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Coming to America: Multiple Origins of New World Geckos

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Coming to America: Multiple Origins of New World Geckos

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Abstract

Geckos in the Western Hemisphere provide an excellent model to study faunal assembly at a continental scale. We generated a time-calibrated phylogeny, including exemplars of all New World gecko genera, to produce a biogeographic scenario for the New World geckos. Patterns of New World gecko origins are consistent with almost every biogeographic scenario utilized by a terrestrial vertebrate with different New World lineages showing evidence of vicariance, dispersal via temporary land bridge, overseas dispersal, or anthropogenic introductions. We also recovered a strong relationship between clade age and species diversity, with older New World lineages having more species than more recently arrived lineages. Our data provide the first phylogenetic hypothesis for all New World geckos and highlight the intricate origins and ongoing organization of continental faunas. The phylogenetic and biogeographical hypotheses presented here provide an historical framework to further pursue research on the diversification and assembly of the New World herpetofauna.

Keywords: biogeography, dispersal, Gekkota, phylogeny, South America, Squamata, vicariance

Introduction

The South American flora and fauna is long thought to have evolved *in situ*, subsequent to Gondwanan vicariance, followed by a long period of isolation (Raven & Axelrod, 1974; Duellman, 1979; Simpson, 1980; Gentry, 1982). Recent use of time-calibrated phylogenies have altered this view, and ample evidence indicates many plant and animal lineages dispersed to South America through a variety of routes after the physical separation from Africa (Carranza *et al.*, 2000; Pennington & Dick, 2004; Renner, 2004; Sanmartin & Ronquist, 2004; Poux *et al.*, 2006; Vidal *et al.*, 2008; Voelker *et al.*, 2009). Indeed, recognizing the importance of overseas dispersal in the assembly of regional floras and faunas has been called a 'counter-revolution' in biogeography (de Queiroz, 2005). It is clear that the reptile fauna of South America, for example, has its origins via both Gondwanan vicariance and overseas dispersal (Duellman, 1979; Bauer, 1993; Noonan & Chippindale, 2006). Some groups, such as skinks (Whiting et al., 2006), blindsnakes (Vidal *et al.*, 2010) and amphisbaenians (Vidal et al., 2008), have particularly complex histories with multiple independent entries into the Western Hemisphere. Similarly, it has long been hypothesized that New World geckos as a whole are composed of several disparate elements (Darlington, 1957; Kluge, 1967; Vanzolini, 1968; Kluge, 1969; Bauer, 1993). This has been corroborated by recent molecular phylogenetic studies showing a vicariant origin for one clade, the Sphaerodactylini (Gamble *et al.*, 2008b) and several independent, trans-Atlantic dispersals in the gekkonid genera *Tarentola* (Carranza et al., 2000) and *Hemidactylus* (Carranza & Arnold, 2006).

Geckos are particularly well suited as models to study faunal origins and subsequent diversification in the Western Hemisphere. First, geckos are a geologically ancient group (Kluge, 1987; Conrad & Norell, 2006), meaning that Gondwanan vicariance likely influenced their global distribution. Second, many gecko lineages are accomplished overseas dispersers, with numerous species distributed on volcanic and coral islands around the world (Bauer, 1994; Carranza *et al.*, 2000; Austin *et al.*, 2004; Rocha *et al.*, 2007). Most gecko species posses a suite of characteristics that makes them amenable to overseas dispersal, including hard-shelled eggs resistant to desiccation (Dunson & Bramham, 1981; Dunson, 1982), eggs that tolerate short-term immersion in sea water (Brown & Alcala, 1957), and a complex, digital-adhesive mechanism (Russell, 2002) that allows geckos to hold on to vegetation and other flotsam. More recently, anthropogenic activities have spread many gecko species across the globe, and several New World gecko species are clearly the result of this human-mediated transportation (Kluge, 1969; Lever, 2003; Fuenmayor *et al.*, 2005).

Geckos are also interesting models to study the relationship between lineage age and species diversity, because they likely arrived in the New World multiple times over tens of millions of years. No consensus exists as to the generality of this relationship, and some studies have found a strong relationship between clade age and diversity (Stephens & Wiens, 2003; Wiens *et al.*, 2006b; McPeek & Brown, 2007; Wiens *et al.*, 2009) while others have not (Magallon & Sanderson, 2001; Ricklefs, 2006; Seehausen, 2006; Ricklefs *et al.*, 2007). The relationship between clade age and diversity can involve the order in which lineages arrive in a region, with potentially higher species diversity for early dispersers, associated with ecological release due to lack of competitors and exploitation of empty niches (Walker & Valentine, 1984; Schluter, 2000; Moore & Donoghue, 2007). Additionally, the length of time a clade has to diversify in a region, the so-called "time-for-speciation effect," may influence species diversity, with older clades having more time to accumulate species than younger clades (Cracraft, 1985; Stephens & Wiens, 2003; Wiens *et al.*, 2006b; McPeek & Brown, 2007). Knowledge of such a relationship in a clade can guide future research and help formulate testable ecological and biogeographic hypotheses.

We conducted a phylogenetic analysis of gekkotan lizards, including exemplars of all described New World genera, with the following objectives: (a) provide a phylogenetic hypothesis for geckos of the Western Hemisphere; (b) estimate divergence dates for all New World gecko lineages and use that time-calibrated phylogeny to evaluate the relative contribution of dispersal and vicariance in the origins of the New World gecko fauna; and (c) determine if clade age is correlated with species richness in New World gecko lineages.

Materials and Methods

Phylogenetic Analyses

We extracted genomic DNA from muscle, liver, or tail clips using the DNeasy Blood & Tissue kit (Qiagen). We used PCR to amplify portions of five nuclear protein-coding genes: recombination activating gene 1 (*RAG1*), recombination activating gene 2 (*RAG2*), oocyte maturation factor MOS (*C-MOS*), acetylcholinergic receptor M4 (*ACM4* or *CHRM4*), and phosducin (*PDC*). Primers, PCR conditions, and sequencing conditions are detailed elsewhere (Bauer *et al.*, 2007; Gamble *et al.*, 2008a) and all PCR reactions were run with negative controls. We aligned sequences using T-Coffee (Notredame et al., 2000) and all sequences were translated to amino acids using MacClade 4.08 (Maddison & Maddison, 1992) to confirm alignment and gap placement.

We analyzed the concatenated dataset using maximum likelihood (ML) with the program RAxML 7.0.3 (Stamatakis, 2006). Data were partitioned by both gene and codon (15 partitions) using the GTR + Γ model for each partition. All partitions were assigned GTR-based models as these are the only models utilized in RAxML (Stamatakis, 2006). All other model parameters were estimated from the data. We assessed nodal support using nonparametric bootstrapping (Felsenstein, 1985) with 1000 pseudoreplicates.

Phylogenetic Hypothesis Testing

The thorough sampling of New World gecko taxa allowed us to test several phylogenetic and biogeographic hypotheses. Alternative phylogenetic hypotheses were produced using the topology constraint function in RAxML. We compared the alternative phylogenetic hypotheses to the optimal ML tree using the Shimodaira-Hasegawa test (SH test) (Shimodaira & Hasegawa, 1999) implemented in RAxML, with data partitioned as before. We also tested alternative phylogenetic hypotheses in a Bayesian framework. We used the filter option in PAUP* (Swofford, 2002) to calculate the posterior probabilities of the constrained trees in the posterior distribution of trees from the BEAST analysis described below (Huelsenbeck et al., 2002).

Tree Calibration and Dating

We estimated divergence dates using a Bayesian uncorrelated relaxed clock as implemented in BEAST 1.4.8 (Drummond et al., 2006; Drummond & Rambaut, 2007). We used a Yule prior on speciation rates and partitioned the dataset by codon with GTR + I + G model for each partition. Model selection was determined using the AIC as implemented in jModeltest (Posada, 2008). Calibration choice is described below. We conducted three independent analyses of 10,000,000 generations each, logging trees every 1,000 generations. Output was analyzed using Tracer (Rambaut & Drummond, 2007) and all runs, minus burn-in, were combined to estimate topology and divergence times.

