable extent before 56 Ma. The two exceptions are two moderately large clades – Lacertidae and Scolecophidia – which we estimate to have originated approximately 100 Ma. We might have failed to record divergence events in these clades before 56 Ma, in which case the LTT plot would slightly underestimate the rate of species accumulation.

We also constructed a LTT plot for passerine birds based on the DNA hybridization-based phylogeny of Sibley & Ahlquist (1990). Relative ages (melting point temperature differences between homoduplexed and heteroduplexed DNA) are provided for 558 nodes representing about one-tenth of the named species. The Sibley–Ahlquist phylogeny samples avian lineages comprehensively to a relative age of about $\Delta T_{50H} = 4$ °C. Time calibrations vary from about 2 to 4 Myr per °C (see Results). Although recent sequence-based analyses have revised some of the relationships in this phylogeny (Barker *et al.*, 2004; Beresford *et al.*, 2005), incorporating these rearrangements would have little effect on the LTT plot.

Clade area and major climate zone

We estimated the area within which each clade has diversified as the total area (10^6 km²) of each of the following regions within which the clade occurs at present: North America (19), Central America (Mexico to Panama, 2.5), West Indies (0.2), South America (18), Eurasia (46), Africa (Ethiopian zoogeographic region, 21), South and Southeast Asia (Oriental zoogeographic region, 9.6), Australasia (8.9), New Guinea (0.8), Madagascar (0.6). Each of the regions was classified as primarily temperate (North America, Eurasia) or primarily tropical. Each clade was then assigned a proportion of tropical distribution (0–1) based on the proportion of its total distribution in tropical and temperate regions. Six clades were primarily temperate (< 0.30), 21 were primarily tropical (> 0.70) and nine were mixed. Then,

following Ricklefs' (2006a) analysis of passerine tribe-level clades, we used multiple regression to evaluate the relationship of the logarithm of the number of species per clade to clade age, log-transformed area and degree of tropical distribution.

Results

The 36 clades of squamates range in size from one (*Shinisaurus* and *Rhineura*) to 2600 (McDiarmid *et al.*, 1999), with a mean of 208 ± 458 SD. Because the standard deviation of clade size considerably exceeds the mean, we infer that the distribution does not reflect a homogeneous random speciation–extinction process. The snakes comprised by far the largest clade; the next largest clades were the gekkonines (875 species) and the lygosomines (760 species), followed by the polychrotines (450 species). However, even with the snake clade removed, the standard deviation of the number of species among the remaining clades (206) still exceeded the mean clade size (140).

One potential source of deviation from a random speciation–extinction process is variation in clade age. The estimated stem ages of the 36 clades averaged 76 Ma ± 24 SD (range 34–160 Ma). All but six clade ages are between 56 and 112 Ma, and all but 12 are between 56 and 84 Ma. However, because the logarithm of the number of species was not related to clade age ($r = 0.170$, $P = 0.32$), clade age *per se* cannot explain the excess variation in clade size above the random speciation–extinction expectation.

Simulated clade size

We simulated clade size distributions with a random speciation model and λt equal to the logarithm of the observed average clade size (208 species), i.e. $\lambda t = 5.33754$. We used 1000 time steps, hence $\lambda = 0.00533754$, and simulated 100 replications of 36 clades. This produced a mean of 209.1 ± 35.8 SE species and a standard deviation of 200.7 ± 41.2 SE, conforming to the expected property (SD \approx mean) of a random speciation–extinction process. However, the simulated maximum clade size of 862 ± 254 SD species (range 427–1788) did not include the 2600 species of the snake clade ($P < 0.01$). Thus, this clade has more species than expected under a process that reproduces the mean of the distribution of squamate clade size.

