

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 biogeographical scenario for the New World geckos. Patterns of New World gecko origins are consistent with almost every biogeographical 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.

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, 1969; Vanzolini, 1968; 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

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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 possess 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 & Alcalá, 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, 2009; McPeck & Brown, 2007), whereas 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 because of 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; McPeck & Brown, 2007). Knowledge of such a relationship in a clade can guide future research and help formulate testable ecological and biogeographical hypotheses.

We conducted a phylogenetic analysis of gekkotan lizards, including exemplars of all described New World genera, with the following objectives: (i) provide a phylogenetic hypothesis for geckos of the Western Hemisphere; (ii) 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 (iii) determine whether 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, Valencia, CA, USA). 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 phosphodiesterase 4 (*PDE4*). Primers, PCR conditions and sequencing conditions are detailed elsewhere (Bauer *et al.*, 2007; Gamble *et al.*, 2008a), and all PCRs 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 analysed 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 general time reversible (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 biogeographical 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 later (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 Akaike information criterion (AIC) as implemented in JMODELTEST (Posada, 2008). Calibration choice is described in the following text. We conducted three independent analyses of 10 000 000 generations each, logging trees every 1000 generations. Output was analysed 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.* (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 carried out 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 biogeographical 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 previously. The excluded calibrations were the following: (i) 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); (ii) a minimum age for the Gekkonoidea at 55 Ma using the oldest known fossils of hard-shelled gecko eggs from Wyoming (Hirsch, 1996); and (iii) 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: (iv) an exponential prior representing the minimum age for the Helodermatidae/Anguinae split using the fossil *Primaderma nessovi*, 99 Ma (Nydam, 2000); (v) 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); (vi) an exponential prior representing the divergence between the *Sphaerodactylus cinereus* group, represented in this study by *Sphaerodactylus elegans* (Hass, 1991), and its sister taxon was calibrated with amber-preserved *Sphaerodactylus* sp., 20 Ma (Kluge, 1995; Iturralde-Vinent & MacPhee, 1996); (vii) 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; Abdрахmatov *et al.*, 1996; Macey *et al.*, 1999). Finally, as mentioned previously (viii), we used a uniform prior to set the maximum age for squamates using the oldest known squamate fossil, *T. 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.

Biogeographical 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 biogeographical 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, 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 *Hemidactylus mabouia* from the analyses as they most likely arrived in the Americas via anthropogenic means (see Conclusions).

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* (Fig. S1; Table S1). 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.*, 2008a,b; 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.*, 2008a,b).

Phylogenetic hypothesis testing

We tested several *a priori* and *a posteriori* hypotheses related to biogeography, previously proposed phylogenetic hypotheses, and taxonomy (Table 1). The biogeographical hypotheses constrained closely related New World taxa as monophyletic. Monophyly in these clades could potentially result in simpler biogeographical 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* lineages, represented by *Hemidactylus brasiliensis* and *Hemidactylus 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.

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: (i) *T. americana* as the sister taxon to remaining *Tarentola* (Carranza *et al.*, 2000, 2002) and (ii) monophyly of *Saurodactylus*. Finally, monophyly of a *Homonota* + *Garthia* clade (Kluge, 1964,

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 maximum likelihood tree	-63 384.26043	n/a	n/a	n/a
<i>Saurodactylus</i> monophyly	-63 384.33134	-0.07090	No	0.5663
<i>Phyllopezus</i> monophyly	-63 385.24020	-0.97976	No	0.0451
<i>Tarentola americana</i> sister taxon to remaining <i>Tarentola</i>	-63 385.68739	-1.42696	No	0.2061
<i>Thecadactylus</i> forms clade with other New World Phyllodactylidae	-63 386.68409	-2.42366	No	0.0009
<i>Aeluroscalabotes</i> sister taxon to remaining Eublepharidae	-63 387.38857	-3.12814	No	0.0042
<i>Coleodactylus</i> monophyly	-63 393.88910	-9.62867	No	0.0093
<i>Hemidactylus brasiliensis</i> + <i>Hemidactylus palaichthus</i>	-63 398.20652	-13.94609	No	0.0000
<i>Garthia</i> + <i>Homonota</i>	-63 418.55371	-34.29328	Yes	0.0000