We assessed the consistency of our divergence date calibrations using the fossil cross-validation method of Near et al. (Near et al., 2005). This method identifies inconsistent fossil calibration points in analyses with multiple calibrations by examining the agreement between each calibration point and all other fossils in the analysis (Near et al., 2005). This was done using each calibration, on its own, to estimate ages of the other calibrations, the so-called "molecular age" of the calibration. Each fossil calibration was assessed using F-tests and only calibrations that minimized the difference between the fossil age and the "molecular age" were used. Cross-validation analyses were conducted in r8s (Sanderson, 2003) using Penalized Likelihood with the TN algorithm and Maximum Likelihood tree. The program r8s has a tendency to unrealistically push back the age of the root when calibrations are close to the tips of the phylogeny (Hugall et al., 2007). We countered this artefact during our cross-validation analyses by imposing a maximum age for squamates using the oldest known squamate fossil, *Tikiguania estesi*, from the late Triassic, 230 Ma (Datta & Rayz, 2006).

We assessed eight fossil and biogeographic calibrations to constrain nodes in the divergence date analyses, and most of these calibrations were used in previously published studies (Vidal & Hedges, 2005; Wiens *et al.*, 2006a; Gamble *et al.*, 2008b). Three of these calibrations were excluded from further analyses by the fossil cross-validation described above. The excluded calibrations were: (1) the minimum age for the divergence between *Euleptes* and the clade containing *Teratoscincus, Quedenfeldtia* and *Aristelliger* as 22.5 Ma using fossil *Euleptes* (Agusti *et al.*, 2001; Muller, 2001); (2) a minimum age for the Gekkonoidea at 55 Ma using the oldest known fossils of hard-shelled gecko eggs from Wyoming (Hirsch, 1996); and (3) a minimum age for the Iguania/Anguimorpha divergence using the fossil *Parviraptor estesi*, 144 Ma (Rieppel, 1994). The remaining calibrations and settings were used in the BEAST analyses: (4) an exponential prior representing the minimum age for the Helodermatidae/Anguidae split using the fossil *Primaderma nessovi*, 99 Ma (Nydam, 2000); (5) an exponential prior representing the minimum age for the *Paradelma orientalis/Pygopus nigriceps* split, calibrated using the fossil *Pygopus hortulanus*, 20 Ma (Hutchinson, 1997; Jennings et al., 2003); (6) an exponential prior representing the divergence between the *Sphaerodactylus cinereus* group, represented in this study by *S. elegans* (Hass, 1991), and its sister taxon was calibrated with amber preserved *Sphaerodactylus* sp., 20 Ma (Kluge, 1995; Iturralde–Vinent & MacPhee, 1996); (7) a normal prior was used for the *Teratoscincus scincus/Teratoscincus roborowskii* split calibrated with the Tien Shan-Pamir uplift in western China, 10 Ma (Tapponnier *et al.*, 1981; Abdrakhmatov *et al.*, 1996; Macey *et al.*, 1999). Finally, as mentioned previously (8), we used a uniform prior to set the maximum age for squamates using the oldest known squamate fossil, *Tikiguania estesi*, 230 Ma (Datta & Rayz, 2006).

We compared the posterior distribution from the results of our BEAST analyses to the prior distribution to ascertain the signal strength in our data (Drummond *et al.*, 2006). The prior distribution was estimated by conducting a BEAST analysis without data sampling only from the prior distribution.

Biogeographic Analyses

We estimated ancestral distributions for Gekkota with both parsimony and likelihood ancestral state reconstruction methods in Mesquite (Maddison & Maddison, 2008). We incorporated phylogenetic uncertainty

into our ancestral state reconstruction by summarizing ancestral states over a random subsample of 5000 post burn-in trees from the BEAST analyses (Lutzoni et al., 2001). Ancestral states were summarized onto the BEAST consensus tree. We performed three separate analyses that used two different coding schemes. First we coded species distributions as a binary character, Old World vs. New World. This simplistic scenario was appropriate because we used it primarily to identify where on the phylogeny lineages moved into the New World. For the likelihood-based analyses, we used both the 1–rate MK1 model (Lewis, 2001) and the asymmetric 2–rate model (Schluter et al., 1997; Pagel, 1999), and used the likelihood-ratio test to determine which model provided the best fit for the data. Second, we coded species distributions in a more biogeographically realistic manner, with species assigned to one of the following five biogeographic areas: North America/Central America; Africa/Madagascar including the Arabian peninsula and Socotra archipelago; South America/Caribbean; Europe/Asia including India; and Australia/Oceania, which included New Caledonia, New Guinea, New Zealand and Pacific Islands. We used the 1–rate MK1 model for this second analysis.

We explored the number and directionality of transitions between the Old World and New World using the "Summarize State Changes Over Trees" function in Mesquite (Maddison & Maddison, 2008). We summarized ancestral states over a random subsample of 5000 of the post burn-in trees from the BEAST analyses using a parsimony reconstruction model. We used parsimony because Mesquite does not count transitions among states in a likelihood framework if they are equivocal with this function. This can underestimate the actual number of transitions that have occurred over the phylogeny. In a parsimony framework, on the other hand, multiple equally parsimonious reconstructions exist, which eliminates the problem of equivocal reconstructions at a node and provides a more realistic count of potential character transitions.

Clade Age and Species Richness

We estimated the relationship between the number of species in each New World gecko lineage and the amount of time that lineage occupied the region. Several interpretations exist for estimating the timing of colonization of a lineage to a new region (Poux et al., 2005). The extremes are to equate colonization age with stem-clade age or the timing of cladogenesis with the sister taxon in the ancestral region (Vences et al., 2003; Vidal et al., 2008), or to associate colonization age with crown-clade age or the timing of the first cladogenic event within the new region (Yoder *et al.*, 2003; Barker *et al.*, 2004). Conservatively, actual colonization occurs sometime between these two values (Poux *et al.*, 2005; Poux *et al.*, 2006). We were unable to estimate the crown-clade age for all New World lineages because we had only one representative taxon for several of our lineages. We therefore used stem-clade age of each New World lineage as a proxy for the timing of colonization. We estimated species richness for each New World lineage using data from the Reptile Database (Uetz, 2010b). We also incorporated potential increases in species richness in some taxa from the data presented here, specifically in the genera *Pseudogonatodes*, *Coleodactylus,* and *Phyllopezus*. Finally, we excluded *Hemidactylus haitianus* and *H. mabouia* from the analyses as they most likely arrived in the Americas via anthropogenic means (see Discussion).

RESULTS

Phylogenetic Analyses

We estimated a maximum likelihood phylogeny from the combined molecular data using fragments of five nuclear protein-coding genes: *RAG1, RAG2, C-MOS, ACM4* and *PDC* (Suppl. Fig. 1; Suppl. Table 1). The dataset consisted of 2652 aligned characters of which, within Gekkota, 1802 characters were variable and 1497 characters were parsimony-informative. Sequence alignment was unambiguous and unique indels in these genes have been commented on elsewhere (Townsend *et al.*, 2004; Gamble *et al.*, 2008b; a; Geurgas *et al.*, 2008). Portions of the phylogeny with short, internal branches were generally poorly supported. This was the case at the base of each of the following clades: Sphaerodactylidae, Phyllodactylidae, and Gekkonidae.

Phylogenetic relationships among higher-level gekkotan clades and among outgroup taxa were largely concordant with previously published phylogenies at well-supported nodes (Han *et al.*, 2004; Townsend *et al.*, 2004; Vidal & Hedges, 2005; Gamble *et al.*, 2008b; a).

Phylogenetic Hypothesis Testing

We tested several *a priori* and *a posteriori* hypotheses related to biogeography, previously proposed phylogenetic hypotheses, and taxonomy (Table 1). The biogeographic hypotheses constrained closely related New World taxa as monophyletic. Monophyly in these clades could potentially result in simpler biogeographic scenarios, e.g. one colonization event vs. two. We considered two biogeographical hypotheses. First, New World Phyllodactylidae, exclusive of species in the *Tarentola americana* clade, form a monophyletic group and dispersed to the New World just once. This *a posteriori* hypothesis compared a clade consisting of *Bogertia, Garthia, Gymnodactylus, Homonota, Phyllodactylus, Phyllopezus,* and *Thecadactylus* to our optimal tree, where *Thecadactylus* was excluded from this clade. We also considered the hypothesis that the *Hemidactylus* lineage, represented by *H. brasilianus* and *H. palaichthus*, formed a clade and colonized the New World just once. We could not reject either of these hypotheses using the likelihood-based SH test, but both were rejected by the Bayesian test.

Table 1 Results of testing alternative phylogenetic hypotheses using the likelihood-based Shimodaira-Hasegawa test (SH) test in RAxML and Bayesian posterior probabilities from the BEAST analysis.