A homogeneous speciation–extinction process produces a distribution of clade sizes in which the logarithm of a clade's size rank is linearly negatively related to the number of species per clade, with slope $\ln(u)$ (Ricklefs, 2003). Average clade size is related to u by the expression $\bar{N} = 1/(1 - u)$, which may then be used to estimate λt for simulating clade diversification. The observed relationship for squamate clades is not linear, however (Fig. 1). Not only are the largest clades too large, but there are

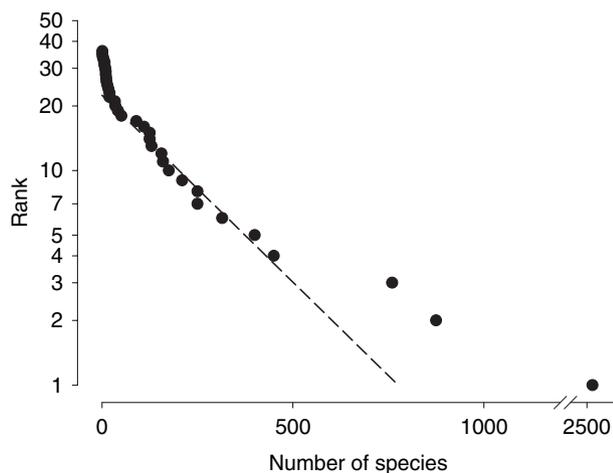


Fig. 1 Relationship between the logarithm of the rank of clade size (largest to smallest) and the number of species in 36 clades of squamate reptiles. The dashed line is fitted to clades of size rank 4–20, which exhibit an approximately geometric distribution of clade sizes.

also too many small clades. The relationship in Fig. 1 is approximately linear over the part of the range of clade size from about 20 to 500 species. Accordingly, we fitted a linear regression to 17 clades with ranks 4 (largest) to 20 (smallest): $\ln(\text{rank}) = 3.110 (\pm 0.036 \text{ SE}) - 0.00401 (\pm 0.00017 \text{ SE}) \text{ species}$ ($F_{1,15} = 562$, $P < 0.0001$, $r^2 = 0.974$). For this distribution, $u = 0.996$, and $\bar{N} = 250.1$. This is larger than the observed mean of 208 species because many small clades were excluded. The intercept of the regression was at a rank of $\exp(3.110) = 22.4$. Thus, for simulations based on this relationship, we included only 22 clades.

We then asked whether the larger clades of rank 3 (lygosomines, 760 species), rank 2 (geckonines, 875 species) and rank 1 (alethinophidian snakes, 2600 species) are too large for a process that yields an average of 250.1 species ($\lambda t = 5.522$). The sizes of the three largest clades determined by simulating 22 clades 100 times are shown in Table 1. Average clade size was 249.5 (± 51.8 SE) species with a SD among clades of 235.8 (± 66.6 SE). As seen in Table 1, the number of species of alethinophidian snakes is beyond the 95th percentile and the maximum of the simulated size distribution, and thus is exceptional by this reckoning. The second and third largest clades are within the 95th percentile and thus not exceptional.

Table 1 Sizes of the three largest clades produced by 100 sets of simulations of 22 clades with the product of speciation rate and time $\lambda t = 5.522$.

Rank	Mean	SD	Minimum	Maximum	5%	95%	Observed
1	911.7	320.8	336	1792	513	1550	2600
2	657.0	189.3	265	1280	425.5	1009	875
3	532.5	139.8	156	881	336	800	760

This simulation produced on average only one clade with fewer than 20 species (rank 22 = 12.8 ± 14.4 species), whereas the 36 clades of squamates include 13 with fewer than 20 species. Thus, other than having a single exceptionally large clade, squamates resemble passerine birds in having more small clades than expected at random. Because clade size is independent of age in squamates (and in passerines, Ricklefs, 2006a), diversification rate appears to be heterogeneous among squamate clades.

Test of phylogenetic conservatism

Abouheif's test-statistic for phylogenetic independence ($C = -0.045$) was exceeded by 263 of 1000 randomized values ($P = 0.263$). Thus, the data provide no indication of phylogenetic conservatism at the level of clade considered in this analysis.

