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Global Patterns of Diversification and Species Richness in Amphibians

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Online enhancements: appendix tables.

abstract: Geographic patterns of species richness ultimately arise through the processes of speciation, extinction, and dispersal, but relatively few studies consider evolutionary and biogeographic processes in explaining these diversity patterns. One explanation for high tropical species richness is that many species-rich clades originated in tropical regions and spread to temperate regions infrequently and more recently, leaving little time for species richness to accumulate there (assuming similar rates of diversification in temperate and tropical regions). However, the major clades of anurans (frogs) and salamanders may offer a compelling counterexample. Most salamander families are predominately temperate in distribution, but the one primarily tropical clade (Bolitoglossinae) contains nearly half of all salamander species. Similarly, most basal clades of anurans are predominately temperate, but one largely tropical clade (Neobatrachia) contains ∼96% of anurans. In this article, I examine patterns of diversification in frogs and salamanders and their relationship to large-scale patterns of species richness in amphibians. I find that diversification rates in both frogs and salamanders increase significantly with decreasing latitude. These results may shed light on both the evolutionary causes of the latitudinal diversity gradient and the dramatic but poorly explained disparities in the diversity of living amphibian clades.

Keywords: amphibians, biogeography, diversification, phylogeny, speciation, species richness.

Explaining the underlying causes of large-scale patterns of species richness is an urgent challenge for ecologists and evolutionary biologists as global biodiversity is increasingly threatened. Some of these patterns, such as the tendency for species diversity to increase from the poles toward the equator, have been noted for centuries but have proved difficult to explain (e.g., Brown and Lomolino 1998). For example, more than a hundred hypotheses have been proposed to explain the latitudinal diversity gradient, but there is little consensus as to the most likely explanation (e.g., Pianka 1966; Rahbek and Graves 2001; Willig et al. 2003).

Many workers have found strong correlations between environmental variables and global diversity patterns and on this basis have considered climatic factors to be the primary explanation (e.g., Francis and Currie 2003, 2004; Hawkins et al. 2003; Willig et al. 2003). However, patterns of species richness ultimately are caused by evolutionary and biogeographic processes such as speciation, extinction, and dispersal; these are the processes that directly increase or decrease the number of species in a region (e.g., Ricklefs 1987, 2004; Wiens and Donoghue 2004). Thus, an adequate explanation for large-scale patterns of species richness must incorporate evolutionary and biogeographic processes at some level, in addition to considering the well-known climatic correlates.

In the 1990s, several evolutionary ecologists converged on a similar explanation for the high species richness of tropical regions, a hypothesis that integrates both evolutionary and ecological factors (e.g., Ricklefs and Schluter 1993; Brown and Lomolino 1998; Futuyma 1998). Wiens and Donoghue (2004) dubbed this explanation the "tropical conservatism hypothesis" (TCH). The TCH is not an entirely new hypothesis but is rather a synthetic explanation that includes some important aspects of previous explanations for the latitudinal diversity gradient.

The TCH has three main parts (Farrell et al. 1992; Ricklefs and Schluter 1993; Brown and Lomolino 1998; Futuyma 1998; Wiens and Donoghue 2004). First, many species-rich tropical clades originated in tropical regions and spread to temperate regions only recently or not at all. The recent dispersal of clades to temperate regions leaves less time for speciation to occur and for species to thereby accumulate in these regions (i.e., the "time-for-speciation effect" reviewed and tested by Stephens and Wiens [2003]), given the important assumption that the diversification rate (rate of speciation − rate of extinction) generally is similar between tropical and temperate regions

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(but see Cardillo 1999; Cardillo et al. 2005; Ricklefs 2006). This aspect is clearly related to the traditional "evolutionary time" hypothesis (e.g., Willis 1922; Stebbins 1974). Second, dispersal between tropical and temperate regions is limited by specialization of lineages to a given climatic regime (i.e., niche conservatism; reviewed by Wiens and Graham [2005]), thereby linking the biogeographic patterns to climatic factors. Third, many clades have originated in the tropics because tropical regions were much more extensive until recently (roughly 30–40 million years ago [Mya]; Behrensmeyer et al. 1992). This third part of the hypothesis is related to the long-standing hypothesis that species richness increases with area (e.g., MacArthur and Wilson 1967; Rosenzweig 1995).

Few studies have thoroughly tested the TCH thus far, although some have addressed aspects of it (e.g., greater age of tropical clades in New World birds; Gaston and Blackburn 1996; Hawkins et al. 2006). Most recently, one study tested and supported the first two parts of the hypothesis in New World treefrogs (Wiens et al. 2006), and another addressed and supported the third part of the hypothesis in trees (Fine and Ree 2006).

Caudate and anuran amphibians (salamanders and frogs) may offer a compelling counterexample to the TCH. Among the 10 currently recognized families of salamanders, nine are predominately temperate (Zug et al. 2001; Pough et al. 2004), including those families generally placed near the base of salamander phylogenies (e.g., Larson and Dimmick 1993; Wiens et al. 2005). However, one clade within one subfamily of the family Plethodontidae is tropical (the tropical bolitoglossines, or supergenus *Bolitoglossa*). This single clade contains nearly half of all recognized salamander species (228 of 555 species; AmphibiaWeb 2006). Taken together, these patterns imply that salamanders are ancestrally temperate, have dispersed extensively into tropical regions only recently, and have undergone accelerated rates of diversification in the tropics.

Patterns of diversity in anurans show many parallels to those in salamanders. Among the 5,356 species of anurans (AmphibiaWeb 2006), most of the basal lineages (Ford and Cannatella 1993; Hoegg et al. 2004; Roelants and Bossuyt 2005; San Mauro et al. 2005) are predominately temperate and relatively species poor, including the ascaphids ($n = 2$ species), bombinatorids ($n = 10$), discoglossids ($n = 12$), leioplematids ($n = 4$), pelodytids ($n = 3$), and pelobatids ($n = 11$). Among these primitive anuran lineages, there are also some clades that are more tropical in distribution and have higher species richness (e.g., megophryids [$n = 131$ species], pipoids [$n = 31$ species]). However, anurans have higher species richness in the tropics overall (e.g., IUCN et al. 2004), and their species diversity in the tropics is dominated by a single, relatively recent clade, Neobatrachia (~5,152 species, or 96% of anuran species).

In contrast to the predictions of the TCH, these patterns in amphibians suggest that the latitudinal diversity gradient may be caused more by differences in speciation and/or extinction rates between temperate and tropical regions than by differences in the timing of biogeographic dispersal. In fact, many ecologically based explanations for the latitudinal diversity gradient implicitly assume or require differences in diversification rates between organisms in temperate and tropical regions (e.g., the productivity, energy, stability, predation, and competition hypotheses; Willig et al. 2003), whereas in some evolutionarily based hypotheses, this link is explicit (e.g., the evolutionary rates and evolutionary speed hypotheses; Willig et al. 2003).

In summary, both salamanders and frogs show patterns of diversity that suggest dramatically higher rates of diversification in predominately tropical clades. Although these basic patterns of diversity and distribution may be common knowledge among herpetologists, no studies have explicitly addressed rates of diversification among major clades of frogs or salamanders and their relationship to latitude and latitudinal diversity patterns. In fact, there has been surprisingly little recent literature that addresses the dramatic disparities in the species diversity of living amphibian clades, and thus few explicit hypotheses have been proposed to explain the high species richness of bolitoglossines or neobatrachians or even the 10-fold difference between the numbers of anuran and caudate species (but see Ryan 1986).

In this article, I examine rates and patterns of diversification in amphibians and their relationship to latitude and global patterns of species richness. I take advantage of new phylogenetic data for frogs and salamanders (e.g., Chippindale et al. 2004; Hoegg et al. 2004; Min et al. 2005; Roelants and Bossuyt 2005; San Mauro et al. 2005; Wiens et al. 2005), new summaries of global amphibian diversity and distribution patterns (e.g., IUCN et al. 2004; AmphibiaWeb 2006), and recent methods for estimating divergence dates and diversification rates (Magallón and Sanderson 2001; Sanderson 2002, 2003). Specifically, I ask whether there is a general relationship between diversification rate and latitude in salamanders and frogs. To address this, I estimate the phylogeny and divergence dates within these groups through new analyses of previously published sequences of the slow-evolving nuclear RAG-1 gene. I use these estimated dates to infer rates of diversification of clades and then test for a relationship between the latitudinal distribution of clades and their rates of diversification.

Material and Methods

Overview

Similar data and methods were used in the analyses of frogs and salamanders. For greater clarity, I first present these methods as applied to salamanders and then briefly summarize differences and relevant details for frogs. Throughout the article, I generally follow the standard taxonomy used by AmphibiaWeb (2006) rather than the novel (but poorly justified) classification of Frost et al. (2006).

Salamander Phylogeny

In order to estimate divergence times for use in calculating diversification rates, it is desirable to have branch lengths based on the same gene for all taxa. I used only the RAG-1 gene, given that data from other nuclear genes are available only for a more limited set of taxa. Furthermore, although mitochondrial data are now available for many salamander species, estimates of higher-level salamander phylogeny based primarily on mitochondrial data seem prone to the problem of long-branch attraction (e.g., Weisrock et al. 2005), and branch lengths from these data may be problematic for estimates of divergence dates.

RAG-1 data were compiled from several sources (table A1 in the online edition of the *American Naturalist*), along with two previously unpublished sequences (*Amphiuma tridactylum*, *Batrachoseps attenuatus*). I also used a slightly corrected sequence to replace the *Batrachoseps major* sequence used by Chippindale et al. (2004). Previous analyses of RAG-1 data across salamanders showed that the $GTR + I + \Gamma$ model provides the best fit and that recognizing separate partitions for codon positions within the gene significantly improves the fit to the data relative to using only one partition (Wiens et al. 2005).

I estimated a phylogeny and branch lengths for a pooled data set of 68 RAG-1 sequences from 66 species, including multiple representatives of all salamander families. I performed two pairs of replicated Bayesian analyses, using MrBayes, version 3.1.2 (Huelsenbeck and Ronquist 2001). Each of the four analyses used 4.0×10^6 generations. Stationarity was evaluated on the basis of (1) plots of log likelihoods over time, (2) the similarity in topologies, branch support (posterior probabilities), and likelihoods between trees, and (3) the average standard deviation of split frequencies between runs within each pair of searches. Stationarity seemingly was achieved after fewer than 100,000 generations, but all trees generated before 400,000 generations were excluded. The final estimate of phylogeny and branch lengths was based on the pooled post–burn-in trees from the four replicate analyses.