Hypothesis	Likelihood	Difference in likelihood	Significant with SH test?	Posterior probability
Best ML tree	−63384.26043	n/a	n/a	n/a
Saurodactylus monophyly	−63384.33134	−0.07090	No	0.5663
Phyllopezus monophyly	−63385.24020	−0.97976	No	0.0451
Tarentola americana sister taxon to remaining *Tarentola*	−63385.68739	−1.42696	No	0.2061
Thecadactylus forms clade with other New World Phyllodactylidae	−63386.68409	−2.42366	No	0.0009
Aeluroscalabotes sister taxon to remaining Eublepharidae	−63387.38857	−3.12814	No	0.0042
Coleodactylus monophyly	−63393.88910	−9.62867	No	0.0093
Hemidactylus brasilianus + H. palaichthus	−63398.20652	−13.94609	No	0.0000
Garthia + Homonota	−63418.55371	−34.29328	Yes	0.0000

Phylogenetic analyses also produced several unexpected relationships inconsistent with either prior published phylogenetic hypotheses or taxonomy. Several of these previously published hypotheses could not be rejected with the SH test, but were rejected with the Bayesian method. These included: *Aeluroscalabotes felinus* as the sister taxon to the remaining Eublepharidae (Grismer, 1988; Jonniaux & Kumazawa, 2008); monophyly of *Phyllopezus*, excluding *Bogertia*; and monophyly of *Coleodactylus.* Two other hypotheses could not be rejected using either test. These included: 1) *Tarentola americana* as the sister taxon to remaining *Tarentola* (Carranza et al., 2000; Carranza et al., 2002), and 2) monophyly of *Saurodactylus*. Finally, monophyly of a *Homonota + Garthia* clade (Kluge, 1964; Kluge, 1993; 2001) was rejected by both the SH test and the Bayesian analysis.

Tree Calibration and Dating

We estimated divergence dates using a Bayesian uncorrelated relaxed clock, with five fossil and biogeographic calibrations (Fig. 1, Suppl. Fig. 3). Fossil cross-validation rejected use of three additional calibrations (Suppl. Fig. 2). Divergence dates were largely concordant with other published studies (Vidal & Hedges, 2005; Gamble *et al.*,

2008b). The topology from the BEAST analysis was congruent with the RAxML analysis at well-supported nodes. Examination of 95% confidence intervals surrounding the stem age for New World gecko clades showed that only the age of Sphaerodactylini overlapped with the timing of the separation of South American and African continents, whereas other New World gecko lineages were younger. Comparing the posterior estimates of clade age to the prior distributions (Suppl. Fig. 3) showed the sequence data had a strong influence on clade age estimates and divergence times were not overwhelmed by our calibration priors.
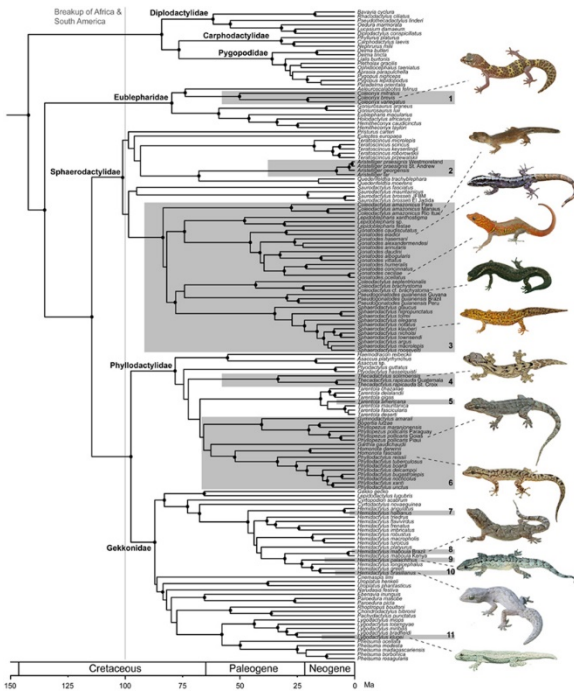

Figure 1 Time-calibrated gecko phylogeny using a Bayesian uncorrelated relaxed clock, with five fossil and biogeographic calibrations. Gray boxes indicate New World species and clade numbers are referred to in Table 1. Black circles at nodes indicate clades with ML bootstrap support > 70. The gray vertical line indicates timing of the Africa/South America split. Photos by LJV and TG.

Biogeographic Analyses

We recovered multiple independent origins of New World geckos (Fig. 1 & 2; Suppl. Figs 3–6). Ancestral areas were difficult to interpret at several nodes, particularly when the ancestral area was considered equivocal or when a node was poorly supported, e.g. the node in question was not recovered in many of the sampled Bayesian trees (Table 1). We compared results from the two coding schemes: coding biogeographic areas as a binary character, e.g. Old World and New World, or as five biogeographic regions, and both analyses were largely congruent, although there were more equivocally reconstructed nodes with the five character analysis. For this reason, we focus on the binary reconstruction for the remainder of the paper. The 1–rate MK1 model (-lnL = 50.81168372) had a rate of 0.00213. The asymmetric 2–rate model (-lnL = 49.76389421) had a forward rate of 0.00259, e.g. Old World to New World transition, and a backward rate of 0.00076, New World to Old World transition. No significant difference was detected between the 1–rate and 2–rate models using a likelihood ratio test (difference -lnL = 1.047789, df = 1, P = 0.1477).
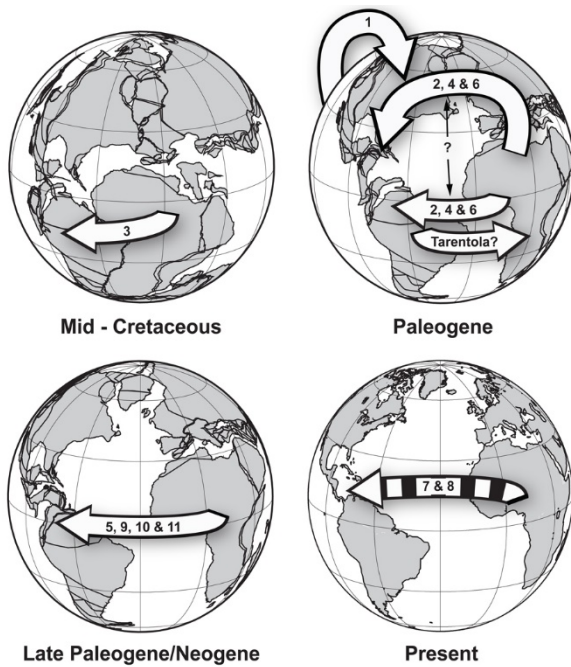
Figure 2 A. Biogeographic hypotheses for the origins of New World geckos at four different historical periods. Numbers inside lines refer to New World clades in Fig. 1. Dashed line indicates likely human-mediated dispersal.

The majority of Old World/New World divergences originated in the Old World with subsequent dispersal to the Western Hemisphere. Using parsimony, we estimated 10 transitions from the Old World to the New World (min = 7, max = 13) and 1 transition from the New World to the Old World (min = 0, max = 5) (Suppl. Fig 7). Two of these entries into the New World, represented by *H. mabouia* and *H. haitianus*, likely resulted from human-mediated dispersal (see Discussion).

Clade Age and Species Richness

We recovered a positive relationship between age and species richness of each New World lineage using linear regression (with species richness log-transformed; r^2 = 0.5972; P = 0.0146; Fig 3) and non-parametric Spearman-rank correlation (ρ = 0.7050; P = 0.0339). Older New World clades had more species overall than more recently arrived lineages.
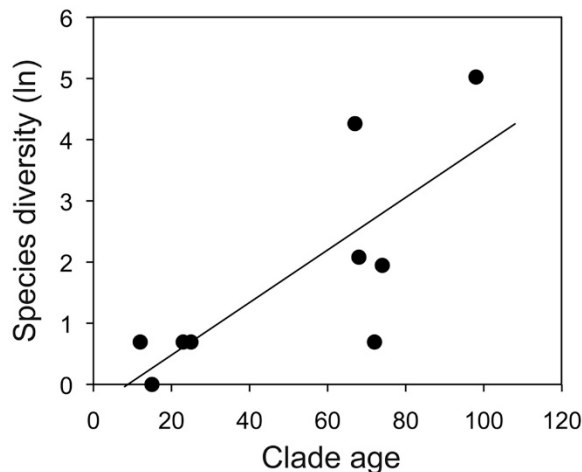

Figure 3 The relationship between clade age and log-transformed species richness for each New World gecko lineage. Clade age is based on the stem age of each New World lineage calculated as the time of divergence with its closest Old World relative.