Lineage-through-time plot

An LTT plot for squamates based on the phylogeny of Townsend *et al.* (2004) is shown in Fig. 2. We believe that the sampling of squamate lineages is reasonably complete up to an estimated age of 56 Ma. The observed

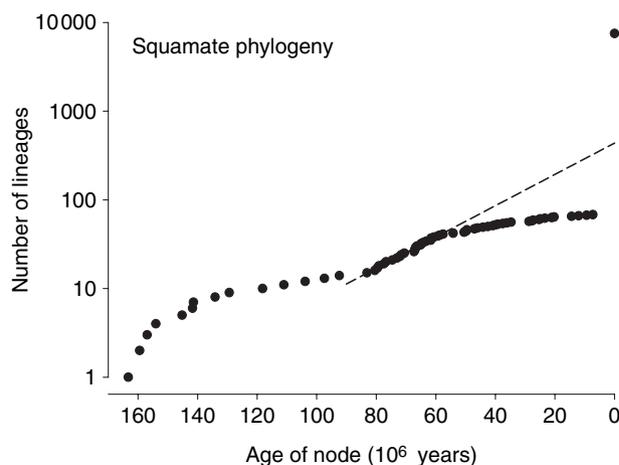


Fig. 2 Increase in the number of lineages in the squamate phylogeny as a function of age since the first branch point ca. 160 Ma to the present. Sampling is probably complete through 56 Ma. The dashed line is fitted to points between 84 and 56 Ma, and extrapolated to the present.

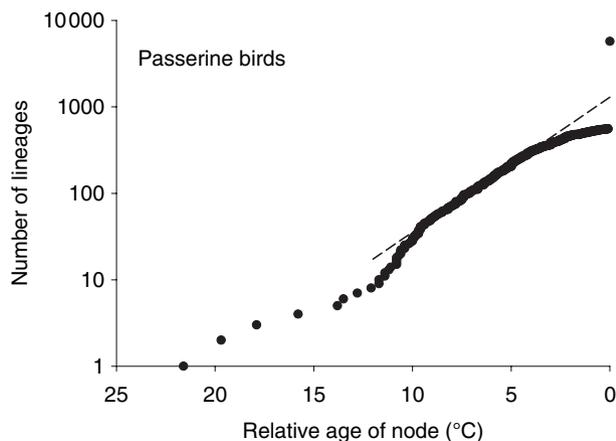


Fig. 3 Lineage-through-time (LTT) plot for passerine birds based on the phylogeny of Sibley & Ahlquist (1990). Dashed line represents the net diversification rate fitted to points between relative ages of 9.5 and 4.0 °C. Calibrations for this scale vary between ca. 2 and 4 Myr °C⁻¹. The lower value places the early split between suboscine and oscine passerines at about 40 Ma, which is consistent with the fragmentary fossil record (Mayr, 2005). A calibration of 4 Myr per °C would place the oscine–suboscine split at about 80 Ma, and thus possibly before the KT boundary, as suggested by van Tuinen & Hedges (2001) and Pereira & Baker (2006). Passerine fossils that are assignable to suboscine and oscine lineages first appear in the early Oligocene, ca. < 36 Ma (Mayr & Manegold, 2004; Mayr, 2005). The LTT plot shows a marked increase in slope between about 12 and 9.5 °C, beginning roughly at the Oligocene–Miocene boundary using the 1 °C = 2 Myr calibration and in the Early Eocene using 1 °C = 4 Myr.

decrease in slope and near levelling of the plot after this time is the result of incomplete lineage sampling. The LTT plot before 56 Ma shows a dramatic change in slope, at a relative age of about 84 Ma, with the characteristic signature of a mass extinction event (Harvey *et al.*, 1994; Heard & Mooers, 2002), although no such event is suggested in the fossil record (Evans, 2003).

To provide a tentative estimate of speciation and extinction rates for modern squamates, we assumed that these rates were constant from 84 Ma to the present and that sampling is complete between 56 and 84 Ma (node ranks 14–41, $n = 28$). Accordingly, the slope of the log(lineage) vs. time regression (0.04064×10^{-6} years) estimates the net speciation rate ($\lambda - \mu$). The difference (a) between this regression extrapolated to the present, i.e. relative time = 0, (6.077) and the logarithm of the present number of species at time 0 ($\ln(7488) = 8.921$) can be used to estimate the speciation rate according to $\lambda = (\lambda - \mu) / \exp(-a)$, after which the extinction rate is calculated by $\mu = \lambda - (\lambda - \mu)$. Thus, we estimated the speciation rate to be 0.698 per Myr, and the extinction 0.658 per Myr, or 94.3% of the speciation rate.