The Bayesian phylogeny was also confirmed with a parsimony analysis. A heuristic search was performed to find the shortest trees, using 200 random-taxon-addition sequence replicates and tree-bisection-reconnection branch swapping. Branch support was estimated with a nonparametric bootstrap analysis (Felsenstein 1985*a*), using 200 pseudoreplicates with five random-taxon-addition sequence replicates each. Parsimony analyses were performed using PAUP, version 4.0b10 (Swofford 2002).

Penalized Likelihood Analysis

Divergence dates for salamander clades were estimated using penalized likelihood (PL; Sanderson 2002) implemented in r8s (ver. 1.6 for Unix; Sanderson 2003). The PL method is a "relaxed" molecular clock method that allows for different rates of evolution across the tree, while minimizing hypothesized changes in rates. The PL analyses used the topology and branch lengths from the Bayesian analysis of RAG-1. Although some recent studies have provided divergence date estimates for various salamander clades, these estimates have been based on more limited taxon sampling with fewer fossil calibration points (e.g., San Mauro et al. 2005) and in some cases have used very fast-evolving characters that may bias branch length estimates (Mueller 2006).

Calibration points from fossil taxa were used to constrain the minimum ages of the following 11 crown-group clades. (1) The most recent common ancestor (MRCA) of *Plethodon* diverged into two clades at least 19 Mya. Tihen and Wake (1981) reported fossil vertebrae of *Plethodon* and *Aneides* from the Arikareean (Lower Miocene) of Montana. One of the *Plethodon* vertebrae was considered to be "very similar" to those of extant *Plethodon* from western North America. I tentatively consider this vertebra to represent a lineage that evolved after the split between the modern eastern and western *Plethodon* clades. The Arikareean extends from 19 to 30 Mya (Barnosky 2001). (2) The MRCA of *Aneides*, *Desmognathus*, and *Phaeognathus* diverged at least 19 Mya. Given the presence of an *Aneides* vertebra in the Arikareean period (Tihen and Wake 1981), the MRCA of the clade containing modern *Aneides* must be at least 19 Mya. (3) The MRCA of *Aneides* diverged at least 5 Mya. A fossil was identified as *Aneides lugubris* from the late Miocene (Hemphillian) by Clark (1985), who estimated its age at 5 Mya. Thus, the MRCA of the two species of *Aneides* sampled (*Aneides aeneus* and *Aneides lugubris*) is at least this old. (4) The MRCA of bolitoglossines diverged at least 5 Mya. Clark (1985) reported a fossil *Batrachoseps* from the late Miocene (Hemphillian) of California estimated to be five million years old. Given that the analyses of the present study show *Batrachoseps* as the sister group of all other included bolitoglossines, the MRCA of bolitoglossines must be at least this old. (5) The MRCA of plethodontids and amphiumids diverged at least 66 Mya. The oldest known amphiumid fossil (*Proamphiuma cretacea*) is late Maastrichtian or Early Paleocene and thus approximately 66 million years old (Gardner 2003). The split between Plethodontidae and Amphiumidae must be at least this old. (6) The MRCA of Salamandroidea (all extand salamanders exclusive of Cryptobranchoidea and Sirenidae) diverged at least 114 Mya (early Barremian, Cretaceous), based on *Galverpeton* and *Valdotriton* (Evans and Milner 1996). (7) The MRCA of *Salamandra* and *Mertensiella* diverged at least 34 Mya, based on fossils of *Salamandra* from the Eocene of Europe (Milner 2000). (8) The MRCA of *Triturus* and *Euproctus* diverged at least 34 Mya, based on fossils of *Triturus* from the Eocene of Europe (Milner 2000). (9) The MRCA of *Notophthalmus* and *Taricha*, based on fossils of *Taricha* from the Upper Oligocene of Oregon, diverged at least 24 Mya (Milner 2000). (10) The MRCA of Dicamptodontidae and Ambystomatidae diverged at least 58 Mya, based on a fossil dicamptodontid (Naylor and Fox 1993). (11) The MRCA of Cryptobranchidae and Hynobiidae diverged at least 161 Mya (Gao and Shubin 2003), based on a fossil cryptobranchid (*Chunerpeton*). Although there are many other fossil salamander taxa known (e.g., Milner 2000), these additional taxa seem unlikely to make the estimated dates of the relevant clades any older. For example, even though various fossil proteids and sirenids are known (e.g., Milner 2000), it is unclear whether they are nested within the crown groups of these clades, and so they cannot be used to constrain the minimum age of these nodes.

Current implementations of PL require specification of an estimated age for at least one clade (rather than just a constraint on the minimum age of the clade). I used three possible dates for the crown-group age of the MRCA of extant caudates: 250, 210, and 170 Mya. Given the presence of the fossil anuran *Triadobatrachus* in rocks of that age, 250 Mya is a minimal age for the split between anurans and caudates. However, the age of the MRCA of extant caudates could be considerably younger than the anuran-caudate split. Fossil caudates are known from roughly 170 Mya (*Marmorerpeton*; Evans and Milner 1996), and fossil cryptobranchids are known from 161 Mya (Gao and Shubin 2003). I used 210 Mya as an intermediate estimate between these two extremes.

The PL analyses were implemented using the truncated Newton algorithm. Cross-validated assessment was used to select the best-fitting smoothing parameter, with values from 10^0 to 10^4 in exponential increments of 0.5. These analyses showed an optimal smoothing parameter of 10 for root ages of 170 and 210 Mya and 31.62 for a root age of 250 Mya. For each root age, 10 replicate optimizations were performed to estimate the ages of clades (using the option "num_time_guesses = 10").

A range of possible dates for each node are presented, based on different dates for the age of the root. The uncertainty in root ages seems likely to be a major source of uncertainty in the estimates of clade ages and diversification rates, and analyses of diversification rates were performed using all three possible root ages. In this article, the relative diversification rates of clades are of primary interest; thus, the relative ages of clades are more important than potential variability in the estimates of absolute ages.

Estimating Diversification Rates

I estimated the diversification rates for 12 nonnested clades of salamanders, which together include all described salamander species. Most clades correspond to traditionally recognized families (i.e., Ambystomatidae, Amphiumidae, Dicamptodontidae, Proteidae, Rhyacotritonidae, Salamandridae, and Sirenidae). However, a single clade (Cryptobranchoidea) was used for the families Cryptobranchidae and Hynobiidae, given that hynobiids appear to be paraphyletic with respect to cryptobranchids (see "Results"). Furthermore, the Plethodontidae were divided into four clades, the minimum number needed to treat the tropical bolitoglossines as a distinct unit in these analyses and simultaneously include all other plethodontid clades. Thus, within Plethodontidae, I utilized (1) Plethodontinae, (2) a single clade for the Hemidactylinae and Spelerpinae, (3) *Batrachoseps*, and (4) the clade of tropical bolitoglossine genera. The subfamilies Hemidactylinae and Spelerpinae form a clade in these analyses (and were traditionally recognized as a single taxon, the tribe Hemidactyliini; Wake 1966), but some previous studies do not place them as sister taxa (e.g., Chippindale et al. 2004; Mueller et al. 2004; Macey 2005). Because Hemidactylinae contains only one species, the inclusion (or exclusion) of this subfamily in a clade with the more species-rich Spelerpinae has little effect on the results (J. J. Wiens, unpublished results). Admittedly, the choice of clades is somewhat arbitrary, and families are not comparable units. However, given that diversification rates are estimated based on divergence dates (see below), no assumptions are made about different families or clades being of equal age.

Diversification rates were estimated using the method-of-moments estimators presented by Magallón and Sanderson (2001) for both stem groups (their eq. [6]) and crown groups (their eq. [7]). The age of the stem group corresponds to the point in time when the clade first split from its sister group, whereas the age of the crown group corresponds to the age of the oldest split between extant lineages in the clade (fig. 1; after fig. 1 of Magallón and Sanderson 2001). Importantly, the stem group may contain extinct lineages that currently are assigned to that

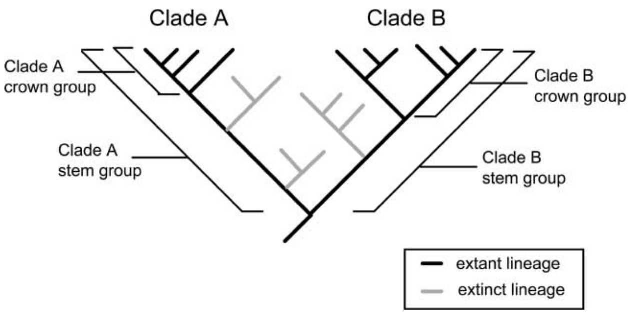


Figure 1: Stem group and crown groups for two hypothetical clades A and B (after Magallón and Sanderson 2001). The stem group is the most inclusive monophyletic group containing all the extant species of a clade (but no other extant species), whereas the crown group is the least inclusive monophyletic group that includes all the extant members of a clade and their most recent common ancestor. In this example, the stem groups of A and B contain extinct lineages that are outside the crown group.

taxon (e.g., family) but diverged before the origin of the crown group.

The method-of-moments estimators have an advantage over the widely used maximum likelihood estimators (e.g., eqq. [3], [4] of Magallón and Sanderson 2001), which require the assumption that the extinction rate is negligible. Given that the relative extinction rate (ε, where ε = speciation rate/extinction rate) is unknown, I attempted to bracket the most likely extinction rates by using two extreme values of the relative extinction rate. Following the arguments of Magallón and Sanderson (2001), I used a value of 0.90 as an upper limit and 0 (no extinction) as a lower limit. Note that when the extinction rate is 0, the diversification rate becomes equivalent to the rate of speciation.