Conclusions

Phylogeny of New World Geckos

Phylogenetic relationships among gekkotan families were congruent with previously published hypotheses (Donnellan *et al.*, 1999; Han *et al.*, 2004; Townsend *et al.*, 2004; Gamble *et al.*, 2008b; a). We confirmed placement of the New World genera *Bogertia, Garthia,* and *Gymnodactylus* as members of the Phyllodactylidae (Gamble *et al.*, 2008a). Within gekkotan families, we recovered several unexpected relationships. These were tested *a posteriori* against the traditional taxonomies or previous phylogenetic hypotheses and, in almost all cases, we could not reject the alternative hypotheses using the likelihood-based SH test. Conversely, most alternative hypotheses had very low Bayesian posterior probabilities. Differences between the likelihood and Bayesian methods for hypothesis testing have been reported elsewhere (Buckley, 2002) and the SH test in particular is known to be conservative (Strimmer & Rambaut, 2002). The short internal branch lengths involved in differentiating alternative hypotheses can also reduce the accuracy of phylogenetic reconstruction and, subsequently, make distinguishing among alternative hypotheses difficult (Jackman et al., 1999; Slowinski, 2001; Poe & Chubb, 2004). The only alternative hypothesis rejected by both tests was the sister-group relationship of *Garthia* and *Homonota*. These South American genera have been synonymised in the past (Kluge, 1965; 2001), but we recovered *Garthia* as the sister taxon to a strongly-supported clade, consisting of *Homonota* and *Phyllodactylus*. Our results verify previous morphological work (Abdala & Moro, 1996; Abdala, 1998) and should remove any lingering doubts as to the validity of *Garthia*.

Both *Phyllopezus* and *Coleodactylus* were polyphyletic with regards to other described genera. Exemplars of *C. amazonicus*, for example, were recovered as the sister taxon to the remaining Sphaerodactylini, a clade consisting of *Gonatodes, Lepidoblepharis, Pseudogonatodes, Sphaerodactylus*, and the remaining sampled *Coleodactylus* species: *C. brachystoma, C.* cf. *brachystoma* and *C. septentrionalis*. This relationship was well supported and the alternative hypothesis of a monophyletic *Coleodactylus* had a very low posterior probability in the Bayesian analysis, although a monophyletic *Coleodactylus* could not be rejected by the SH test. Geurgas et al. (Geurgas et al., 2008) recovered a monophyletic *Coleodactylus* in their phylogenetic analysis of the genus using both mitochondrial and nuclear genes, but the relationship was poorly supported. These results suggest additional work is needed to clarify the taxonomy and monophyly of these New World gecko genera.

Our results provide evidence that we still have a poor understanding of species richness among Neotropical geckos. We included multiple exemplars from different localities for several individual species in our analyses. In most cases, large genetic divergences existed among individuals from different localities, with genetic distance as great or greater than distances among recognized sister species within our dataset (Fig.1). This suggests undescribed species-level diversity in the following currently recognized species: *Coleodactylus amazonicus, Phyllopezus pollicaris, Pseudogonatodes guianensis,* and *Thecadactylus rapicauda*. Undescribed diversity within some of these taxa has been reported by others, e.g. *C. amazonicus* (Geurgas et al., 2008) and *T. rapicauda* (Kronauer et al., 2005), but is newly reported for *P. guianensis* and *P. pollicaris*. Other studies have shown that current knowledge of amphibian species richness in the Neotropics may be dramatically underestimated (Fouquet et al., 2007), so it is no surprise that the same could be said for reptiles. Indeed, 19 species of gecko have been described from the Western Hemisphere since 2000 (Uetz, 2010a). Our preliminary results, along with results of Geurgas et al. (Geurgas *et al.*, 2008; Geurgas & Rodrigues, 2010), suggest that gekkotan species-level diversity in the Neotropics is still under-reported, perhaps substantially so.

Biogeography of New World Geckos

We used our phylogeny, along with the molecular clock analyses and ancestral area reconstruction, to generate a hypothesis for origins of geckos in the Western Hemisphere. Our data suggest multiple independent origins of New World geckos via several routes, including vicariance, dispersal, and human-mediated transport.

We confirmed the Gondwanan origin of the oldest New World lineage (clade 3, Fig. 1) that diverged from the its closest Old World relative, the North African *Saurodactylus*, approximately 82–114 Ma. Gamble et al. (2008b) recovered similar divergence dates between Sphaerodactylini and *Saurodactylus* using non-parametric rate smoothing that lacked non-gekkotan calibrations. These dates broadly overlap with the separation of Africa and South America 99–112 Ma (Parrish, 1993; Maisey, 2000; Eagles, 2007). Evidence that West Africa and eastern South America maintained a connection until this time is strengthened by the existence of shared faunal components between the two regions (Buffetaut & Taquet, 1979; Maisey, 2000; Sereno *et al.*, 2003; Sereno *et al.*, 2004).

Terrestrial dispersal via a Beringean land bridge was the most likely point of entry for the ancestors of the eublepharid genus *Coleonyx* (clade 1, Fig. 1). Dispersal to the New World could have occurred any time after the divergence between *Coleonyx* and its closest Old World relative, the Southeast Asian *Aeluroscalabotes*, between 55–93 Ma and was likely facilitated by warm climatic cycles during the late Paleocene and early Eocene (Peters & Sloan, 2000; Sanmartin *et al.*, 2001; Thomas, 2004).

Several New World clades (clades 2, 4 & 6, Fig 1) show clear evidence of trans-Atlantic dispersal. The timing of these events allows for overseas rafting or terrestrial dispersal via an intermittent land bridge connecting Europe to North America from the late Cretaceous to the late Eocene (Sanmartin *et al.*, 2001; Smith *et al.*, 2006). The presence of a high latitude European gecko fossil from the Eocene (Bauer et al., 2005) and non-eublepharid, gecko eggshell fossils from western North America from the same period (Hirsch, 1996) certainly make the land bridge hypothesis a possibility. Dispersal via trans-Atlantic landbridge would still require overseas dispersal to South America and proto-Caribbean islands from North America.

Poor phylogenetic resolution at the base of Phyllodactylidae made it difficult to distinguish among several alternative biogeographic hypotheses surrounding the origin of its three New World lineages. Given our optimal topology, two equally likely biogeographic hypotheses exist, each involving multiple trans-Atlantic dispersal events (Fig 4). Hypothesis 1 involves three separate dispersals from the Old World to the New World in the ancestors of clades 4, 5, and 6 respectively. Hypothesis 2 involves a single dispersal to the New World of the ancestor of the clade containing 4,5 & 6, followed by dispersal back to the Old World by the ancestor of *Tarentola*; and another westward trans-Atlantic trip by the ancestor of *T. americana* (clade 5). One way of testing these alternative scenarios is to compare a 1–rate transition model, where transitions between the Old and New World are equally likely, favouring Hypothesis 2, to a 2–rate model, where movement between the Old and New World is asymmetric and potentially unidirectional, favouring Hypothesis 1. We found no significant difference between these two models and, therefore, cannot reject the bidirectionality of dispersal rates between Africa and the Americas. While westward trans-Atlantic dispersal from Africa to South America is the most commonly seen pattern in vertebrates (Vidal *et al.*, 2010) dispersal in the opposite direction is common in invertebrates and plants (Sanmartin & Ronquist, 2004). It should also be noted that trans-Atlantic dispersal in either direction involved much shorter distances during the timeframe of basal divergences within Phyllodactylidae and such trips could be accomplished in a matter of weeks (Houle, 1998; Houle, 1999). The overseas dispersal of Neotropical *Tarentola* (clade 5) to the New World 7–17 Ma is well established (Carranza et al., 2000) and involves trans-Atlantic dispersal in both hypotheses.
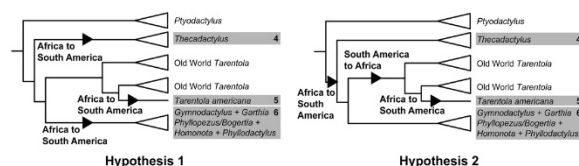
Figure 4 Two equally parsimonious biogeographic hypotheses for the origins of New World Phyllodactylidae. Arrows indicate dispersal events. Gray boxes enclose New World species and clade numbers are referred to in Fig. 1.

