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Evidence for Gondwanan Vicariance In an Ancient Clade of Gecko Lizards

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Abstract

Aim

Geckos (Reptilia: Squamata), due to their great age and global distribution, are excellent candidates to test hypotheses of Gondwanan vicariance against post-Gondwanan dispersal. Our aims are: to generate a phylogeny of the sphaerodactyl geckos and their closest relatives; evaluate previous phylogenetic hypotheses of the sphaerodactyl geckos with regard to the other major gecko lineages; and to use divergence date estimates to inform a biogeographical scenario regarding Gondwanan relationships and assess the roles of vicariance and

dispersal in shaping the current distributions of the New World sphaerodactyl geckos and their closest Old World relatives.

Location

Africa, Asia, Europe, South America, Atlantic Ocean.

Methods

We used parsimony and partitioned Bayesian methods to analyse data from five nuclear genes to generate a phylogeny for the New World sphaerodactyl geckos and their close Old World relatives. We used dispersal–vicariance analysis to determine ancestral area relationships among clades, and divergence times were estimated from the phylogeny using nonparametric rate smoothing.

Results

We recovered a monophyletic group containing the New World sphaerodactyl genera, *Coleodactylus*, *Gonatodes*, *Lepidoblepharis*, *Pseudogonatodes* and *Sphaerodactylus*, and the Old World Gekkotan genera *Aristelliger*, *Euleptes*, *Quedenfeldtia*, *Pristurus*, *Saurodactylus* and *Teratoscincus*. The dispersal–vicariance analysis indicated that the ancestral area for this clade was North Africa and surrounding regions. The divergence between the New World spaherodactyl geckos and their closest Old World relative was estimated to have occurred *c*. 96 Myr BP.

Main conclusions

Here we provide the first molecular genetic phylogenetic hypothesis of the New World sphaerodactyl geckos and their closest Old World relatives. A combination of divergence date estimates and dispersal–vicariance analysis informed a biogeographical scenario indicating that the split between the sphaerodactyl geckos and their African relatives coincided with the Africa/South America split and the opening of the Atlantic Ocean. We resurrect the family name Sphaerodactylidae to represent the expanded sphaerodactyl clade.

Introduction

Vicariance hypotheses of Gondwanan fragmentation have been the prevailing explanation for the distributions of plant and animal taxa in the Southern Hemisphere since the widespread acceptance of plate tectonics in the late, 1960s (**Bauer, 1993**; **Sanmartín & Ronquist, 2004**). Recently, several molecular studies comparing the timing of cladogenic and vicariant events have shown that oceanic dispersal may be more common than once thought by many biogeographers because the estimated time of divergence between focal taxa occurred after the vicariant event (**Lundberg, 1993**; **Raxworthy *et al.*, 2002**; **Nagy *et al.*, 2003**; **Vences *et al.*, 2004**; **Whiting *et al.*, 2006**). The recognition that oceanic dispersal may be the most important factor in the distributions of many animal taxa has been called a 'counter-revolution' in biogeography (**de Queiroz, 2005**) and has caused many biogeographers to rethink some long-held hypotheses. The same phylogenetic tools that have allowed biogeographers to reject Gondwanan vicariance for many taxonomic groups can conversely reject dispersalist hypotheses in favour of vicariance. The combination of robust, multi-gene phylogenies, relaxed dating techniques, and event-based methods of biogeographical reconstruction should not be seen as favouring one paradigm over another (preferring dispersal over vicariance), but should instead be viewed as a major step forward in biogeographical research as a whole.

The distribution of gecko lizards on continents in the southern Hemisphere is presumed to have been heavily influenced by Gondwanan vicariance (**Cracraft, 1974**; **Bauer, 1990, 1993**) and the ancient origin of geckos 165–180 Myr BP (**Kluge, 1987**) makes this a plausible scenario. While overseas dispersal is likely for some genera of New World geckos (**Kluge, 1969**; **Carranza *et al.*, 2000**), the majority of South American gecko species are thought to be closely related to African taxa, with distributions shaped by the opening of the Atlantic Ocean