These estimators require information on the ages of clades and their present species richness. The ages of clades were estimated using PL analysis, as described above. I initially used the intermediate estimate of the root age of Caudata for estimates of diversification rates (210 Mya); use of other root ages influences estimates of absolute diversification rates but appears to have little effect on comparisons of relative diversification rates between clades (J. J. Wiens, unpublished results). Estimates of species richness were taken from the AmphibiaWeb (2006) database, which lists all currently recognized caudate species and is updated as new species are described. Of course, new salamander species continue to be discovered, and these estimates of extant species richness cannot be considered extremely precise. Nevertheless, the overall patterns of relative species richness in extant clades likely will be maintained as new species are described, and I address the potential effects of new species discoveries on estimates of diversification rates in the "Discussion."

An important issue is whether enough species in the phylogeny have been sampled to span the common ancestor of the crown group of each selected clade. For example, diversification rate estimates for a family may be biased if the estimated species richness is based on all the species in the family but the estimated age is based on a subclade within the family that includes only a limited set of species. For most clades this does not seem to be a problem. For example, I included all the recognized genera for three clades (Plethodontinae, Proteidae, and Sirenidae), multiple representatives of the two critical lineages for two other clades (Cryptobranchoidea, Hemidactylinae + Spelerpinae clade), and all the recognized species for one family (Amphiumidae). For other groups (e.g., Ambystomatidae, Salamandridae, and tropical Bolitoglossinae), available within-clade phylogenies suggest that the most basal split within each group was included (e.g., Elias and Wake 1983; Shaffer et al. 1991; Titus and Larson 1995). For three clades, it is possible that one or possibly two species from the crown groups have been excluded, specifically *Batrachoseps* (clade including *Batrachoseps campi* and *Batrachoseps wrighti* not included; Jockusch and Wake 2002), Dicamptodontidae (two species not included, one possibly basal; Steele et al. 2005), and Rhyacotritonidae (one species not included but phylogeny uncertain; Good and Wake 1992). One way to account for this problem is to adjust the estimated species numbers when calculating crown-group diversification rates (alternatively, one could adjust the age of the crown group, but the age of the crown group is uncertain without sampling more species). Readjusting species numbers for these three clades has little effect on overall patterns of diversification rates for crown groups (J. J. Wiens, unpublished results), whereas stem-group estimates are completely unaffected.

Latitudinal Position versus Diversification Rate of Clades

I tested for a significant relationship between the latitudinal position of a clade and its estimated diversification rate. The latitudinal position of a clade was estimated using the midpoint of the southernmost and northernmost localities for that clade. The overall geographic ranges of families and other clades were initially estimated from Zug et al. (2001) and Pough et al. (2004). The range maps for individual species provided in the Global Amphibian Assessment database (GAA; IUCN et al. 2004) were used to determine the overall range limits of clades in terms of the distribution of individual species. The specific latitudes of the range limits were estimated using the GAA range maps and ArcView GIS 3.3 (ESRI 1992). The following species ranges were used to estimate the extreme northern and southern range limits of the 12 clades (northern, southern): (1) Cryptobranchoidea (*Salamandrella keyserlingii*, *Hynobius arisanensis*), (2) Sirenidae (*Siren intermedia*, *Pseudobranchus axanthus*), (3) Proteidae (*Necturus maculosus*, *Necturus beyeri*), (4) Salamandridae (*Triturus vulgaris*, *Notophthalmus meridionalis*), (5) Ambystomatidae (*Ambystoma gracile*, *Ambystoma rivulare*), (6) Dicamptodontidae (*Dicamptodon tenebrosus*, *Dicamptodon ensatus*), (7) Rhyacotritonidae (*Rhyacotriton olympicus*, *Rhyacotriton variegatus*), (8) Amphiumidae (*Amphiuma means*, northern and southern), (9) Plethodontidae, subfamily Plethodontinae (*Plethodon cinereus*, *Desmognathus auriculatus*), (10) Plethodontidae, Hemidactylinae + Spelerpinae clade (*Eurycea bislineata*, *Eurycea quadridigitata*), (11) Plethodontidae, *Batrachoseps* (*Batrachoseps wrightorum*, *B. major*), and (12) Plethodontidae, tropical bolitoglossines (*Pseudoeurycea bellii*, *Bolitoglossa altamazonica*). The latitudinal extremes and midpoints for each clade are provided in table 1. Note that all of these clades occur exclusively in the Northern Hemisphere (except tropical bolitoglossines), such that the latitudinal midpoint of each clade reflects whether it is primarily temperate or tropical.

Admittedly, georeferenced locality data would be superior to inferring range limits from maps. However, georeferenced museum localities are not yet available for most salamander species and may not be available for the extreme southernmost and northernmost localities of the critical species. Similarly, using the average of the geographic midpoint of the ranges of all species within a clade might be preferable to using the overall latitudinal midpoint of the clade. Again, the former approach is hampered by the lack of georeferenced locality data for all caudate species. Furthermore, it seems that the average midpoint of individual species within clades would be similar to the latitudinal midpoint estimated from the extreme range limits within each clade (i.e., the midpoints seem to reflect the central tendency of latitudinal species ranges rather than outliers). For the purposes of this study, the most important aspect of the geographic position of a clade is whether it is primarily temperate or tropical, and this index does appear to reflect that (table 1).

The geographic location of clades (and the possible effect of geographic location on diversification rate) may be shared between clades because of their shared phylogenetic history. Therefore, I analyzed independent contrasts (Felsenstein 1985*b*) of diversification rate and latitudinal midpoint of clades. Independent contrasts were calculated using COMPARE, version 4.06 (Martins 2004), and regressions were forced through the origin following Garland et al. (1992). All regression analyses were performed using Statview (Abacus, Berkeley, CA). Diversification rates were multiplied by 10,000 to maintain precision when using COMPARE (which uses only two decimal places). In order to calculate contrasts, I used the phylogeny estimated from the Bayesian analysis of the RAG-1 data and branch lengths estimated from PL (with branch lengths based on absolute age estimates of clades). Analyses were also performed using equal branch lengths and using the raw data (without contrasts). Regression results were generally similar for the three sets of branch lengths (i.e., using root ages of 170, 210, and 250 Mya), equal branch lengths, and raw data. Note that for calculating independent contrasts of stem-group diversification rates, the length of the branch for the ancestor of each of the 11 clades was ar-

Table 1: Species richness and latitudinal midpoints for the clades of salamanders used in this study

Clade	No. species	Latitudinal midpoint (°)	Range limits (°; northern, southern)[a]
Cryptobranchoidea (Cryptobranchidae + Hynobiidae)	53	46.875	71.25, 22.50
Sirenidae	4	33.20	41.40, 25.00
Proteidae	6	40.12	50.50, 29.75
Salamandridae	74	43.90	67.30, 20.50
Ambystomatidae	31	37.45	56.30, 18.60
Dicamptodontidae	4	43.04	49.12, 36.96
Rhyacotritonidae	4	43.64	48.37, 38.90
Amphiumidae	3	31.50	38.00, 25.00
Plethodontidae:			
Plethodontinae	93	38.96	50.24, 27.69
Hemidactylinae + Spelerpinae clade	35	38.23	51.45, 25.01
Bolitoglossinae:			
Batrachoseps	20	37.91	45.67, 30.15
Tropical bolitoglossine clade	228	5.31	28.367, −17.74

[a] Negative value indicates degrees south.

bitrarily reduced to 1 million years, given that the stem group begins with the origin of the entire clade (thus, using the time interval between the origin of the stem and crown group is inappropriate).

Analyses of Anurans

Methods generally followed those described for salamanders. As for salamanders, some recent studies have estimated divergence dates for major anuran clades using relaxed molecular clock methods, but these studies used relatively limited taxon sampling (e.g., Roelants and Bossuyt 2005; San Mauro et al. 2005). For this study, the phylogeny and branch lengths were estimated using RAG-1 data from 84 anuran species and six outgroups (two caecilians, four salamanders), including representatives of almost all typically recognized anuran families (AmphibiaWeb 2006). Most sequences were derived from a variety of recent studies on amphibian phylogeny (e.g., Biju and Bossuyt 2003; Hoegg et al. 2004; van der Meijden et al. 2004, 2005; Evans et al. 2005; Roelants and Bossuyt 2005; San Mauro et al. 2005; Wiens et al. 2005, 2007*a*; Pramuk 2006). GenBank numbers and literature sources for these sequences are provided in table A2 in the online edition of the *American Naturalist.* This study focuses primarily on the basal clades of anurans, given that sampling is weak within the Neobatrachia (relative to the >5,000 species) and that there is considerable uncertainty regarding the phylogeny and taxonomy within this clade (e.g., Darst and Cannatella 2004; Frost et al. 2006; this study). Furthermore, basal anurans are more comparable in age to the major groups of salamanders. Methods followed those described above for salamanders (i.e., partitioned Bayesian analysis). The phylogenetic results of this study are broadly concordant with those of other recent studies of basal anuran clades (e.g., Hoegg et al. 2004; Roelants and Bossuyt 2005; San Mauro et al. 2005; Frost et al. 2006).

For divergence date estimation, I used PL analysis, as described above. Ten fossil calibration points were used: (1) crown-group age of the MRCA of hynobiids and cryptobranchids, at least 161 Mya (Gao and Shubin 2003), based on a fossil cryptobranchid (*Chunerpeton)*; (2) MRCA of frogs and salamanders, at least 242 Mya, based on a fossil anuran (*Triadobatrachus*) from the Early Triassic of Madagascar (Carroll 1988); (3) MRCA of pipoids and all other frogs, at least 144 Mya, given *Rhadinosteus parvus*, ostensibly a rhinophrynid but clearly a pipoid, from the Late Jurassic (Tithonian; Rocek 2000); (4) MRCA of Pipidae + Rhinophrynidae, at least 121 Mya, given the pipid *Cordicephalus* from the Early Cretaceous (Barremian; Rocek 2000); (5) MRCA of Pelodytidae, Pelobatidae, and Megophryidae, at least 33.7 Mya, given fossil *Pelodytes* from the Late Eocene (Rocek and Rage 2000); (6) MRCA of *Caudiverbera* and Myobatrachidae, at least 61.0 Mya, given fossil *Caudiverbera* from the Early Paleocene (Baez 2000); (7) MRCA of Bufonidae, at least 23.8 Mya, given fossil *Bufo* from the Early Miocene (Rocek and Rage 2000); (8) MRCA of Ranoidea, at least 33.7 Mya, given fossil *Rana* from the Late Eocene (Rocek and Rage 2000); (9) MRCA of Pelodryadinae (*Litoria caerulea*)-Phyllomedusinae (*Agalychnis callidryas*) clade of Hylidae, at least 28 Mya, given that Sanmartín and Ronquist (2004) summarize evidence suggesting that the last terrestrial connection between Australia and South America was sundered at least 28 Mya; (10) MRCA of *Hyla meridionalis*–*Hyla cinerea*, at least 16 Mya, given that Sanchiz (1998) noted fossil *Hyla* similar to extant *Hyla meridionalis* in the Lower Miocene of Austria (∼16 Mya), and that a fossil *Hyla* (*Hyla goini*) from North America is known from the Miocene Hemingfordian North American Land Mammal Age (15–19 Mya) that is very similar to (if not conspecific with) *Hyla squirella*, the sister group to *H. cinerea* (Holman 2003). Although many more fossil anuran taxa are known in addition to those listed here, most of those excluded are either redundant with those used here (i.e., younger fossils within the same group) or else appeared to be of uncertain phylogenetic placement.