Presence of three New World lineages within Gekkonidae cannot be attributed to human-mediated transport. The lineage represented here by *Lygodactylus klugei* most likely arrived in South America via trans-Atlantic dispersal and the remaining *Lygodactylus* species are found in sub-Saharan Africa and Madagascar. The New World species, *L. klugei* and *L. wetzeli*, had been hypothesized to be allied with the New World sphaerodactylid geckos and placed in a separate genus, *Vanzoia* (Smith et al., 1977). Morphological data suggest South American *Lygodactylus* are allied with African *Lygodactylus* (Bons & Pasteur, 1977), a hypothesis corroborated by the molecular data and analyses presented here.

Two lineages of the widespread genus *Hemidactylus* appear to have arrived in the New World via trans-Atlantic dispersal. Carranza and Arnold (2006) provided convincing evidence that the clades containing *H. palaichthus* and *H. brasilianus*, resulted from an ancient, trans-Atlantic dispersal. Applying a sequence evolution rate of 1.35–3.2%/my to their data, Carranza and Arnold (2006) hypothesized that the ancestors of *H. palaichthus* and *H. brasilianus* dispersed from the Old World to the Neotropics, at most between 6–16 Ma. This is within the bounds of our estimated divergences dates for these two lineages from their Old World sister taxa, 7.4–21.9 Ma.

We included both New World and Old World exemplars of *Hemidactylus mabouia* and *H. haitianus/H. angulatus* in our dataset. Presence of these species in the New World has been attributed to human-mediated dispersal (Kluge, 1969; Carranza & Arnold, 2006; Weiss & Hedges, 2007). Our results are similar to recently published results utilizing molecular data (Carranza & Arnold, 2006; Weiss & Hedges, 2007; Bauer *et al.*, In Press), and we also found little genetic variance between trans-Atlantic exemplars within these two species. *Hemidactylus haitianus* was recently synonymised with *H. angulatus* based on this close relationship (Weiss & Hedges, 2007), but *H. angulatus* appears to be a species complex (Carranza & Arnold, 2006; Bauer *et al.*, In Press). A full revision of this group is warranted before such nomenclatural changes should be considered.

North and South America have quite different biogeographic histories with varying levels of biotic exchange occurring between the two continents (Simpson, 1980). We recovered several instances of movement between South America and the Caribbean with North America. All North American taxa arrived from South America or the Caribbean with the exception of *Coloeonyx*, which, as mentioned above, arrived in North America via a Beringean land bridge. Our taxon sampling within most genera that occur on both continents was not complete enough to accurately estimate the timing of this movement. It appears though that in at least one instance, *Phyllodactylus*, dispersal into North America predated the connection of North and South America via the Panamanian land bridge 3 mya (Cody *et al.*, 2010).

Clade Age and Species Richness

We found that older New World gecko lineages possessed more species than more recent arrivals. The idea that older clades would have more species than younger clades is not new (Wallace, 1878; Darlington, 1957; Fischer, 1960). Several empirical studies support this phenomenon, describing an increase in species diversity over time (Stephens & Wiens, 2003; Wiens *et al.*, 2006b; McPeek & Brown, 2007; Wiens *et al.*, 2009). Indeed, in many animal lineages it appears that clade age alone is a sufficient explanation for species richness (McPeek & Brown, 2007). Other studies have found no relationship between clade age and species richness (Magallon & Sanderson, 2001; Ricklefs, 2006; Seehausen, 2006; Ricklefs *et al.*, 2007). One possible explanation for the lack of a relationship between clade age and species richness is that species diversity in a region is ecologically limited and there is a maximum number of species that a given region can support (Pianka, 1966; Rabosky, 2009a; b).

This ecological limit hypothesis predicts a relationship between clade age and species richness in younger clades but the relationship will disappear over time as clades reach their carrying capacity (Rabosky, 2009a).

Several likely explanations for a positive relationship between clade age and species richness in New World geckos emerge. The first involves the "time-for-speciation effect" (Stephens & Wiens, 2003), that is, more recently arrived lineages (e.g. clades 5, 9, 10 & 11) have simply not had time necessary to accumulate species. Another explanation is that early gekkotan lineages could have increased diversification rates due to lack of competitors and the exploitation of empty niches or lack of predators (Walker & Valentine, 1984; Schluter, 2000; Moore & Donoghue, 2007). Other organisms have shown increased diversification rates associated with movement into new regions (Cracraft, 1985; Slowinski & Guyer, 1993; Weir, 2006; Moore & Donoghue, 2007; Wiens, 2007; Van Bocxlaer et al., 2010) and New World geckos could certainly follow this pattern. Another explanation is that potentially available niches may have already been occupied by earlier gecko lineages resulting in decreased speciation rates and/or increased extinction rates in the recently arrived lineages. This last scenario could result in a near permanent suppression of species diversity in more recent arrivals and help maintain a clade age and species diversity relationship over time. Differentiating between these hypotheses is beyond the scope of the current paper and dataset and none of these explanations are mutually exclusive.

It is also possible that the relationship between clade age and species richness is simply an artefact based on the presence of newly arrived lineages. The positive relationship between clade age and species richness in New World geckos appears to be strongly influenced by the very small number of species in clades occupying the lower left hand corner of Figure 3. These are the four most recently arrived New World gecko lineages represented in our dataset by: *Tarentola americana; H. palaichthus; H. brasilianus;* and *L. klugei* (clades 5, 9, 10 and 11). The clade age/species richness relationship breaks down if these recently arrived lineages are removed revealing large disparities in species richness among the older New World lineages. *Thecadactylus, Coleonyx* and *Aristelliger* (clades 1, 2 and 4), for example, have substantially fewer extant species than the clade consisting of *Bogertia, Garthia, Gymnodactylus, Homonota, Phyllodactylus,* and *Phyllopezus* (clade 6) even though these four clades diverged from their Old World sister taxa at about the same time. This variation in species richness among clades of similar age is evidence that clade age alone is not responsible for the number of species in any individual New World gecko lineage and that speciation and extinction rates are also important in determining the number of species in a particular clade. The ecological limit hypothesis predicts an apparent relationship between clade age and species richness when older clades have reached saturation but younger clades are still growing (Rabosky, 2009a). The pattern we observe in New World geckos is consistent with this hypothesis.

Table 2 New World gecko lineages recovered in the phylogenetic analyses and their most likely route of entry into the Western Hemisphere. Clade number refers to Figs 1 & 2. Citations refer to other published sources that have used phylogenies to identify the indicated taxa as independent New World lineages.

Clade	Taxa	Posterior Stem Age (95% CI) (Ma)	Origin	New World species diversity	Citation
1	*Coleonyx*	74 (55 – 93)	Beringean landbridge	7	(Grismer, 1988; Jonniaux & Kumazawa, 2008)
2	*Aristelliger*	68 (49 – 88)	Trans-Atlantic dispersal /North Atlantic land bridge	8	(Gamble et al., 2008b)
3	*Coleodactylus, Gonatodes,*	98 (82 – 114)	Gondwanan vicariance	152	(Gamble et al., 2008b)

3	Lepidoblepharis, Pseudogonatodes & Sphaerodactylus				
4	Thecadactylus	72 (58 – 87)	Trans-Atlantic dispersal /North Atlantic land bridge	2	This study
5	Tarentola americana	12 (7 – 17)	Trans-Atlantic dispersal	2	(Carranza et al., 2000)
6	Bogertia, Garthia, Gymnodactylus, Homonota, Phyllodactylus & Phyllopezus	67 (53 – 81)	Trans-Atlantic dispersal /North Atlantic land bridge	71	This study
7	Hemidactylus haitianus	4 (1 – 8)	Anthropogenic dispersal	1	(Carranza & Arnold, 2006; Weiss & Hedges, 2007)
8	Hemidactylus mabouia	2.5 (1 – 5)	Anthropogenic dispersal	1	(Kluge, 1969; Carranza & Arnold, 2006)
9	Hemidactylus palaichthus	23 (16 – 30)	Trans-Atlantic dispersal	2	(Carranza & Arnold, 2006)
10	Hemidactylus brasilianus	15 (9 – 21)	Trans-Atlantic dispersal	1	(Carranza & Arnold, 2006)
11	Lygodactylus klugei	25 (16 – 35)	Trans-Atlantic dispersal	2	This study