The data used to construct an LTT plot are cumulative, and therefore not independent, and so we cannot

provide confidence limits on these estimates. Variation in the slope of the LTT plot would inversely affect calculated speciation and extinction rates. For example, if the slope of the line were 1.5 times steeper, and crossed the original line at 70 Ma, the estimates would change to $\lambda = 0.206$ and $\mu = 0.145$, with the μ/λ ratio equal to 0.704. If the slope were decreased by a factor of 1.5, λ would increase to 0.981, μ to 0.954 and μ/λ to 0.972. This range of speciation rates (0.21–0.98) and μ/λ ratios (0.70–0.97) is very likely to include the actual value, even considering that some lineages within the 56–84 Ma age range might have been undersampled.

The LTT plot for passerine birds is relatively straight over a range of depth from 9.5 to 4.0 °C, which we used to estimate the net diversification rate ($\lambda - \mu$) to be 0.359 °C^{-1} . From the difference between the extrapolation of this line to 0 °C (the present) and the natural logarithm of the present-day number of species of passerines (5712), $a = 1.487$, $\lambda = 1.59$ and $\mu = 1.23 \text{ °C}^{-1}$. The ratio of the extinction to the speciation rate was therefore 0.774. Following Sibley & Ahlquist's (1990) calibration for passerine birds of ca. 2 Myr per 1 °C, these rates would be $\lambda = 0.79$ and $\mu = 0.62 \text{ Myr}^{-1}$. This calibration places the base of the passerine radiation at about 44 Ma. Although there is some debate about this age, no estimate has been more than twice this age (van Tuinen & Hedges, 2001; Pereira & Baker, 2006), in which case the rates would be $\lambda = 0.40$ and $\mu = 0.31 \text{ Myr}^{-1}$. In both cases, these rates fall within the range estimated for squamates.

Age, area and tropical distribution

In a multiple regression of log-transformed number of species on clade age, log-transformed area and proportion tropical distribution, age was not a significant effect ($F_{1,31} = 0.24$, $P = 0.62$). When age was dropped from the regression model, proportion tropical distribution was only marginally significant ($F_{1,32} = 3.74$, $P = 0.062$), although the trend indicated more species in tropical areas (slope = 1.45 ± 0.75 , suggesting an approximately fourfold difference between tropical and temperate regions). With both age and tropical proportion removed from the model, the log-transformed number of species per clade increased with log-transformed area with a slope of 0.78 ± 0.19 ($F_{1,34} = 16.95$, $P = 0.0002$, $r^2 = 0.33$) (Fig. 4).

Discussion

Squamate reptiles and passerine birds are two of the dominant vertebrate elements in the modern fauna. We investigated the extent to which patterns of evolutionary diversification have been similar in these two clades. To accomplish this, we examined squamate diversity in a phylogenetic context, paralleling the methods used

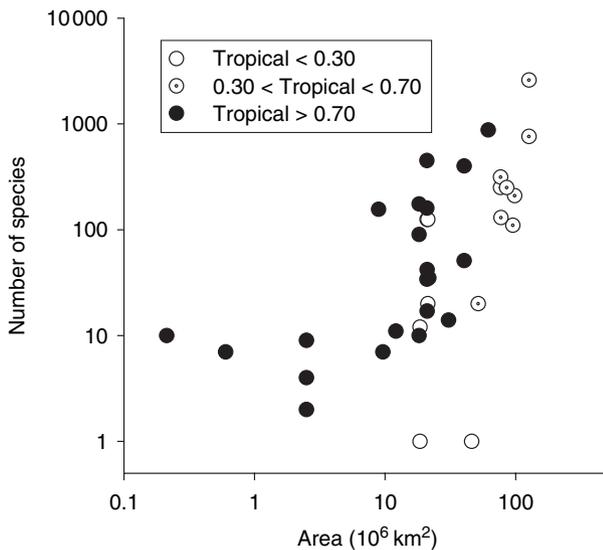


Fig. 4 Species–area relationship among squamate clades. The representation of each clade in tropical vs. temperate regions is indicated by different symbols.

previously to study passerine birds. In particular, we focused on clades that originated as new lineages within a narrow range of time (squamates: averaging 56 Ma; passerines: ca. 10–15 Ma) and determined the extent to which some clades were exceptionally species rich or species poor. In addition, by examining the accumulation of lineages through time, we were able to investigate the extent to which the rate of diversification appears to have been homogeneous through time and to estimate approximate rates of speciation and extinction. Our results indicate that the evolutionary diversification of squamates and passerines has been remarkably similar in broad outline while differing in some details.