I used three possible ages for the age of the root of the tree (the MRCA of anurans and caudates). Recent molecular clock studies estimate dates of ∼300–360 Mya for this clade (reviewed in San Mauro et al. 2005). I used the oldest date from molecular analyses (357 Mya; San Mauro et al. 2005), a more recent age based on the approximate age of the oldest unambiguous member of this clade, *Triadobatrachus* (∼242 Mya, but rounded up to 250), and an intermediate age between the molecular and fossil estimates (300 Mya). Use of these alternate root ages has very little effect on the relationship between diversification rate and latitude (J. J. Wiens, unpublished results), and so only results based on the root age of 300 Mya are presented.

For analyses of diversification rate and latitude, methods similar to those described for salamanders were used. I used 15 clades as units in these analyses: (1) Ascaphidae (genus *Ascaphus*), (2) Leiopelmatidae (*Leiopelma*), (3) Pipoidea (Rhinophrynidae and Pipidae were combined into a single clade, given that Rhinophrynidae contains only one species and is therefore an inappropriate unit for analyses of diversification rate and that monophyly of extant Pipoidea is unequivocal), (4) Bombinatoridae (*Bombina*, *Barbourula*), (5) Discoglossidae (*Alytes*, *Discoglossus*), (6) Scaphiopidae (*Scaphiopus*, *Spea*), (7) Pelodytidae (*Pelodytes*), (8) Pelobatidae (*Pelobates*), (9) Megophryidae, (10) Heleophrynidae, (11) *Caudiverbera* + *Telmatobufo* (traditionally classified in Leptodactylidae, but recent studies suggest that they are the sister group of Myobatrachidae; San Mauro et al. 2005; Frost et al. 2006), (12) Myobatrachidae (including Limnodynastinae and Myobatrachinae), (13) Sooglossidae, (14) Ranoidea (including Arthroleptidae [50 species], Astylosternidae [29], Hemisotidae [9], Hyperoliidae [259], Mantellidae [164], Microhylidae [443], Ranidae [784], and Rhacophoridae [285]), and (15) Hyloidea (including Allophrynidae [1 species], Brachycephalidae [10], Bufonidae [486], Centrolenidae [139], Dendrobatidae [248], Hylidae [824], and Leptodactylidae [1,278]). Nasikabatrachidae and Rhinodermatidae are two species-poor neobatrachian families that were not included as separate units; Nasikabatrachidae (1 species) is sister group to Sooglossidae (Biju and Bossuyt 2003), and Rhinodermatidae (2 species) is most likely nested inside of Leptodactylidae within Hyloidea (Roelants and Bossuyt 2005; Frost et al. 2006). The latitudinal extremes and midpoints for each clade are provided in table 2.

Given the limited sampling of species within anuran clades, I analyzed diversification rates using only the stem-group estimator, using both low and high extinction rates. The latitudinal midpoint of each clade was estimated as described for salamanders. I analyzed the relationship between diversification rate and latitude (the absolute value of the latitudinal midpoint of each clade), using both the raw data and independent contrasts. To confirm the robustness of the results to alternate divergence dates using alternate methods (i.e., Bayesian), the analyses were redone using the phylogeny and divergence dates estimated by San Mauro et al. (2005).

Results

Salamanders

The Bayesian phylogeny, branch support values, and one set of estimated divergence dates are summarized as a chronogram (fig. 2; for alternate dates, see tables 3, 4). The phylogeny estimated from RAG-1 generally is strongly supported (posterior probability ≥0.95 for most nodes) and similar to that from combined morphological and molecular data (Wiens et al. 2005). The only major difference is in the placement of proteids, which is weakly supported in both this tree and that of Wiens et al. (2005). Importantly, the branch that places the proteids is relatively short, suggesting that alternate phylogenetic placements should have little effect on the estimated age (and associated diversification rates) for this clade. The phylogeny estimated from the parsimony analysis (not shown) is nearly identical to that from the Bayesian analysis and has similar levels of branch support.

The estimated rates of diversification differ considerably, depending on whether the stem group or the crown group is considered and whether extinction rates are considered negligible or very high (tables 3, 4). Considering the stem-group ages (the time when the clade first diverged from its ancestor), tropical bolitoglossines have a higher diversification rate than any other salamander clade. However, considering the crown-group ages (the age of the common ancestor of all the extant species of the clade), tropical bolitoglossines do not have the highest diversification rate when rates of extinction are considered negligible; specifically, diversification rates in the primarily temperate clades *Batrachoseps* and Ambystomatidae exceed those of tropical bolitoglossines.

There is a significant negative relationship between latitude and diversification rate based on stem groups, which is driven largely by the high diversification rate of the tropical bolitoglossines. When based on independent contrasts with branch lengths based on the chronogram in

Table 2: Species richness and latitudinal midpoints for the clades of anurans used in this study

Clade	No. species	Latitudinal midpoint (°)[a]	Range limits (°; northern, southern)[a]
Leiopelmatidae	4	−38.50	−35.82, −41.19
Ascaphidae	2	46.97	55.05, 38.89
Pipoidea	31	−4.22	26.42, −34.85
Bombinatoridae	10	27.77	56.27, −.73
Discoglossidae	12	41.57	52.84, 30.30
Scaphiopidae	7	34.35	51.50, 17.20
Pelodytidae	3	43.54	51.06, 36.02
Pelobatidae	4	45.04	58.32, 31.75
Megophryidae	131	13.38	35.48, −8.78
Heleophrynidae	6	−29.07	−23.76, −34.38
Caudiverbera + *Telmatobufo*	4	−35.45	−30.02, −40.88
Myobatrachidae	126	−22.00	−.36, −43.63
Sooglossidae	4	−4.58	−4.47, −4.70
Ranoidea	2,023	17.82	71.05, −35.42
Hyloidea	2,986	10.30	69.33, −48.72

[a] Negative value indicates degrees south.

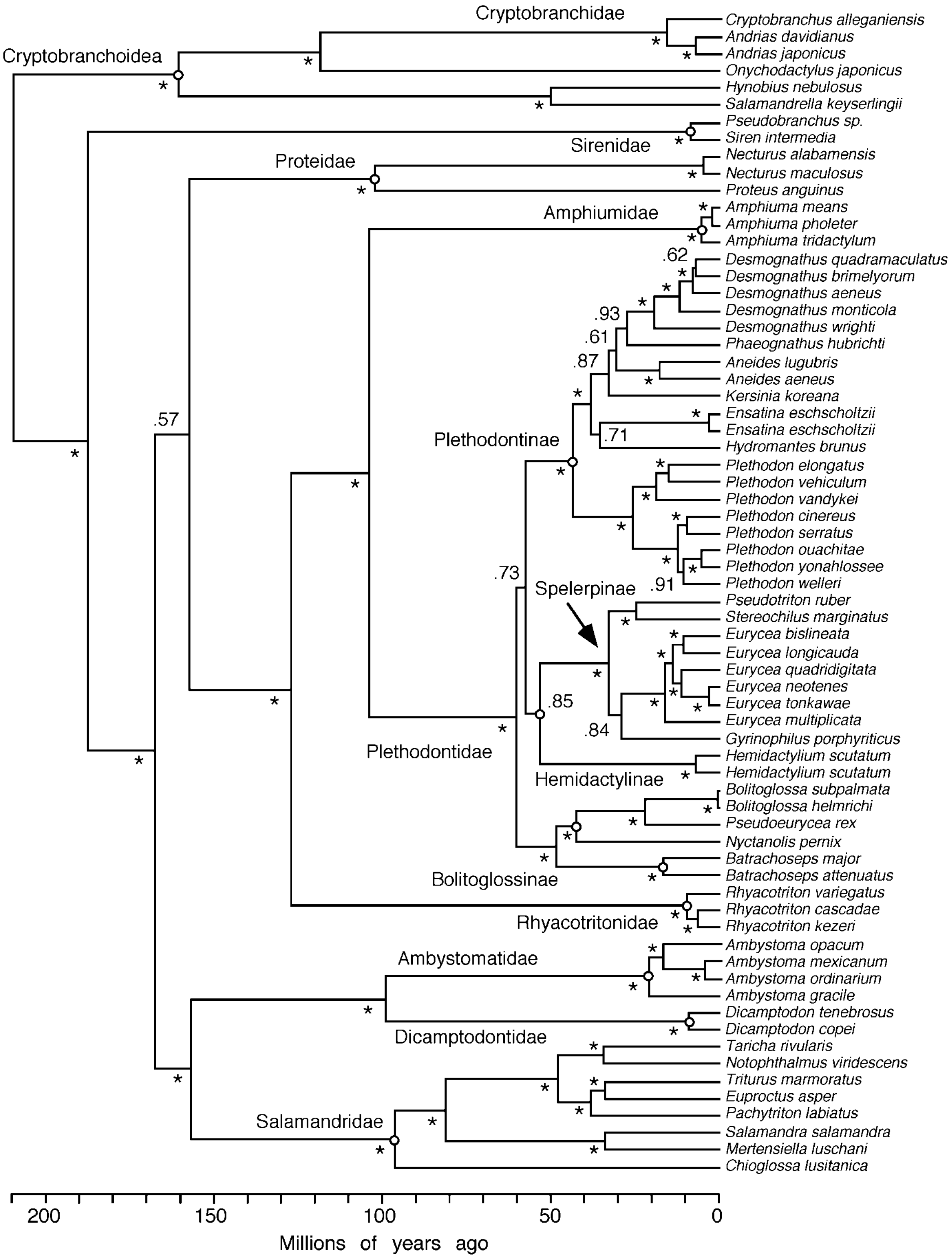


Figure 2: Phylogeny and divergence date estimates for salamanders based on analyses of the RAG-1 gene, using a root age for the crown group of salamanders of 210 Mya. Branches with asterisks have Bayesian posterior probabilities ≥0.95; values ≥0.50 but <0.95 are shown adjacent to clades (values <0.50 not shown). Crown groups of clades used in analyses of diversification rates are indicated with open circles.