Acknowledgements

References

1. Abdala V, Moro S. Cranial musculature of South American Gekkonidae. Journal of Morphology. 1996;229:59–70.

2. Abdala V. Análisis cladístico de las especies del género *Homonota* (Gekkonidae) Revista Española de Herpetología. 1998;12:55–62.
3. Abdrakhmatov KY, Aldazhanov SA, Hager BH, Hamburger MW, Herring TA, Kalabaev KB, Makarov VI, Molnar P, Panasyuk SV, Prilepin MT, Reilinger RE, Sadybakasov IS, Souter BJ, Trapeznikov YA, Tsurkov VY, Zubovich AV. Relatively recent construction of the Tien Shan inferred from GPS measurements of present–day crustal deformation rates. Nature. 1996;384:450–453.
4. Agusti J, Cabrera L, Garces M, Krijgsman W, Oms O, Pares JM. A calibrated mammal scale for the Neogene of Western Europe: State of the art. Earth–Science Reviews. 2001;52:247–260.
5. Austin JJ, Arnold EN, Jones CG. Reconstructing an island radiation using ancient and recent DNA: the extinct and living day geckos (*Phelsuma*) of the Mascarene islands. Molecular Phylogenetics and Evolution. 2004;31:109–122.
6. Barker FK, Cibois A, Schikler P, Feinstein J, Cracraft J. Phylogeny and diversification of the largest avian radiation. Proceedings of the National Academy of Sciences of the United States of America. 2004;101:11040–11045.
7. Bauer AM. African–South American relationships: A perspective from the Reptilia. In: Goldblatt P, editor. Biological relationships between Africa and South America. New Haven: Yale University Press; 1993. pp. 244–288.
8. Bauer AM. Familia Gekkonidae (Reptilia, Sauria) Part I Australia and Oceania. Das Tierreich. 1994;109:i–xiv. 1–306. (303)
9. Bauer AM, Bohme W, Weitschat W. An Early Eocene gecko from Baltic amber and its implications for the evolution of gecko adhesion. Journal of Zoology. 2005;265:327–332.
10. Bauer AM, De Silva A, Greenbaum E, Jackman TR. A new species of day gecko from high elevation in Sri Lanka, with a preliminary phylogeny of Sri Lankan *Cnemaspis* (Reptilia: Squamata: Gekkonidae) Mitteilungen aus dem Museum für Naturkunde in Berlin. Zoologische Reihe, Supplement. 2007;83:22–32.
11. Bauer AM, Jackman TR, Greenbaum E, Giri VB, de Silva A. South Asia supports a major endemic radiation of *Hemidactylus* geckos. Molecular Phylogenetics and Evolution. In Press.
12. Bons J, Pasteur G. Solution histologique a un probleme de taxinomic herpetologique interessant les rapports paleobiologiques de l'Amerique du Sud et de l'Afrique. C. R. Acad. Sc. Paris. 1977;248:2547–2550.
13. Brown WC, Alcala AC. Viability of lizard eggs exposed to sea water. Copeia. 1957;1957:39–41.
14. Buckley TR. Model misspecification and probabilistic tests of topology: Evidence from empirical data sets. Systematic Biology. 2002;51:509–523.
15. Buffetaut E, Taquet P. An early Cretaceous terrestrial crocodilian and the opening of the South Atlantic. Nature. 1979;280:486–487.
16. Carranza S, Arnold EN, Mateo JA, Lopez–Jurado LF. Long–distance colonization and radiation in gekkonid lizards, *Tarentola* (Reptilia : Gekkonidae), revealed by mitochondrial DNA sequences. Proceedings of the Royal Society Biological Sciences Series B. 2000;267:637–649.
17. Carranza S, Arnold EN, Mateo JA, Geniez P. Relationships and evolution of the North African geckos, *Geckonia* and *Tarentola* (Reptilia : Gekkonidae), based on mitochondrial and nuclear DNA sequences. Molecular Phylogenetics and Evolution. 2002;23:244–256.
18. Carranza S, Arnold EN. Systematics, biogeography, and evolution of *Hemidactylus* geckos (Reptilia : Gekkonidae) elucidated using mitochondrial DNA sequences. Molecular Phylogenetics and Evolution. 2006;38:531–545.
19. Cody S, Richardson JE, Rull V, Ellis C, Pennington RT. The great American biotic interchange revisited. Ecography. 2010;33:326–332.
20. Conrad JL, Norell MA. High-resolution X-ray computed tomography of an early Cretaceous gekkonomorph (Squamata) from Öösh (Övörkhangai; Mongolia) Historical Biology. 2006;18:405–431.
21. Cracraft J. Biological diversification and its causes. Annals of the Missouri Botanical Garden. 1985;72:794–822.

22. Darlington PJ. Zoogeography: The geographical distribution of animals. 1st edn. London, England: John Wiley and Sons, Inc.; 1957.
23. Datta PM, Rayz S. Earliest lizard from the Late Triassic (Carnian) of India. Journal of Vertebrate Paleontology. 2006;26:795–800.
24. de Queiroz A. The resurrection of oceanic dispersal in historical biogeography. Trends in Ecology & Evolution. 2005;20:68–73.
25. Donnellan SC, Hutchinson MN, Saint KM. Molecular evidence for the phylogeny of Australian gekkonoid lizards. Biological Journal of the Linnean Society. 1999;67:97–118.
26. Drummond AJ, Ho SYW, Phillips MJ, Rambaut A. Relaxed phylogenetics and dating with confidence. PLoS Biology. 2006;4:699–710.
27. Drummond AJ, Rambaut A. BEAST: Bayesian evolutionary analysis by sampling trees. Bmc Evolutionary Biology. 2007;7:214.
28. Duellman WE. The South American Herpetofauna: A panoramic view. In: Duellman WE, editor. The South American Herpetofauna: Its Orgin evolution and Dispersal. Kansas: Museum of Natural History The University of Kansas, Lawrence; 1979. pp. 1–28.
29. Dunson WA, Bramham CR. Evaporative water loss and oxygen consumption of three small lizards from the Florida Keys: *Sphaerodactylus cinereus, S. notatus*, and *Anolis sagrei*. Physiological Zoology. 1981;54:253–259.
30. Dunson WA. Low water vapor conductance of hard–shelled eggs of the gecko lizards *Hemidactylus* and *Lepidodactylus*. Journal of Experimental Zoology. 1982;219:377–379.
31. Eagles G. New angles on South Atlantic opening. Geophysical Journal International. 2007;168:353–361.
32. Felsenstein J. Confidence-limits on phylogenies - an approach using the bootstrap. Evolution. 1985;39:783–791.
33. Fischer AG. Latitudinal variations in organic diversity. Evolution. 1960;14:64–81.
34. Fouquet A, Gilles A, Vences M, Marty C, Blanc M, Gemmell NJ. Underestimation of species richness in Neotropical frogs revealed by mtDNA analyses. PLoS ONE. 2007;2:e1109.
35. Fuenmayor GR, Ugueto G, Bauer AM, Barros T, Manzanilla J. Expansion and Natural History of a successful colonizing gecko in Venezuela (Reptilia: Gekkonidae: *Hemidactylus mabouia*) and the discovery of *H. frenatus* in Venezuela. Herpetological Review. 2005;36:121–125.
36. Gamble T, Bauer AM, Greenbaum E, Jackman TR. Out of the blue: a novel, trans-Atlantic clade of geckos (Gekkota, Squamata) Zoologica Scripta. 2008a;37:355–366.
37. Gamble T, Bauer AM, Greenbaum E, Jackman TR. Evidence for Gondwanan vicariance in an ancient clade of gecko lizards. Journal of Biogeography. 2008b;35:88–104.
38. Gentry AH. Neotropical Floristic Diversity - Phytogeographical Connections between Central and South America, Pleistocene Climatic Fluctuations, or an Accident of the Andean Orogeny. Annals of the Missouri Botanical Garden. 1982;69:557–593.
39. Geurgas SR, Rodrigues MT, Moritz C. The genus *Coleodactylus* (Sphaerodactylinae, Gekkota) revisited: A molecular phylogenetic perspective. Molecular Phylogenetics and Evolution. 2008;49:92–101.
40. Geurgas SR, Rodrigues MT. The hidden diversity of *Coleodactylus amazonicus* (Sphaerodactylinae, Gekkota) revealed by molecular data. Molecular Phylogenetics and Evolution. 2010;54:583–593.
41. Grismer LL. Phylogeny, taxonomy, classification, and biogeography of eublepharid geckos. In: Estes R, Pregill G, editors. Phylogenetic relationships of the lizard families. Stanford, CA: Stanford University Press; 1988. pp. 369–469.
42. Han D, Zhou K, Bauer AM. Phylogenetic relationships among gekkotan lizards inferred from C–mos nuclear DNA sequences and a new classification of the Gekkota. Biological Journal of the Linnean Society. 2004;83:353–368.
43. Hass CA. Evolution and biogeography of West–Indian Sphaerodactylus (Sauria, Gekkonidae) – a molecular approach. Journal of Zoology. 1991;225:525–561.
44. Hirsch KF. Parataxonomic classification of fossil chelonian and gecko eggs. Journal of Vertebrate Paleontology. 1996;16:752–762.