(1) Species richness is unrelated to clade age

Simple models of evolutionary diversification predict that the species richness of a clade should be a function of its age (Bailey, 1964; Pielou, 1977; Nee *et al.*, 1992). Thus, the relationship between clade size and age can reveal whether modern clades have tended to increase in size over long periods. Alternatively, speciation might be approximately balanced by extinction, with larger clades having experienced the good fortune of above-average rates of diversification (Raup *et al.*, 1973; Gould *et al.*, 1977; Head & Rodgers, 1997). In neither squamates nor passerines is species richness related to clade age over the range of clade ages included in these analyses.

This result should not be surprising. Most clades do not increase at constant rates over long periods; rather, they grow and decline, most eventually perishing (e.g. Simpson, 1953; Gould *et al.*, 1987; Foote, 1992; Nee, 2006). Indeed, the sister taxon of Squamata, Rhynchocephalia,

proliferated extensively in the Triassic, but now is represented by just two closely related sibling species (Evans *et al.*, 2001). In addition, when extinction balances speciation, average clade size does not change over time even though the size of individual clades may increase or decrease. Simulations with equal speciation and extinction rates show that the average size of extant clades initially increases rapidly as small clades go extinct, and then levels off because larger clades tend to gain and lose species at an equal rate without a high risk of extinction (R. E. Ricklefs, unpublished data).

Differences in clade diversity at which speciation and extinction are balanced could be set by variation in the capacity of the region or environment to support different types of species, or driven by variation in the rate of species production among clades resulting from regional factors. Unfortunately, we cannot distinguish between these alternatives.

(2) Few clades are exceptionally large

Among squamates, only the alethinophidian snakes have unusually great species richness. Among passerines, the largest tribe-level clades are not exceptional. Several family-level clades are larger than expected from a random diversification process, but their size can be attributed in several cases to expanded ranges or other regional factors, rather than specific ecological position or ecomorphological innovations. Whether the great species richness of alethinophidian snakes is related to their worldwide distribution (see below) or the evolution of some trait that has enhanced the rate of speciation or reduced the rate of extinction, or both, remains to be seen.

(3) Clade size exhibits no phylogenetic signal

The distribution of clade sizes among most of the squamate clades could not be distinguished from a geometric distribution, which characterizes a homogeneous random speciation–extinction process. The random nature of diversification is further supported by the absence of phylogenetic signal in clade size. That is, a test of phylogenetic independence detected no significant association of the number of species among related clades. Such phylogenetic lability would not be expected if diversification rates were related to consequential morphological adaptations that arose deep in squamate phylogeny (Vitt *et al.*, 2003). Ricklefs (2003) found similar phylogenetic independence in species number for both family- and tribe-level clades of passerine birds.

(4) Many clades are exceptionally species poor

Based on the approximately geometric distribution of clade sizes among clades having 20–500 species, only

one squamate clade with fewer than 20 species would be predicted by chance. In fact, however, 13 such clades exist. Similarly, in passerine birds, as many as 26 of 106 tribe-level clades, all with fewer than five species, were exceptionally small relative to the geometric distribution of the number of species in larger clades (Ricklefs, 2003). In the passerine sample, most of the small clades are conspicuously marginal either geographically or ecologically (Ricklefs, 2006a). By contrast, the small squamate clades do not appear to possess unusual features. To be sure, some have unusual morphology or ecology (e.g. *Shinisaurus*, helodermatids, basiliscines and xantusiids), but most are unexceptional with respect to their ecology and morphology (e.g. oplurines, crotaphytids and *Leiocephalus*, *Leiolepis*). A few clades have restricted geographic distributions (*Shinisaurus*: Guangxi Province, China; *Rhineura*: northern Florida, but with widespread fossil localities in North America) or insular distributions (*Leiocephalus*: West Indies; oplurines: Madagascar), but most are continental, and many have sizeable geographic ranges. The geographic locations of these clades also provide little insight: slightly more than half the clades are found in the New World, mostly in the Neotropics, and most are tropical. In sum, although the Squamata contains a large excess of species-depauperate clades, no general pattern explains why some clades have so few species.