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 and 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	Citations
1	<i>Coleonyx</i>	74 (55–93)	Beringean landbridge	7	Grismer (1988); Jonniaux & Kumazawa (2008)
2	<i>Aristelliger</i>	68 (49–88)	Trans-Atlantic dispersal/North Atlantic land bridge	8	Gamble <i>et al.</i> (2008b)
3	<i>Coleodactylus</i> , <i>Gonatodes</i> , <i>Lepidoblepharis</i> , <i>Pseudogonatodes</i> & <i>Sphaerodactylus</i>	98 (82–114)	Gondwanan vicariance	152	Gamble <i>et al.</i> (2008b)
4	<i>Thecadactylus</i>	72 (58–87)	Trans-Atlantic dispersal/North Atlantic land bridge	2	This study
5	<i>Tarentola americana</i>	12 (7–17)	Trans-Atlantic dispersal	2	Carranza <i>et al.</i> (2000)
6	<i>Bogertia</i> , <i>Garthia</i> , <i>Gymnodactylus</i> , <i>Homonota</i> , <i>Phyllodactylus</i> & <i>Phyllopezus</i>	67 (53–81)	Trans-Atlantic dispersal/North Atlantic land bridge	71	This study
7	<i>Hemidactylus haitianus</i>	4 (1–8)	Anthropogenic dispersal	1	Carranza & Arnold (2006); Weiss & Hedges (2007)
8	<i>Hemidactylus mabouia</i>	2.5 (1–5)	Anthropogenic dispersal	1	Kluge (1969); Carranza & Arnold (2006)
9	<i>Hemidactylus palaichthus</i>	23 (16–30)	Trans-Atlantic dispersal	2	Carranza & Arnold (2006)
10	<i>Hemidactylus brasiliensis</i>	15 (9–21)	Trans-Atlantic dispersal	1	Carranza & Arnold (2006)
11	<i>Lygodactylus klugei</i>	25 (16–35)	Trans-Atlantic dispersal	2	This study

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 biogeographical calibrations (Fig. 1; Table 2; Fig. S3). Fossil cross-validation rejected the use of three additional calibrations (Fig. S2). 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 (Fig. S3) showed the sequence data had a strong influence on clade age estimates and divergence times were not overwhelmed by our calibration priors.

Biogeographical analyses

We recovered multiple independent origins of New World geckos (Figs 1 and 2; Table 2; Figs S3–S6). 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 biogeographical areas as a binary character, e.g. Old World and New World, or as five biogeographical 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 ($-\ln L = 50.81168372$) had a rate of 0.00213. The asymmetric 2-rate model ($-\ln L = 49.76389421$) 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 $-\ln L = 1.047789$, d.f. = 1, $P = 0.1477$).

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) (Fig. S7). Two of these entries into the New World, represented by *H. mabouia* and *H. haitianus*, likely resulted from human-mediated dispersal (see Conclusions).

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;