Table 3: Estimated ages (in millions of years) and diversification rates (net speciation events per million years) for salamander clades, based on the stem groups for these clades

		Diversification rate	
Clade	Stem age	Relative extinction rate = 0	Relative extinction rate = .90
170 million years:			
Cryptobranchoidea	170.00	.023355	.010733
Sirenidae	153.04	.009058	.001714
Proteidae	129.07	.013882	.003141
Salamandridae	129.57	.033218	.016333
Ambystomatidae	81.08	.042353	.017098
Dicamptodontidae	81.08	.017098	.003236
Rhyacotritonidae	103.32	.013417	.002539
Amphiumidae	83.96	.013085	.002172
Plethodontinae	46.07	.098385	.050410
Hemidactylinae + Spelerpinae clade	46.07	.077173	.032160
Batrachoseps	38.68	.077449	.027526
Tropical bolitoglossine clade	38.68	.140366	.081838
210 million years:			
Cryptobranchoidea	210.00	.018906	.008688
Sirenidae	187.73	.007385	.001398
Proteidae	157.88	.011349	.002568
Salamandridae	157.13	.027392	.013468
Ambystomatidae	99.41	.034544	.013945
Dicamptodontidae	99.41	.013945	.002639
Rhyacotritonidae	127.52	.010871	.002057
Amphiumidae	104.19	.010544	.001750
Plethodontinae	57.77	.078459	.040201
Hemidactylinae + Spelerpinae clade	57.77	.061543	.025647
Batrachoseps	48.54	.061717	.021935
Tropical bolitoglossine clade	48.54	.111853	.065214
250 million years:			
Cryptobranchoidea	250.00	.015881	.007298
Sirenidae	221.55	.006257	.001184
Proteidae	183.34	.009773	.002212
Salamandridae	182.79	.023547	.011578
Ambystomatidae	112.62	.030492	.012309
Dicamptodontidae	112.62	.012309	.002330
Rhyacotritonidae	146.16	.009485	.001795
Amphiumidae	118.67	.009258	.001536
Plethodontinae	65.14	.069582	.035652
Hemidactylinae + Spelerpinae clade	65.14	.054580	.022745
Batrachoseps	54.67	.054797	.019475
Tropical bolitoglossine clade	54.67	.099311	.057902

Note: Results based on three different root ages for caudates are presented (170, 210, and 250 million years).

figure 2, the relationship is significant regardless of whether relative extinction rates are considered negligible ($r^2 = 0.748$, $P < .001$; fig. 3*A*) or high ($r^2 = 0.804$, $P < .001$). For crown groups, however, there is no significant relationship between independent contrasts of diversification and latitude if the extinction rate is low ($r^2 = 0.131$, $P = .248$; fig. 3*B*), although there is a significant relationship if extinction rates within the crown-group clades are considered to be high ($r^2 = 0.450$, $P = .017$). For both stem and crown groups, results are very similar when based on the raw data, on independent contrasts with equal branch lengths, or on independent contrasts with branch lengths estimated from chronograms with alternate root ages (170 and 250 Mya).

Anurans

The Bayesian phylogeny, branch support values, and one set of estimated divergence dates are summarized as a

Table 4: Estimated ages (in millions of years) and diversification rates (net speciation events per million years) for salamander clades, based on the crown groups for these clades

Clade	Stem age	Diversification rate: Relative extinction rate = 0	Diversification rate: Relative extinction rate = .90
170 million years:			
Cryptobranchoidea	161.00	.020355	.010733
Sirenidae	7.22	.096004	.001714
Proteidae	83.53	.013152	.003141
Salamandridae	83.39	.043302	.016333
Ambystomatidae	17.69	.154937	.017098
Dicamptodontidae	7.36	.094178	.003236
Rhyacotritonidae	8.06	.085998	.002539
Amphiumidae	4.67	.086823	.002172
Plethodontinae	35.34	.108643	.050410
Hemidactylinae + Spelerpinae clade	42.68	.067062	.032160
Batrachoseps	13.33	.172737	.027526
Tropical bolitoglossine clade	34.34	.137921	.081838
210 million years:			
Cryptobranchoidea	161.00	.020355	.011011
Sirenidae	8.93	.077620	.022683
Proteidae	102.61	.010707	.003403
Salamandridae	96.77	.037314	.021335
Ambystomatidae	21.52	.127362	.061997
Dicamptodontidae	9.18	.075506	.022066
Rhyacotritonidae	10.04	.069039	.020176
Amphiumidae	5.85	.069310	.020134
Plethodontinae	44.16	.086944	.051423
Hemidactylinae + Spelerpinae clade	53.60	.053399	.026671
Batrachoseps	17.18	.134027	.058912
Tropical bolitoglossine clade	43.00	.110144	.072420
250 million years:			
Cryptobranchoidea	161.00	.020355	.011011
Sirenidae	10.50	.066014	.019292
Proteidae	117.58	.009344	.002969
Salamandridae	108.69	.033222	.018995
Ambystomatidae	24.90	.110074	.053581
Dicamptodontidae	9.96	.069593	.020338
Rhyacotritonidae	11.30	.061340	.017926
Amphiumidae	6.51	.062283	.018093
Plethodontinae	50.28	.076361	.045164
Hemidactylinae + Spelerpinae clade	60.21	.047537	.023743
Batrachoseps	18.37	.125345	.055096
Tropical bolitoglossine clade	48.66	.097332	.063997

chronogram (fig. 4; see table 5 for alternate dates). The phylogeny for the basal clades is generally strongly supported and concordant with other recent studies (e.g., Roelants and Bossuyt 2005; San Mauro et al. 2005; Frost et al. 2006). In general, the basal clades of anurans show higher diversification rates at lower latitudes (see table 2 for latitudinal ranges and species richness of clades and table 5 for ages and diversification rates). The relationship for the raw data is weak but significant, assuming either a low relative extinction rate ($r^2 = 0.308$; $P = .032$) or a high rate ($r^2 = 0.285$, $P = .040$). The weakness of this relationship is seemingly related to two clades with tropical distributions but low diversification rates (the aquatic and burrowing pipoids and the highly restricted Seychellian endemics, the Sooglossidae). This relationship is stronger when based on independent contrasts with estimated branch lengths (low relative extinction: $r^2 = 0.522$, $P = .002$ [fig. 5]; high relative extinction: $r^2 = 0.496$, $P = .003$), but it is marginally nonsignificant when equal branch lengths are used (low relative extinction: $r^2 =$

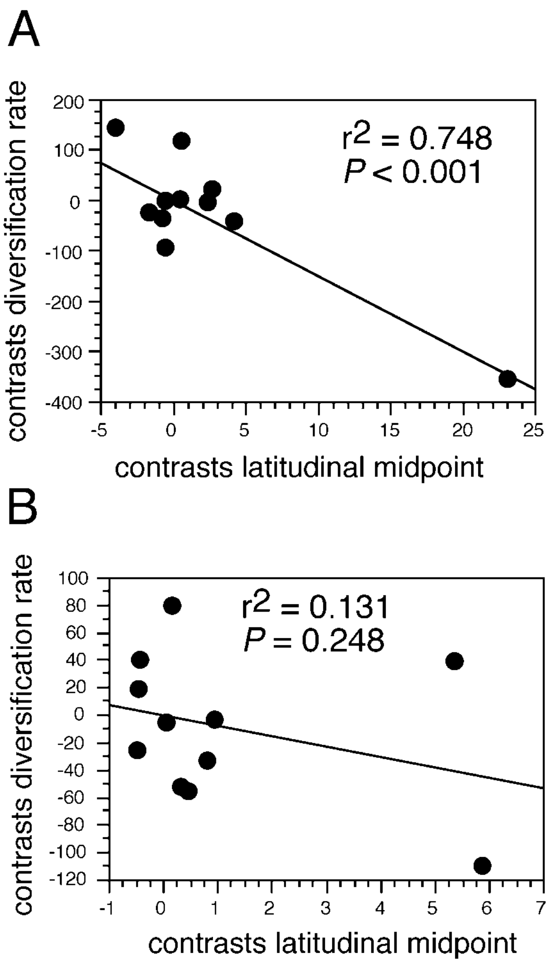


Figure 3: Linear regression analysis showing (*A*) increasing diversification rates with decreasing latitudinal midpoint based on the stem group ages of salamander clades but (*B*) no relationship using the crown group ages. The analyses shown assume a pure-birth model for estimating diversification rates and branch lengths from the chronogram in figure 2 for calculating independent contrasts.

0.235, $P = .067$; high relative extinction: $r^2 = 0.208$, $P = .087$). Although some may find the lack of a strong relationship under equal branch lengths troubling, it is clear that the branch lengths are not equal, and these same branch lengths are assumed to calculate the diversification rates. Results (not shown) were nearly identical when the phylogeny and Bayesian divergence date estimates from San Mauro et al. (2005) were used.