(5) Clade size is related to the size of the region within which a clade has diversified

The slope of the log–log relationship between species diversity and region area for squamates (0.78) did not differ significantly from 1.00 or from the slope for clades of passerine birds (0.73). This pattern could result from a capacity of larger areas to support larger clades, or from a positive effect of region area on speciation, clade longevity or both, recognizing that many clades had radically different, often more extensive, distributions in the past. The absence of a relationship between clade size and age suggests that clade size is constrained by ecological or regional factors, although the LTT plot shows no indication of a slowing of diversification towards the present (e.g. Pybus & Harvey, 2000). Although the effect of tropical vs. temperate distribution on clade size was only marginally significant for squamates ($P = 0.062$), the slope of the relationship was equivalent to tropical clades being larger than temperate clades, as in the case of passerine birds, by a factor of $\exp(1.45) = 4.26$.

(6) Squamates and passerines exhibit similar rates of speciation and extinction

An LTT plot for South American tyrannids (suboscines, which constitute the largest clade of passerines) suggested an extinction rate of about 82% of the speciation rate

over the history of the clade. A comparison of clade size and age in a variety of North and South American passerine clades gave an estimate of about 94% (Ricklefs, 2006a). For passerines as a whole, the LTT analysis in this study yielded an extinction–speciation ratio of 77%. An analysis of a small portion of the LTT plot for squamates suggested that the extinction rate was about 94% of the speciation rate. Each of these estimates undoubtedly has broad confidence limits, which we have not attempted to evaluate because of the small sample of nodes and lack of sampling toward the present. However, although the estimates also are based on the unascertainable assumption of time homogeneity, they are consistent with extinction having been frequent during the diversification of both squamates and passerines. Variation in the estimated slope of the LTT plot would not alter this conclusion.

The rate of speciation estimated from the LTT plot for squamates was 0.70 per Myr. The LTT plot for South American tyrannids indicated a speciation rate of 0.43–0.86 per Myr, depending on the calibration used (Ricklefs, 2006c). For a sample of North American and South American clades of passerine birds, the value was 0.62–1.23 or 0.50–1.00, depending on whether tropical vs. temperate was included as an effect in the analysis and on the time calibration (Ricklefs, 2006a). For all passerines, a speciation rate of 0.79 per Myr was estimated using a time calibration of 2 Myr per °C DNA hybridization melting point difference (Sibley & Ahlquist, 1990). The most extreme calibration of 4 Myr per °C would suggest a speciation rate of 0.40 per Myr. Regardless of the calibration used, estimates of the speciation rate in squamates appear to be roughly similar to those for passerines. And although broad confidence limits are associated with these rates, their general similarity, with waiting times to speciation or extinction in the range of 1–2 Myr, is striking.

Differences in patterns of diversification of squamates and birds

Compared with passerine birds, squamates showed more evidence of rate heterogeneity over time and over clades, and a weaker latitude effect. Heterogeneity in the rate of diversification through time can be perceived in LTT plots. The LTT plot for squamates portrayed in Fig. 2 reveals a reduced rate of increase followed by a sharp upturn at approximately 84 Ma. This pattern is characteristic of a mass extinction event that prunes many branches in a phylogeny (Heard & Mooers, 2002), although it could also result from variation in the net diversification rate. The fossil record of squamates is moderately well known, with many taxa from Laurasia (reviewed in Evans, 2003). No suggestion has been made based on the fossil record of a mid-Cretaceous mass extinction event, nor is there evidence of a mass

extinction event at the Cretaceous/Tertiary boundary at 65 Ma.