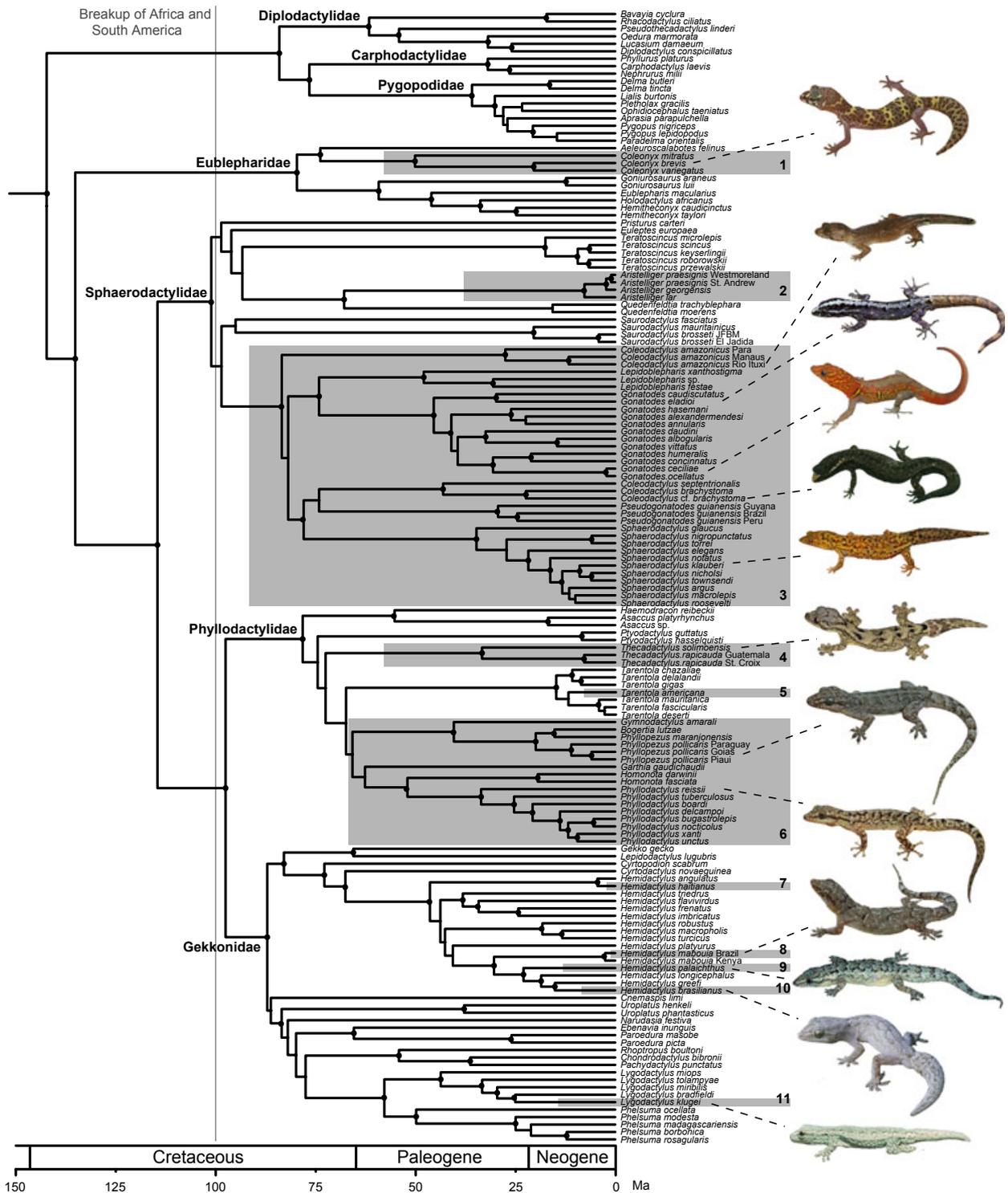


Fig. 1 Time-calibrated gecko phylogeny using a Bayesian uncorrelated relaxed clock, with five fossil and biogeographic calibrations. Grey boxes indicate New World species and clade numbers are referred to in Table 1. Black circles at nodes indicate clades with maximum likelihood bootstrap support > 70.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

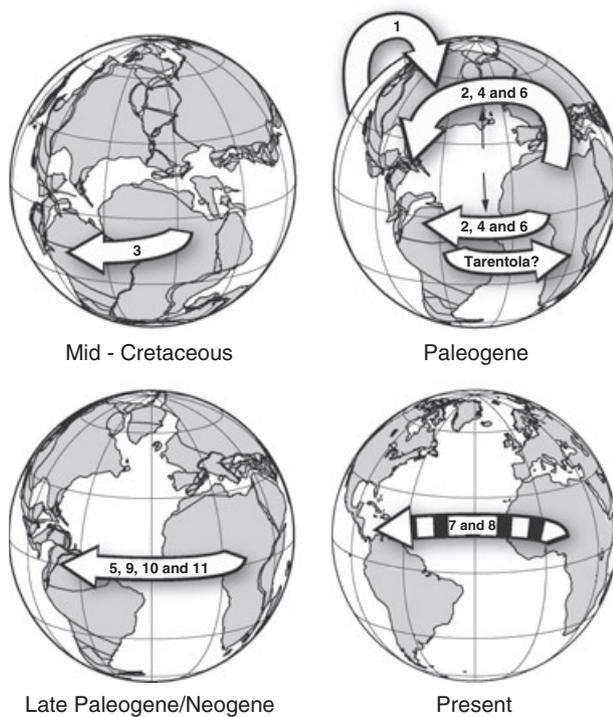


Fig. 2 Biogeographical hypotheses for the origins of New World geckos at four different historical periods. Numbers inside lines refer to New World clades in Fig. 1. Dashed line indicates likely human-mediated dispersal.

$r^2 = 0.5972$; $P = 0.0146$; Fig. 3) and nonparametric Spearman-rank correlation ($\rho = 0.7050$; $P = 0.0339$). Older New World clades had more species overall than more recently arrived lineages.