Discussion

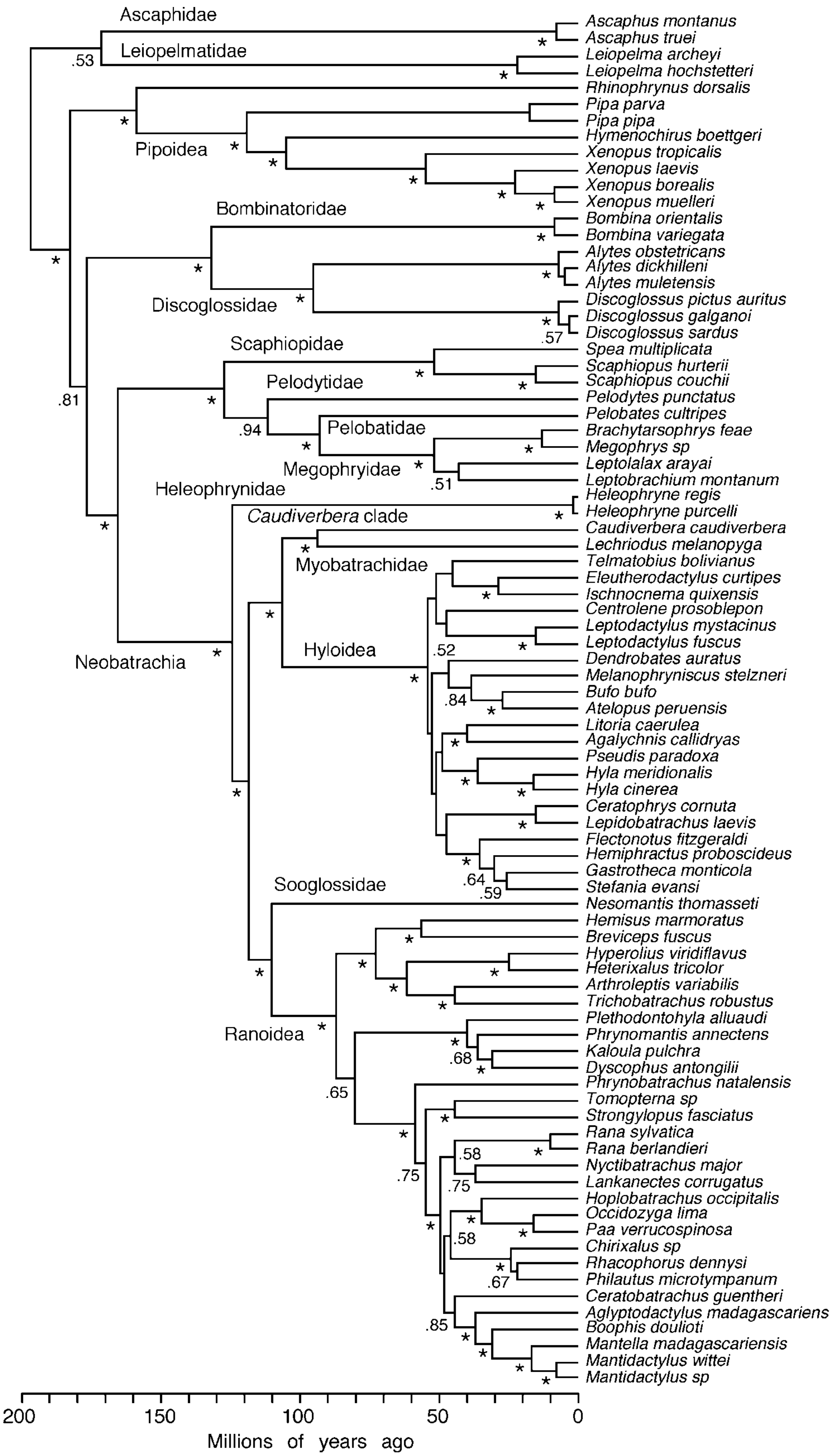
Salamanders and basal frogs offer a counterexample to the hypothesis that the latitudinal diversity gradient results largely from limited and recent dispersal from tropical regions into temperate regions with little difference in diversification rates between climatic regimes (e.g., Farrell et al. 1992; Ricklefs and Schluter 1993; Brown and Lomolino 1998; Futuyma 1998; Wiens and Donoghue 2004). In salamanders, most families are temperate, and based on the phylogeny and divergence time estimates presented here, the invasion of tropical regions has been relatively recent. Nevertheless, the one primarily tropical clade of salamanders has a relatively high diversification rate (based on the stem-group estimator), and there is a significant relationship between diversification rate and latitude. This result implies that the invasion of the tropical climate regime led to accelerated rates of diversification in this clade.

Similarly, in frogs, most basal clades are predominately temperate in distribution and have limited species richness. However, several clades appear to have independently invaded tropical regions (e.g., megophryids, pipids, most neobatrachians), and many of these predominately tropical clades have high rates of diversification (e.g., Megophryidae, and Myobatrachidae, Ranoidea, and Hyloidea within Neobatrachia). Frogs appear to be ancestrally temperate, given that the basal members of their sister group (salamanders) clearly are temperate and that the sister group to all other anurans is temperate as well (also supported by ancestral-state reconstruction; J. J. Wiens, unpublished results). There is clearly a strong latitudinal gradient in amphibian diversity at the global scale (IUCN et al. 2004), and perusal of species lists for countries in the most species-rich regions (e.g., northern South America, central Africa, and southeast Asia) reveals that these regions are dominated by neobatrachian frogs of the Ranoidea and Hyloidea (AmphibiaWeb 2006).

I address three major questions below. First, does the geographic distribution of the tropical amphibian clades explain their high species richness, or might some other intrinsic biological traits (e.g., "key innovations") do so? Second, if the occurrence of these lineages in the tropics does explain their higher diversification rates, what is the primary cause of this pattern? For example, do tropical clades speciate more quickly, or are they more buffered from extinction? Third, what are the implications of these results for the TCH and for explaining the latitudinal diversity gradient in other groups of organisms?

Geography versus Key Innovation

From the results in salamanders and basal frogs, it appears that the latitudinal position of clades can influence their diversification rates (see also Cardillo 1999; Cardillo et al. 2005; Ricklefs 2006). However, these patterns are associated with a limited number of amphibian clades that have invaded tropical regions, and it is worthwhile to consider whether the high diversification rates of these clades are


Ascaphidae
Leiopelmatidae
.53
Pipoidea
Bombinatoridae
Discoglossidae
.57
Scaphiopidae
Pelodytidae
.94
.81
Pelobatidae
Megophryidae
.51
Heleophrynidae
Caudiverbera clade
Myobatrachidae
Hyloidea
.52
.84
.64
.59
Neobatrachia
Sooglossidae
Ranoidea
.65
.68
.75
.58
.75
.58
.67
.85
Ascaphus montanus
Ascaphus truei
Leiopelma archeyi
Leiopelma hochstetteri
Rhinophrynus dorsalis
Pipa parva
Pipa pipa
Hymenochirus boettgeri
Xenopus tropicalis
Xenopus laevis
Xenopus borealis
Xenopus muelleri
Bombina orientalis
Bombina variegata
Alytes obstetricans
Alytes dickhilleni
Alytes muletensis
Discoglossus pictus auritus
Discoglossus galganoi
Discoglossus sardus
Spea multiplicata
Scaphiopus hurterii
Scaphiopus couchii
Pelodytes punctatus
Pelobates cultripes
Brachytarsophrys feae
Megophrys sp
Leptolalax arayai
Leptobrachium montanum
Heleophryne regis
Heleophryne purcelli
Caudiverbera caudiverbera
Lechriodus melanopyga
Telmatobius bolivianus
Eleutherodactylus curtipes
Ischnocnema quixensis
Centrolene prosoblepon
Leptodactylus mystacinus
Leptodactylus fuscus
Dendrobates auratus
Melanophryniscus stelzneri
Bufo bufo
Atelopus peruensis
Litoria caerulea
Agalychnis callidryas
Pseudis paradoxa
Hyla meridionalis
Hyla cinerea
Ceratophrys cornuta
Lepidobatrachus laevis
Flectonotus fitzgeraldi
Hemiphractus proboscideus
Gastrotheca monticola
Stefania evansi
Nesomantis thomasseti
Hemisus marmoratus
Breviceps fuscus
Hyperolius viridiflavus
Heterixalus tricolor
Arthroleptis variabilis
Trichobatrachus robustus
Plethodontohyla alluaudi
Phrynomantis annectens
Kaloula pulchra
Dyscophus antongilii
Phrynobatrachus natalensis
Tomopterna sp
Strongylopus fasciatus
Rana sylvatica
Rana berlandieri
Nyctibatrachus major
Lankanectes corrugatus
Hoplobatrachus occipitalis
Occidozyga lima
Paa verrucospinosa
Chirixalus sp
Rhacophorus dennysi
Philautus microtympanum
Ceratobatrachus guentheri
Aglyptodactylus madagascariens
Boophis doulioti
Mantella madagascariensis
Mantidactylus wittei
Mantidactylus sp
200
150
100
50
0
Millions of years ago

related to one or more intrinsic biological traits rather than to their tropical distributions.

In salamanders, only one clade occurs primarily in the tropics (supergenus *Bolitoglossa*). However, it seems that the most likely key innovations of tropical bolitoglossines are shared with other clades and that these other clades are found in temperate regions and do not have unusually high diversification rates.

In the traditional classification of the clade, most bolitoglossine salamanders were considered to have a striking evolutionary novelty (and potential key innovation) in the feeding mechanism, a free projectile tongue that can, in some taxa, be extended up to half the body length (Lombard and Wake 1986). The most extreme example of this trait occurs in *Hydromantes*, which occurs in temperate North America and Europe (Deban et al. 1997). Although *Hydromantes* was considered a bolitoglossine (e.g., Wake 1966; Lombard and Wake 1986), recent molecular evidence (Mueller et al. 2004; Min et al. 2005; this study) shows that it is a plethodontine. The results here show that the *Hydromantes* stem group appears to be moderately old (>30 Mya [fig. 2]) and contains only 10 species (AmphibiaWeb 2006), suggesting a diversification rate similar to that of other temperate plethodontids (e.g., 0.077 net speciation events per million years for the stem group, with no extinction). Furthermore, other temperate plethodontid lineages have acquired free projectile tongues (i.e., most spelerpines) but do not have exceptional diversification rates (tables 3, 4). Bolitoglossine salamanders are also unusual among major salamander clades in having direct development; they lack an aquatic larval stage and do not require standing or running water for reproduction, as many other salamanders do (Zug et al. 2001; Pough et al. 2004). However, direct development also occurs in several temperate lineages (most plethodontines, *Batrachoseps*, and some salamandrids). Thus, it seems unlikely that direct development alone is the cause of the high diversification rate of tropical bolitoglossines.