Among passerine birds, a LTT plot for the endemic South American radiation of suboscine passerines (Ricklefs, 2006c), and for passerines as a whole (this study), suggests relatively homogeneous proliferation over time (Ricklefs, 2006a). This is not true of all birds analysed in this manner. For example, a similar analysis of the Australasian Corvida radiation indicated a slowing of the proliferation rate through the latter part of the Tertiary as the Australian continent became more arid (Ricklefs, 2005a). Both squamates and passerines exhibit heterogeneity in diversification rates among clades, as shown by the large proportion of small clades in both groups, and by the exceptionally large clade of alethinophian snakes among the squamates. Heterogeneity is indicated by a ratio of the standard deviation to the mean exceeding one. Among squamate clades, this ratio is 2.20 (or 1.48 excluding the snake clade); among passerine tribe-level clades, this ratio was 1.35 (Ricklefs, 2003).

Compared with passerine birds, diversification rates of squamate clades do not appear to be as strongly tied to latitude, although relatively few clades of squamates are distributed primarily in temperate regions.

Comparison with diversification in mammals

A recently assembled supertree for all mammals (Bininda-Emonds *et al.*, 2007) permits comparison of diversification between mammals (4510 species in total), squamates and passerine birds. As in the case of squamates and passerines, the number of species in orders of mammals is unrelated to clade age ($r = 0.24$, $P = 0.239$, $n = 25$). Estimated net diversification (speciation–extinction) rates for mammals varied between 0.05 and 0.10 Myr⁻¹ over the past 100 Ma. The comparable value for squamates is 0.042 Myr⁻¹, and for passerine birds 0.092–0.18 Myr⁻¹, depending on the age calibration. Because the contemporary number of species is similar in the three groups, it is not surprising that net diversification rates are inversely related to the relative ages of the modern groups (squamates > mammals > passerines). Like squamates and passerines, mammal orders exhibit heterogeneity in the rate of diversification. The ratio of the standard deviation of the number of species per order to the mean is 2.34 – or 1.51 excluding the exceedingly diverse Rodentia (1969 species) and Chiroptera (915 species) (Bininda-Emonds *et al.*, 2007, Table 1). In addition, based on an LTT plot, the number of ancestral lineages of contemporary mammals was unaffected by the end-Cretaceous mass extinction, as was the case for squamates. Thus, three major groups of terrestrial vertebrates exhibit rather similar patterns of diversification and contemporary clade diversity.

Conclusion

Squamates and passerines are similar in terms of body size, primarily terrestrial habits, generally active foraging mode, and typically generalized diets, but differ in average body temperature and mobility. The apparently comparable rates of speciation and extinction in the two groups suggest that body temperature (Rohde, 1992; Allen *et al.*, 2006; Allen & Gillooly, 2006) and dispersal capabilities (Belliere *et al.*, 2000) do not have strong impacts on the rate of diversification, or that these effects are compensated by other differences between squamates and passerines. Both squamates and birds exhibit larger clade size in the tropics, although the effect of latitude is weak in squamates. Many factors might be responsible for these patterns, but it is not possible to distinguish among them at this point. A high relative rate of extinction (94% of the speciation rate) and the absence of a relationship between species richness and clade age suggest that species turnover is high and that extinction has approximately balanced speciation over the long history of squamate and passerine diversification. Mammalian orders exhibit similar patterns. Analyses of modern clades focus primarily on clades that have grown, giving the appearance of overall positive rates of proliferation. However, it is evident that the biased sampling implicit in an LTT plot is misleading, and that squamates 50 Ma might have been as diverse as they are today.

One of the major differences between squamates and passerines is the relative ages of the clades. Passerines are probably post-Cretaceous for the most part; the first fossils are from ca. 55 Ma and they are apparently not assignable to modern groups (Mayr, 2005). Thus, although squamates have been diversifying several times longer than passerines, the result has been a similar number of species. This reinforces the conclusion that both clades have been in a speciation–extinction balance for a long time and have primarily undergone replacement and turnover, at apparently similar rates. A logical consequence of this inference is that the total numbers of squamate and passerine species are regulated regionally at about the same level and that speciation and/or extinction rates are species-richness dependent, as suggested by Rosenzweig (1995) and others. This inference would appear to be at odds with the estimated excess of speciation rate over extinction rate based on LTT plots for both clades. However, these estimates are based on the surviving clades, which have replaced many others that have disappeared. This creates the illusion of long-term increase in diversity. Alternatively, if diversification is diversity dependent, then species richness might have been regulated with balanced speciation and extinction over long periods by prevalent conditions at the surface of the earth, including climate and geography. For example, the fossil records of plant species richness in the Andes of South