45. Houle A. Floating islands: A mode of long-distance dispersal for small and medium-sized terrestrial vertebrates. Diversity and Distributions. 1998;4:201–216.
46. Houle A. The origin of platyrrhines: An evaluation of the antarctic scenario and the floating island model. American Journal of Physical Anthropology. 1999;109:541–559.
47. Huelsenbeck JP, Larget B, Miller RE, Ronquist F. Potential applications and pitfalls of Bayesian inference of phylogeny. Systematic Biology. 2002;51:673–688.
48. Hugall AF, Foster R, Lee MSY. Calibration choice, rate smoothing, and the pattern of tetrapod diversification according to the long nuclear gene RAG-1. Systematic Biology. 2007;56:543–563.
49. Hutchinson MN. The first fossil pygopod (Squamata, Gekkota), and a review of mandibular variation in living species. Memoirs of the Queensland Museum. 1997;41:355–366.
50. Iturralde–Vinent MA, MacPhee RDE. Age and paleogeographical origin of Dominican amber. Science. 1996;273:1850–1852.
51. Jackman TR, Larson A, de Queiroz K, Losos JB. Phylogenetic relationships and tempo of early diversification in *Anolis* lizards. Systematic Biology. 1999;48:254–285.
52. Jennings WB, Pianka ER, Donnellan S. Systematics of the lizard family pygopodidae with implications for the diversification of Australian temperate biotas. Systematic Biology. 2003;52:757–780.
53. Jonniaux P, Kumazawa Y. Molecular phylogenetic and dating analyses using mitochondrial DNA sequences of eyelid geckos (Squamata : Eublepharidae) Gene. 2008;407:105–115.
54. Kluge AG. A revision of the South American Gekkonid lizard genus *Homonota* Gray. American Museum Novitates. 1964;2193:1–41.
55. Kluge AG. Noteworthy records of the gekkonid lizard genus *Homonota* Gray from Argentina. Bulletin of the Southern California Academy of Sciences. 1965;64:127–131.
56. Kluge AG. Higher taxonomic categories of gekkonid lizards and their evolution. Bulletin of the American Museum of Natural History. 1967;135:1–60. + 65 plates.
57. Kluge AG. The evolution and geographical origin of the New World *Hemidactylus mabouia–brookii* complex (Gekkonidae, Sauria) Miscellaneous Publications Museum of Zoology University of Michigan. 1969;138:1–78.
58. Kluge AG. Cladistic relationships in the Gekkonoidea (Squamata, Sauria) Miscellaneous Publications Museum of Zoology University of Michigan. 1987;173:1–54.
59. Kluge AG. Gekkonoid lizard taxonomy. San Diego, CA: International Gecko Society; 1993.
60. Kluge AG. Cladistic relationships of sphaerodactyl lizards. American Museum Novitates. 1995;3139:1–23.
61. Kluge AG. Gekkotan lizard taxonomy. Hamadryad. 2001;26:i–ii. 1–209.
62. Kronauer DJC, Bergmann PJ, Mercer JM, Russell AP. A phylogeographically distinct and deep divergence in the widespread Neotropical turnip-tailed gecko, *Thecadactylus rapicauda*. Molecular Phylogenetics and Evolution. 2005;34:431–437.
63. Lever C. Naturalized reptiles and amphibians of the world. New York: Oxford University Press; 2003.
64. Lewis PO. A likelihood approach to estimating phylogeny from discrete morphological character data. Systematic Biology. 2001;50:913–925.
65. Lutzoni F, Pagel M, Reeb V. Major fungal lineages are derived from lichen symbiotic ancestors. Nature. 2001;411:937–940.
66. Macey JR, Wang YZ, Ananjeva NB, Larson A, Papenfuss TJ. Vicariant patterns of fragmentation among gekkonid lizards of the genus *Teratoscincus* produced by the Indian collision: A molecular phylogenetic perspective and an area cladogram for Central Asia. Molecular Phylogenetics and Evolution. 1999;12:320–332.
67. Maddison WP, Maddison DR. MacClade, analysis of phylogeny and character evolution, Sinauer. Sunderland, MA: 1992.
68. Maddison WP, Maddison DR. Mesquite: a modular system for evolutionary analysis. 2008
69. Magallon S, Sanderson MJ. Absolute diversification rates in angiosperm clades. Evolution. 2001;55:1762–1780.

70. Maisey JG. Continental break up and the distribution of fishes of Western Gondwana during the Early Cretaceous. Cretaceous Research. 2000;21:281–314.
71. McPeek MA, Brown JM. Clade age and not diversification rate explains species richness among animal taxa. American Naturalist. 2007;169:E97–E106.
72. Moore BR, Donoghue MJ. Correlates of diversification in the plant clade dipsacales: Geographic movement and evolutionary innovations. American Naturalist. 2007;170:S28–S55.
73. Muller J. A new fossil species of *Euleptes* from the early Miocene of Montaigu, France (Reptilia, Gekkonidae) Amphibia-Reptilia. 2001;22:341–348.
74. Near TJ, Meylan PA, Shaffer HB. Assessing concordance of fossil calibration points in molecular clock studies: An example using turtles. American Naturalist. 2005;165:137–146.
75. Noonan BP, Chippindale PT. Vicariant origin of Malagasy reptiles supports late cretaceous Antarctic land bridge. American Naturalist. 2006;168:730–741.
76. Notredame C, Higgins DG, Heringa J. T–Coffee: A novel method for fast and accurate multiple sequence alignment. Journal of Molecular Biology. 2000;302:205–217.
77. Nydam RL. A new taxon of helodermatid–like lizard from the Albian–Cenomanian of Utah. Journal of Vertebrate Paleontology. 2000;20:285–294.
78. Pagel M. The maximum likelihood approach to reconstructing ancestral character states of discrete characters on phylogenies. Systematic Biology. 1999;48:612–622.
79. Parrish JT. The paleogeography of the opening South Atlantic. In: George W, Lavocat R, editors. The Africa-South America connection. Oxford, UK: Clarendon Press; 1993. pp. 8–27.
80. Pennington RT, Dick CW. The role of immigrants in the assembly of the South American rainforest tree flora. Philosophical Transactions of the Royal Society of London B Biological Sciences. 2004;359:1611–1622.
81. Peters RB, Sloan LC. High concentrations of greenhouse gases and polar stratospheric clouds: A possible solution to high-latitude faunal migration at the latest Paleocene thermal maximum. Geology. 2000;28:979–982.
82. Pianka ER. Latitudinal gradients in species diversity: A review of concepts. The American Naturalist. 1966;100:33–46.
83. Poe S, Chubb AL. Birds in a bush: Five genes indicate explosive evolution of avian orders. Evolution. 2004;58:404–415.
84. Posada D. j Model Test: Phylogenetic model averaging. Molecular Biology and Evolution. 2008:1253–1256.
85. Poux C, Madsen O, Marquard E, Vieites DR, de Jong WW, Vences M. Asynchronous colonization of Madagascar by the four endemic clades of primates, tenrecs, carnivores, and rodents as inferred from nuclear genes. Systematic Biology. 2005;54:719–730.
86. Poux C, Chevret P, Huchon D, de Jong WW, Douzery EJP. Arrival and diversification of caviomorph rodents and platyrrhine primates in South America. Systematic Biology. 2006;55:228–244.
87. Rabosky DL. Ecological limits and diversification rate: alternative paradigms to explain the variation in species richness among clades and regions. Ecology Letters. 2009a;12:735–743.
88. Rabosky DL. Ecological limits on clade diversification in higher taxa. American Naturalist. 2009b;173:662–674.
89. Rambaut A, Drummond AJ. Tracer, version 1.5 Distributed by authors. 2007
90. Raven PH, Axelrod DI. Angiosperm biogeography and past continental movements. Annals of the Missouri Botanical Garden. 1974;61:539–673.
91. Renner S. Plant dispersal across the tropical Atlantic by wind and sea currents. International Journal of Plant Sciences. 2004;165:S23–S33.
92. Ricklefs RE. Global variation in the diversification rate of passerine birds. Ecology. 2006;87:2468–2478.
93. Ricklefs RE, Losos JB, Townsend TM. Evolutionary diversification of clades of squamate reptiles. Journal of Evolutionary Biology. 2007;20:1751–1762.