Anurans offer a stronger case for the effects of geography on diversification rate, given that there appear to have been multiple invasions of tropical regions (e.g., pipoids, megophryids, myobatrachids, and neobatrachians). There are no obvious intrinsic biological traits that are uniquely shared among these diverse tropical clades. The diversification rates of megophryids, myobatrachids, hyloids, and ranoids are roughly similar to each other and dramatically higher than those of other anuran clades (table 5). Ryan (1986) suggested that the high species richness of neobatrachians might be explained by neuroanatomical traits that increased their speciation rate (i.e., possibly related to mating calls and reproductive isolation), but a recent study that reconsidered the neuroanatomical evidence did not support this hypothesis (Richards 2006). Neobatrachians clearly are monophyletic, based on morphological and molecular data, but none of their morphological synapomorphies have been proposed as key innovations, and these traits lack any intuitive relationship to increased diversification rates (e.g., neopalatine bone, fusion of third distal carpal to other carpals, separation of sartorius and semitendinosus muscles, accessory head of adductor longus muscle, and loss of parahyoid bone; Ford and Cannatella 1993). Furthermore, the increase in diversification rates is not necessarily associated with the origin of Neobatrachia per se but rather is associated with clades within Neobatrachia (e.g., myobatrachids, hyloids, and ranoids). The diversification rates of the hyloids and ranoids are higher than those of any of the other anuran clades included, but the only trait that they seem to share uniquely is that they are both almost globally distributed.

Speciation versus Extinction

What is the specific cause of the seemingly high diversification rates in tropical amphibian clades? Assuming that the high diversification rates of these clades are related to their geographic distribution, the possible causes might include (1) increased speciation rate in tropical regions, (2) increased extinction rate in temperate regions, (3) decreased speciation rate in temperate regions, and (4) decreased extinction rate in tropical regions. These hypotheses are not mutually exclusive and can be very difficult to distinguish. However, I speculate that a higher extinction rate in temperate regions may be a more likely explanation than higher speciation rates in tropical regions, at least for salamanders.

The evidence for the higher diversification rate in tropical bolitoglossines comes from considering the entire history of the clades (the stem group; table 3). If one compares the crown-group diversification rates with the assumption of minimal extinction (table 4), then it appears that the rate of origin of species in the tropical bolitoglossines is similar to those of other primarily temperate

Figure 4: Phylogeny and divergence date estimates for frogs based on analyses of the RAG-1 gene, using a root age for the crown group of Batrachia (frogs + salamanders) of 300 Mya (note that frog and caecilian outgroups are not shown, and so the oldest clade shown is <300 million years old). Branches with asterisks have Bayesian posterior probabilities ≥0.95; values ≥0.50 but <0.95 are shown adjacent to clades (values <0.50 not shown). Clades used in analyses of diversification are labeled, along with Neobatrachia. Assignment of neobatrachian species to families is provided in table A1.

Table 5: Estimated ages (in millions of years) and diversification rates (net speciation events per million years) for basal anuran clades, based on the stem groups for these clades and using three possible ages for the Anura + Caudata crown-group clade

		Diversification rate	
Clade	Stem age	Relative extinction rate = 0	Relative extinction rate = .90
250 million years:			
Leiopelmatidae	143.70	.009647	.001826
Ascaphidae	143.70	.004824	.000663
Pipoidea	155.30	.022112	.008927
Bombinatoridae	111.70	.020614	.005746
Discoglossidae	111.70	.022246	.006642
Scaphiopidae	109.64	.017748	.004287
Pelodytidae	96.49	.011386	.001890
Pelobatidae	80.81	.017155	.003247
Megophryidae	80.81	.060329	.032658
Heleophrynidae	107.63	.016647	.003767
Caudiverbera + *Telmatobufo* clade	81.75	.016958	.003209
Myobatrachidae	81.75	.059159	.031837
Sooglossidae	95.50	.014516	.002747
Ranoidea	95.50	.079710	.055646
Hyloidea	92.31	.086683	.061771
300 million years:			
Leiopelmatidae	172.18	.008051	.001524
Ascaphidae	172.18	.004026	.000554
Pipoidea	183.00	.018765	.007575
Bombinatoridae	131.92	.017454	.004865
Discoglossidae	131.92	.018836	.005624
Scaphiopidae	127.46	.015267	.003687
Pelodytidae	111.76	.009830	.001631
Pelobatidae	93.26	.014865	.002813
Megophryidae	93.26	.052275	.028298
Heleophrynidae	124.65	.014374	.003253
Caudiverbera + *Telmatobufo* clade	94.35	.014693	.002781
Myobatrachidae	94.35	.051259	.027585
Sooglossidae	110.17	.012583	.002381
Ranoidea	110.17	.069096	.048236
Hyloidea	106.43	.075183	.053576
357 million years:			
Leiopelmatidae	200.00	.006931	.001312
Ascaphidae	200.00	.003466	.000477
Pipoidea	221.43	.015508	.006261
Bombinatoridae	158.57	.014521	.004048
Discoglossidae	158.57	.015671	.004679
Scaphiopidae	158.29	.012293	.002969
Pelodytidae	139.85	.007856	.001304
Pelobatidae	117.61	.011787	.002231
Megophryidae	117.61	.041452	.022439
Heleophrynidae	154.85	.011571	.002618
Caudiverbera + *Telmatobufo* clade	117.52	.011796	.002233
Myobatrachidae	117.52	.041153	.022147
Sooglossidae	137.95	.010049	.001902
Ranoidea	137.95	.055182	.038523
Hyloidea	132.84	.060236	.042925

Note: Stem ages for sister clades are identical.

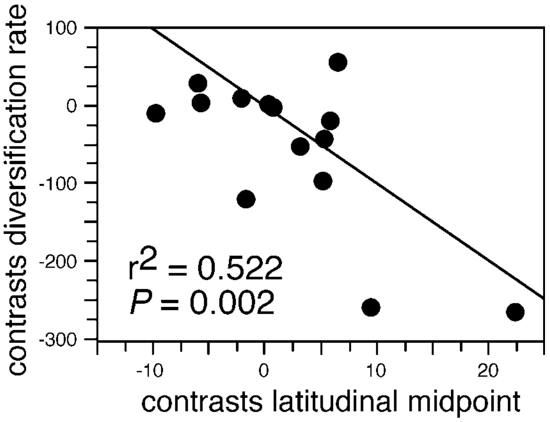


Figure 5: Linear regression analysis showing increasing diversification rates with decreasing latitudinal midpoints for anuran clades, utilizing stem group ages and a pure-birth model for estimating diversification rates and branch lengths from the chronogram in figure 4 for calculating contrasts.

clades (e.g., *Batrachoseps*, ambystomatids). In fact, when the ages of crown groups are compared (fig. 2; table 4), tropical bolitoglossines are older than most salamander families (i.e., Ambystomatidae, Amphiumidae, Cryptobranchidae, Dicamptodontidae, and Rhyacotritonidae), older than the plethodontid subfamily Spelerpinae, and similar in age to the subfamily Plethodontinae (the most species-rich clade of salamanders after the tropical bolitoglossines). Furthermore, estimates of the rate of species origination in other temperate crown-group clades will likely be higher than those for tropical bolitoglossines after additional species in these temperate clades are formally described (e.g., amphiumids [R. Bonett and P. Chippindale, unpublished data] and sirenids [Petranka 1998]). Thus, adding only one species to amphiumids or two to sirenids will show them to have higher rates of crown-group diversification than tropical bolitoglossines, whereas adding many species to the tropical bolitoglossines (e.g., 20) will not substantially change their estimated diversification rate (J. J. Wiens, unpublished results). In summary, I speculate that in salamanders, species seem to originate at generally similar rates within temperate and tropical crown-group clades. If this is the case, then the higher diversification rate of the tropical bolitoglossine stem group may be explained by less extinction over time rather than by more rapid speciation.

The difference in diversification rates may be explained not solely by extinction within crown-group clades but instead by the failure of many older temperate clades to survive until the present day. Thus, when we examine a chronogram of living taxa (fig. 2), we see many salamander clades that were unbranched for tens of millions of years and then underwent several speciation events within the past 10–20 million years (e.g., Amphiumidae, Rhyacotritonidae, and Sirenidae). It seems more plausible to assume that there has been origination and extinction of clades along these lineages throughout their history (and that we see only a few surviving clades today) than to assume that conditions have been favorable for speciation in these clades only in the recent past. On the other hand, if one assumes a uniformly high rate of extinction within every crown-group clade (table 4), then speciation would have to be more rapid in tropical bolitoglossines to account for their higher diversification rate.

The idea that there has been extinction along the branches leading to the modern crown-group clades is supported by the fossil record (e.g., Milner 2000). Many temperate families contain additional genera that are entirely extinct (e.g., Proteidae and Salamandridae), and some families have more extinct genera than extant genera (e.g., Amphiumidae, Cryptobranchidae, Dicamptodontidae, and Sirenidae). Many of these extinct lineages are considerably older than the estimated ages for living genera, suggesting that they are outside the living crown-group clades. For example, the amphiumid *Proamphiuma* is at least 66 million years old (Gardner 2003), whereas the crown group of extant amphiumids is 4.7–6.5 million years old (table 4). There are additional families of salamanders (which may fall within the stem groups of extant families) that are known only from fossils (e.g., Batrachosauroididae and Scapherpetontidae; Milner 2000).

Why might there be more extinction in temperate regions than tropical regions? This question is beyond the scope of this article to address. Nevertheless, many previous authors have suggested that climatic fluctuations and variability in temperate regions might be an important cause of extinction and that tropical regions may be buffered against extinction because of their overall climatic stability (reviews in Pianka 1966; Brown and Lomolino 1998; Willig et al. 2003). The climatic instability of temperate regions may be important at longer temporal scales (e.g., glaciation) and/or shorter scales (e.g., seasonal variability). The limited geographic extent of temperate regions before the Cenozoic expansion may also have contributed to higher extinction rates (see below), especially when coupled with climatic variability.