America (Jaramillo *et al.*, 2006) and of diversity of North American mammals (Stuckey, 1990; Van Valkenburgh & Janis, 1993; Alroy, 2000) show variation rather than continual increase over most of the Tertiary. Further comparisons of diversification in other groups will help to establish or refute the generality of these conclusions.

Acknowledgments

We are grateful to Shai Meiri and several reviewers for constructive comments.

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Received 24 February 2007; revised 12 May 2007; accepted 17 May 2007

Appendix

Squamate clades treated in this analysis.

Clade	Species	Distribution	
1	Eublepharid geckos	20	Southwestern USA, Central America, East and West Africa, southern Asia, extreme southeastern Asia, islands on Sunda Shelf
2	Gekkonine geckos	875	Cosmopolitan except northern North America and Eurasia
3	Diplodactyline geckos + gygopodids	156	Australia, New Zealand, New Caledonia
4	<i>Dibamus</i>	11	Mexico and rain forests of southeast Asia, Indonesia, Philippine Islands, western New Guinea
5	<i>Uromastyx</i>	14	Northern Africa (deserts) across in arid regions to India
6	Chameleons	130	Africa, Madagascar, Middle East, Sri Lanka, India, Spain, Greece
7	<i>Leiolepis</i>	7	Thailand and surrounding area
8	Agamine agamids	400	Africa, south and central Asia, Indonesia, Australia, New Guinea
9	<i>Leiocephalus</i>	10	West Indies
10	Phrynosomatines	125	Southern Canada to Panama
11	Basiliscines	9	Central Mexico to northwestern South America
12	Iguanines	34	Central and tropical South America, West Indies, southwestern USA, Fiji, Galapagos
13	Anolines	450	Southeastern USA, West Indies, all of Central and South America
14	Hoplocercids	10	Panama, northwestern South America, Amazonia, cerrados of Brazil and Bolivia
15	Oplurines	7	Madagascar
16	Liolaemines	175	Nontropical South America
17	Crotaphytids	12	South central and southwestern USA, northern Mexico
18	Tropidurines	90	South America, Galapagos
19	<i>Xenosaurus</i>	4	Southern Mexico to Guatemala
20	<i>Heloderma</i>	2	Southwestern USA to Guatemala
21	Anguids	110	Most of the Americas, West Indies, western Eurasia, Sunda Shelf isles, northwestern Africa
22	<i>Shinisaurus</i>	1	Guangxi Province, China
23	Varanids + <i>Lanthanotus</i>	51	Africa, across southern Asia to China, islands from there to Australia, all of Australia
24	Scolecophidian snakes	315	Central and South America, West Indies, Eurasia, Australasia, Africa, Middle East
26	Alethinophidian snakes	2600	Cosmopolitan except northern NA and Eurasia
26	Lacertids	250	Africa, Eurasia, islands of Sunda Shelf
27	<i>Rhineura</i>	1	Northern Florida
28	Other amphisbaenians	250	West Indies, South America, Sub-Saharan Africa, circum Mediterranean, northern Africa, Middle East, Baja California, Mexico
29	Teids	125	Northern USA through Central America, most of South America, West Indies
30	Gymnophthalmids	160	Southern Mexico to Argentina, southern Lesser Antilles
31	Lygosomine skinks	760	Cosmopolitan except northern Eurasia and northern and western North America
32	Scincine and feylinine skinks	210	North and Central America, Africa, Madagascar, southern Europe, Asia to Japan and Philippines
33	Acontine skinks	17	Southern Africa and Kenya
34	Xantusiids	20	Cuba, southwestern USA to Panama
35	Cordylids	42	Eastern and southern Africa
36	Gerrhosaurids	35	Sub-Saharan Africa and Madagascar