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.*, 2008a,b). 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

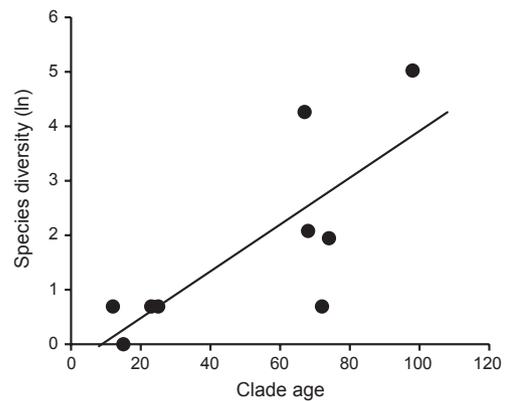


Fig. 3 The relationship between clade age and log-transformed species richness for each New World gecko lineage. Clade age is based on the stem age of each New World lineage calculated as the time of divergence with its closest Old World relative.

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 synonymized 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 regard to other described genera. Exemplars of *Coleodactylus 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.* (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: *C. 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.* (2008) and 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 nonparametric 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, 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 and 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 noneublepharid, 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 Phyllocladylidae made it difficult to distinguish among several alternative biogeographical hypotheses surrounding the origin of its three New World lineages. Given our optimal topology, two equally likely biogeographical 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. Whereas 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 Phyllocladylidae, and such trips could be accomplished in a matter of weeks (Houle, 1998, 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.

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 *Lygodactylus 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*

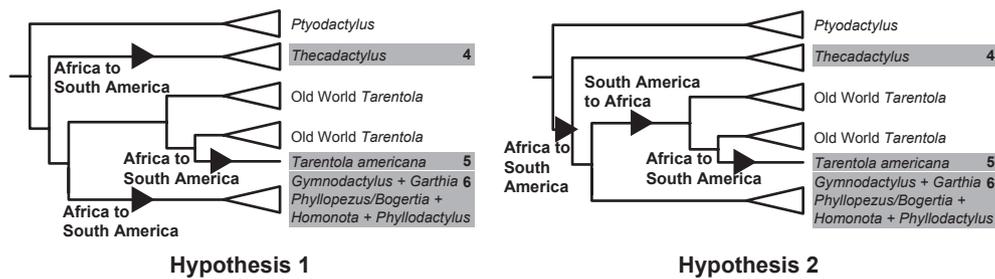


Fig. 4 Two equally parsimonious biogeographical hypotheses for the origins of New World Phyllodactylidae. Arrows indicate dispersal events. Grey boxes enclose New World species and clade numbers are referred to in Fig. 1.

(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 & Arnold (2006) provided convincing evidence that the clades containing *H. palaichthus* and *H. brasiliensis* resulted from an ancient, trans-Atlantic dispersal. Applying a sequence evolution rate of 1.35–3.2%/my to their data, Carranza & Arnold (2006) hypothesized that the ancestors of *H. palaichthus* and *H. brasiliensis* dispersed from the Old World to the Neotropics, at most between 6 and 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 *H. mabouia* and *H. haitianus*/*Hemidactylus 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.*, 2010), and we also found little genetic variance between trans-Atlantic exemplars within these two species. *Hemidactylus haitianus* was recently synonymized 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.*, 2010). A full revision of this group is warranted before such nomenclatural changes should be considered.

North and South America have quite different biogeographical 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 *Coloonyx*, which, as mentioned previously, arrived in North America via a Beringian 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, 2009; McPeck & Brown, 2007). Indeed, in many animal lineages, it appears that clade age alone is a sufficient explanation for species richness (McPeck & 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 because of 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 Fig. 3. These are the four most recently arrived New World gecko lineages represented in our dataset by: *T. americana*; *H. palaichthus*; *H. brasili-anus*; and *L. kluzei* (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 *Phyllo-lopezus* (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.

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Supporting information

Additional Supporting Information may be found in the online version of this article:

Figure S1 Maximum likelihood tree of gekkotan taxa from the RAXML analysis.

Figure S2 Results of fossil cross-validation showing the effect of removing individual calibrations on the difference between fossil age and estimated molecular age.

Figure S3 Time-calibrated phylogeny of geckos with 95% credibility intervals of the posterior divergence times and joint prior divergence times.

Figure S4 Ancestral area reconstruction using parsimony and distributions coded as binary characters.

Figure S5 Ancestral area reconstruction using maximum likelihood with distributions coded as a binary character.

Figure S6 Ancestral area reconstruction using maximum likelihood with distributions coded as one of five biogeographic regions.

Figure S7 The number of biogeographical transitions between the Old World and New World calculated for 5000 Bayesian trees using parsimony.

Table S1 Details of material examined.

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