The hypothesis that more temperate extinctions drive the latitudinal trend in diversification rates is speculative, and alternatives should also be considered. Another major hypothesis is that there are accelerated speciation rates in tropical regions. However, preliminary studies of diversification rates within tropical bolitoglossines suggest two intriguing patterns that cast some doubt on the idea that tropical environments accelerate speciation in this group (Wiens et al. 2007*b*). First, the majority of tropical bolitoglossine species are montane (with the highest species richness from 1,000 to 2,500 m above sea level) and so occur in relatively cool tropical environments that may resemble temperate climates in some respects (but differ in reduced seasonality; Janzen 1967). In fact, field body temperatures of tropical plethodontids are, on average, very similar to those of temperate plethodontids in North America (average for 43 species of tropical bolitoglossines = 14.2°C; average for 28 species of temperate plethodontids = 13.5°C; Feder et al. 1982). Second, there are no consistent elevational differences in diversification rates within bolitoglossines. Thus, there is no evidence that tropical montane regions drive high speciation rates (e.g., Janzen 1967; Rahbek and Graves 2001) or that tropical lowland environments with high energy and productivity do so (or else these two effects largely cancel each other out).

In anurans, distinguishing the relative roles of speciation and extinction in driving latitudinal differences in diversification rates is even more difficult than in salamanders, given the more limited taxon sampling and higher diversity. However, some observations may support the idea that extinction of ancient temperate clades is important in patterns of species richness and diversification in frogs as well as salamanders. First, there are many extinct lineages associated with many of these ancient temperate anuran clades (e.g., Rocek 2000; Rocek and Rage 2000). Second, within hylid frogs (a group of hyloid neobatrachians), there is little evidence for differences in diversification rate between tropical and temperate clades (Wiens et al. 2006). This pattern is inconsistent with the idea that there are pervasive differences in speciation rates between tropical and temperate regions but is not inconsistent with the idea that entire clades are occasionally driven to extinction in temperate regions.

This study suggests several avenues for future research. First, a detailed species-level phylogeny for all or most salamanders with estimates of divergence times is likely to be completed in the next few years and may allow application of statistical methods that can potentially tease apart the relative contributions of extinction and speciation (although this may be very difficult; e.g., Paradis 2004). Second, extensive comparisons of diversification rates are needed for younger tropical and temperate anuran and salamander clades that are of similar age. If extinction of ancient temperate clades is the primary cause of the observed latitudinal differences in diversification rates, then comparisons of younger clades should reveal no consistent differences in diversification rates (e.g., Wiens et al. 2006). Alternately, if diversification rates are consistently higher in young tropical clades, then processes that accelerate speciation in tropical regions may explain this pattern instead. Third, analyses are needed to address specifically how climate might drive higher extinction rates in temperate regions (if this pattern is supported), considering both present-day patterns of climate and distribution and those in the ancient past.

Shifts in Diversification Rate versus the Tropical Conservatism Hypothesis

In general, salamanders and basal anurans do not seem to support the predictions of the TCH. The TCH predicts tropical origin and recent dispersal of groups into temperate regions and assumes that patterns of species richness are driven largely by the timing of colonization, not by differences in rates of diversification between tropical and temperate regions. In salamanders and basal frogs, there has been recent dispersal from temperate into tropical regions, and these shifts seemingly are associated with changes in diversification rates.

Nevertheless, salamanders do support some predictions of the TCH. The TCH predicts that some groups will have a reverse latitudinal gradient (e.g., Ricklefs and Schluter 1993; Brown and Lomolino 1998; Futuyma 1998; Wiens and Donoghue 2004) because the same two factors that are thought to drive higher tropical richness will also operate in groups of temperate origin: (1) higher species richness in the region of origin and (2) limitation of dispersal between regions with different climatic regimes due to niche conservatism. Both of these factors do seem to have some signatures in salamanders.

First, despite the major shift in diversification rates in the tropical bolitoglossines suggested by the analysis of stem groups, salamanders do have higher overall species richness in temperate regions than in tropical regions (the tropical bolitoglossines account for slightly less than half of all salamander species; AmphibiaWeb 2006). Thus, even though rates of diversification are not equal between temperate and tropical regions (possibly through more extinction in temperate regions), the accumulation of species in temperate regions throughout the long phylogenetic history of salamanders still appears to have had a larger effect on overall patterns of salamander diversity, leading to somewhat higher temperate species richness.

Salamanders also seem to support the idea of niche conservatism, in that they generally have failed to successfully colonize and/or persist in tropical regions (with the obvious exception of tropical bolitoglossines). This failure is remarkable for two reasons. First, salamanders are very old and widely distributed and have therefore have had ample time to spread into tropical regions. In general, the fossil record suggests that salamanders have had a similar climatic distribution throughout their evolutionary history, with the possible exception of some questionably sirenid fossils from Africa and South America

(Milner 2000). Second, there has been extensive dispersal of some clades within temperate regions. For example, plethodontine plethodontids and salamandrids have each dispersed throughout Europe, North America, and Asia, cryptobranchids occur in both North America and Asia, and proteids occur in both North America and Europe (Pough et al. 2004; Min et al. 2005). Thus, their failure to disperse into tropical regions cannot be ascribed to a lack of time or dispersal ability. The salamander clades that have successfully extended into tropical regions have done so primarily in the mountains, where the climate is more similar to that of temperate regions (e.g., salamandrids in Asia and ambystomatids and most bolitoglossines in Middle America; IUCN et al. 2004). In many cases, it seems that salamanders of temperate origin may have retained a somewhat similar climatic niche even as they extended their ranges into tropical regions (for a similar example in hylid frogs, see Smith et al. 2005).

Basal anurans show some evidence of niche conservatism but none of a time-for-speciation effect. Some basal anuran clades have widespread distributions in temperate regions (e.g., pelobatoids occur throughout the Northern Hemisphere) with little or no penetration into tropical regions. Although anurans seem to have originated in temperate regions, they clearly reach their highest species richness in tropical regions (IUCN et al. 2004; AmphibiaWeb 2006), in contrast to the expectations of the time-for-speciation effect.

In some ways, these results appear to offer a compelling counterexample to the TCH. Yet they may also help to address one of its most challenging components. The most difficult aspect of the TCH is the problem of explaining why more clades (not species) originate in tropical regions than in temperate regions. Previous authors attributed this hypothesized pattern to the greater geographic extent of the tropics before the Cenozoic expansion of the temperate regions (e.g., Ricklefs and Schluter 1993; Futuyma 1998; Wiens and Donoghue 2004).

But why should greater area lead to more species? At the global scale, it seems that increased area can lead to higher species richness only by influencing diversification rates of clades (i.e., sampling scale cannot increase further, and species cannot colonize from elsewhere). Clades that occur over larger geographic areas may have higher diversification rates because they have greater opportunities for allopatric speciation and decreased likelihood of extinction (Rosenzweig 1995). In fact, it is somewhat difficult to explain why the greater area of the tropics should lead to the origin of more clades (and species) without invoking some difference in diversification rates between clades in tropical and temperate regions. Thus, the high diversification rates in basal anuran clades that have invaded the tropics may reflect the greater area of tropical habitats before the Cenozoic expansion of temperate regions. Of course, if one attributes all differences in diversification rate to the TCH, then it becomes impossible to distinguish the TCH from competing hypotheses. Older clades that originated before the Cenozoic temperate expansion (∼30–40 Mya) may have some signature of differences in area on their diversification rates, whereas such differences may be absent among younger groups. Differences in diversification rates between younger tropical and temperate clades may instead reflect other latitudinal effects on rates of diversification and would serve as evidence against the TCH. As an example, the results for basal clades of frogs suggest that there are latitudinal differences in diversification rates among ancient clades (>100 Mya), but results within hylids show no such pattern (Wiens et al. 2006). Further study is needed to determine whether area itself is the primary factor causing higher diversification rates in these ancient tropical clades and, if so, how.

Explaining the Diversity of Major Amphibian Clades

In this study, I have used patterns of age and diversity among amphibian clades to make inferences about latitudinal variation in diversification rates and the causes of global patterns of species richness. These results may also shed light on some intriguing but poorly explained differences in diversity among major amphibian clades. I propose that the remarkable diversity of bolitoglossine salamanders (∼50% of salamanders) and neobatrachian frogs (∼96% of frogs) are associated with the influence of their tropical geographic distribution on diversification rates. There have been surprisingly few alternate hypotheses proposed to explain the remarkable diversity of these clades (e.g., Ryan 1986). These results may also be relevant for explaining another striking pattern of diversity, that fact that there are nearly 10 times as many frog species as salamanders (5,356 vs. 555; AmphibiaWeb 2006). If the presence of clades in tropical environments is associated with higher diversification rates, then the limited diversity of salamanders may be explained by the fact that there was only a single invasion of tropical regions in the relatively recent past (∼50 Mya), which was largely confined to Middle America. Conversely, in frogs, there appear to have been multiple invasions of tropical regions, each one seemingly at least twice as old as the tropical bolitoglossines. Many of these invasions have spread to multiple continents, and the two clades with the widest distributions have the highest diversification rates (hyloids and ranoids). If the predominately tropical clades of salamanders and frogs are excluded from overall species numbers to leave only the primitively temperate clades, then the number of species in each group is considerably more similar (327 salamanders vs. 59 frogs). Of course, it must be acknowledged that the tropical but species-poor caecilians (the third major clade of amphibians, with only 171 species) do not fit this pattern, although one might argue that the highly specialized ecology of caecilians may have limited their diversification (i.e., caecilians are limbless burrowers).

Conclusions

In order to understand the underlying causes of large-scale patterns of species richness, we must relate these patterns to the processes that directly change species numbers: speciation, extinction, and dispersal. In this study, I find a significant association between tropical distribution and diversification rates in both salamanders and frogs. Although it is possible that this pattern is caused by generally higher speciation rates in tropical regions, some evidence suggests that this pattern may be caused by higher extinction rates of entire clades in temperate regions. Overall, these results offer an important counterexample to some predictions of the TCH, which postulates that limited and recent dispersal to temperate regions, coupled with similar rates of diversification in temperate and tropical regions, is the primary explanation for higher tropical diversity. However, the TCH also suggests that the greater area of tropical regions in the past (>40 Mya) might have led to a larger number of clades in the tropics, a hypothesis that should be reflected in higher diversification rates for ancient tropical clades (>40 Mya), as we observe here. These results show how latitudinal differences in diversification rates may have shaped present-day patterns of species richness of regions and clades.

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