94. Rieppel O. The Lepidosauromorpha: an overview with special emphasis on the Squamata. In: Fraser NC, Sues HD, editors. In the shadow of the dinosaurs: Early Mesozoic tetrapods. New York, NY: Cambridge University Press; 1994. pp. 23–37.

95. Rocha S, Posada D, Carretero MA, Harris DJ. Phylogenetic affinities of Comoroan and East African day geckos (genus *Phelsuma*): Multiple natural colonisations, introductions and island radiations. Molecular Phylogenetics and Evolution. 2007;43:685–692.

96. Russell AP. Integrative functional morphology of the gekkotan adhesive system (Reptilia: Gekkota) Integrative and Comparative Biology. 2002;42:1154–1163.

97. Sanderson MJ. r8s: inferring absolute rates of molecular evolution and divergence times in the absence of a molecular clock. Bioinformatics. 2003;19:301–302.

98. Sanmartin I, Enghoff H, Ronquist F. Patterns of animal dispersal, vicariance and diversification in the Holarctic. Biological Journal of the Linnean Society. 2001;73:345–390.

99. Sanmartin I, Ronquist F. Southern Hemisphere biogeography inferred by event-based models: Plant versus animal patterns. Systematic Biology. 2004;53:216–243.

100. Schluter D, Price T, Mooers AØ, Ludwig D. Likelihood of ancestor states in adaptive radiation. Evolution. 1997;51:1699–1711.

101. Schluter D. The Ecology of Adaptive Radiations. Oxford, UK: Oxford University Press; 2000.

102. Seehausen O. African cichlid fish: a model system in adaptive radiation research. Proceedings of the Royal Society B: Biological Sciences. 2006;273:1987–1998.

103. Sereno PC, Sidor CA, Larsson HCE, Gadow B. A new notosuchian from the early Cretaceous of Niger. Journal of Vertebrate Paleontology. 2003;23:477–482.

104. Sereno PC, Wilson JA, Conrad JL. New dinosaurs link southern landmasses in the Mid-Cretaceous. Proceedings of the Royal Society B-Biological Sciences. 2004;271:1325–1330.

105. Shimodaira H, Hasegawa M. Multiple comparisons of log–likelihoods with applications to phylogenetic inference. Molecular Biology and Evolution. 1999;16:1114–1116.

106. Simpson GG. Splendid isolation: The curious history of South American mammals. New Haven, CT: Yale University Press; 1980.

107. Slowinski JB, Guyer C. Testing whether certain traits have caused amplified diversification - an improved method based on a model of random speciation and extinction. American Naturalist. 1993;142:1019–1024.

108. Slowinski JB. Molecular polytomies. Molecular Phylogenetics and Evolution. 2001;19:114–120.

109. Smith HM, Martin RL, Swain TA. A new genus and two new species of South American geckos (Reptilia: Lacertilia) Papeis Avulsos de Zoologia (Sao Paulo) 1977;30:195–213.

110. Smith T, Rose KD, Gingerich PD. Rapid Asia-Europe-North America geographic dispersal of earliest Eocene primate *Teilhardina* during the Paleocene-Eocene Thermal Maximum. Proceedings of the National Academy of Sciences of the United States of America. 2006;103:11223–11227.

111. Stamatakis A. RAxML-VI-HPC: Maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. Bioinformatics. 2006;22:2688–2690.

112. Stephens PR, Wiens JJ. Explaining species richness from continents to communities: The time-for-speciation effect in emydid turtles. American Naturalist. 2003;161:112–128.

113. Strimmer K, Rambaut A. Inferring confidence sets of possibly misspecified gene trees. Proceedings of the Royal Society of London. Series B, Biological Sciences. 2002;269:137–142.

114. Swofford D. PAUP*. Phylogenetic analysis using parsimony (*and other methods), Sinauer. Sunderland, MA: 2002.

115. Tapponnier P, Mattauer M, Proust F, Cassaigneau C. Mesozoic ophiolites, sutures, and large-scale tectonic movements in Afghanistan. Earth and Planetary Science Letters. 1981;52:355–371.

116. Thomas DJ. Evidence for deep-water production in the North Pacific Ocean during the early Cenozoic warm interval. Nature. 2004;430:65–68.

117.	Townsend TM, Larson A, Louis E, Macey JR. Molecular phylogenetics of Squamata: The position of snakes, Amphisbaenians, and Dibamids, and the root of the Squamate tree. Systematic Biology. 2004;53:735–757.

118.	Uetz P. The original descriptions of reptiles. Zootaxa. 2010a;2334:59–68.

119.	Uetz P. The TIGR Reptile Database. 2010b. Retrieved 1 July, 2010, from http://www.reptile-database.org/

120.	Van Bocxlaer I, Loader SP, Roelants K, Biju SD, Menegon M, Bossuyt F. Gradual adaptation toward a range-expansion phenotype initiated the global radiation of toads. Science. 2010;327:679–682.

121.	Vanzolini PE. Geography of the South American Gekkonidae (Sauria) Arquivos de Zoologia (Sao Paulo) 1968;17:85–112.

122.	Vences M, Vieites DR, Glaw F, Brinkmann H, Kosuch J, Veith M, Meyer A. Multiple overseas dispersal in amphibians. Proceedings of the Royal Society Biological Sciences Series B. 2003;270:2435–2442.

123.	Vidal N, Hedges SB. The phylogeny of squamate reptiles (lizards, snakes, and amphisbaenians) inferred from nine nuclear protein–coding genes. Comptes Rendus Biologies. 2005;328:1000–1008.

124.	Vidal N, Azvolinsky A, Cruaud C, Hedges SB. Origin of tropical American burrowing reptiles by transatlantic rafting. Biology Letters. 2008;4:115–118.

125.	Vidal N, J M, M M, S D, R BW, R T, M V, A W, C C, B HS. Blindsnake evolutionary tree reveals long history on Gondwana. Biology Letters. 2010;6:558–561.

126.	Voelker G, Rohwer S, Outlaw DC, Bowie RCK. Repeated trans–Atlantic dispersal catalysed a global songbird radiation. Global Ecology and Biogeography. 2009;18:41–49.

127.	Walker TD, Valentine JW. Equilibrium models of evolutionary species diversity and the number of empty niches. 1984;124:887–899.

128.	Wallace AR. Tropical Nature and Other Essays. London: Macmillan and Co.; 1878.

129.	Weir JT. Divergent timing and patterns of species accumulation in lowland and highland Neotropical birds. Evolution. 2006;60:842–855.

130.	Weiss AJ, Hedges SB. Molecular phylogeny and biogeography of the Antillean geckos *Phyllodactylus wirshingi, Tarentola americana*, and *Hemidactylus haitianus* (Reptilia, Squamata) Molecular Phylogenetics and Evolution. 2007;45:409–416.

131.	Whiting AS, Sites JW, Pellegrino KCM, Rodrigues MT. Comparing alignment methods for inferring the history of the new world lizard genus *Mabuya* (Squamata: Scincidae) Molecular Phylogenetics and Evolution. 2006;38:719–730.

132.	Wiens JJ, Brandley MC, Reeder TW. Why does a trait evolve multiple times within a clade? Repeated evolution of snakelike body form in squamate reptiles. Evolution. 2006a;60:123–141.

133.	Wiens JJ, Graham CH, Moen DS, Smith SA, Reeder TW. Evolutionary and ecological causes of the latitudinal diversity gradient in hylid frogs: Treefrog trees unearth the roots of high tropical diversity. American Naturalist. 2006b;168:579–596.

134.	Wiens JJ. Global patterns of diversification and species richness in amphibians. American Naturalist. 2007;170:S86–S106.

135.	Wiens JJ, Sukumaran J, Pyron RA, Brown RM. Evolutionary and biogeographic origins of high tropical diversity in old world frogs (Ranidae) Evolution. 2009;63:1217–1231.

136.	Yoder AD, Burns MM, Zehr S, Delefosse T, Veron G, Goodman SM, Flynn JJ. Single origin of Malagasy Carnivora from an African ancestor. Nature. 2003;421:734–737.