100–120   Myr BP (**Bauer, 1993**; **Hay _et al._, 1999**). There are few well resolved phylogenies containing both New World and Old World gecko genera, which has made testing hypotheses of Gondwanan vicariance impossible. The matter has been complicated by the fact that some lineages of geckos are perhaps the most capable overseas dispersalists among non-volant, terrestrial vertebrates, which best explains their widespread distribution on volcanic and coral islands. Geckos possess two main characteristics that make them amenable to overseas dispersal: eggs that are resistant to desiccation and temporary immersion in sea water (**Brown & Alcala, 1957**); and a well developed digital adhesive mechanism (**Russell, 2002**; **Vanhooydonck _et al._, 2005**) that allows individuals to hold tightly to flotsam. Overseas dispersal is the best explanation for the distribution of geckos in the Pacific Ocean (**Moritz _et al._, 1993**), Indian Ocean (**Austin _et al._, 2004**) and Caribbean (**Hedges, 1996**). Trans-Atlantic dispersal from Africa to the West Indies and South America is also strongly supported by molecular phylogenetic data in the gecko genera _Tarentola_ and _Hemidactylus_ (**Carranza _et al._, 2000**; **Carranza & Arnold, 2006**).

The Sphaerodactylinae, a monophyletic subfamily endemic to the New World, seems to be closely related to the African and Arabian genus _Pristurus_ (**Kluge, 1987, 1995**), and offers the only phylogenetically informed hypothesis of trans-Atlantic relationships above the generic level in geckos (**Bauer, 1993**). The subfamily Sphaerodactylinae (_sensu_**Han _et al._, 2004**), which we refer to hereafter as 'sphaerodactyl geckos', comprise 145 species in five genera, _Sphaerodactylus, Coleodactylus, Lepidoblepharis, Pseudogonatodes_ and _Gonatodes_, all of which are confined to the Western Hemisphere. All species are small –_Sphaerodactylus ariasae_ is the smallest terrestrial amniote (**Hedges & Thomas, 2001**) – and most are diurnal (**Werner, 1969**; **Vitt _et al._, 2005**). The sphaerodactyl geckos posses many morphological synapomorphies, including a short or absent maxillary process of the palatine, a long, deep choanal canal (**Kluge, 1995**), a reduced hypoischium (**Noble, 1921**; **Kluge, 1995**), and lack of beta generation glands (**Kluge, 1983, 1995**). **Underwood (1954)** was the first to place the five genera of sphaerodactyl geckos into their own family, the Sphaerodactylidae. **Kluge (1967)** maintained this grouping, although he changed the taxonomic rank to subfamily and hypothesized that the Sphaerodactylinae were the sister clade to the Gekkoninae. **Kluge (1987)** offered a revised hypothesis using a cladistic analysis of 44 morphological characters and found strong affinities between the sphaerodactyl geckos and the North African genus _Pristurus_. **Kluge's (1995)** cladistic analysis of spaherodactyl geckos reaffirmed the existence of the sphaerodactyl + _Pristurus_ clade and utilized as outgroups the gekkonid genera _Cnemaspis_, _Narudasia_, _Saurodactylus_ and _Quedenfeldtia_, which were assumed to be closely related on the basis of the absence of cloacal sacs and bones (**Arnold, 1990a,b, 1993**; **Kluge & Nussbaum, 1995**). Molecular phylogenetic analyses have recovered sphaerodactyl exemplars as sister taxa to the remaining Gekkonidae either by themselves (**Han _et al._, 2004**) or with the central Asian genus _Teratoscincus_ (**Townsend _et al._, 2004**). While the monophyly of the sphaerodactyl geckos has never been in doubt, its placement with relation to the remaining Gekkonidae is still in question.

Geckos, owing to their small size and light build, are poorly represented in the fossil record (**Evans, 2003**), and the fragmentary nature of most existing gekkotan fossils makes identification below the family level all but impossible. Several Jurassic fossils, such as _Ardeosaurus_, _Bavarisaurus_ and _Eichstaettisaurus_, are of questionable gekkotan affinity (**Estes, 1983**; **Kluge, 1987**; **Evans, 2003**; **Conrad & Norell, 2006**). Cretaceous fossils such as _Hoburogecko_ and _Gobekko_ are most certainly geckos, but their relationships to fossil and extant species are unknown (**Alifanov, 1989**; **Borsuk-Bialynicka, 1990**; **Conrad & Norell, 2006**). Similarly, the Eocene _Rhodanogekko_, _Cadurcogekko_, and the amber-preserved _Yantarogekko_ remain _incertae sedis_ (**Hoffstetter, 1946**; **Bauer _et al._, 2004**). There are only a handful of fossil geckos that have been assigned to extant clades and can be used in a calibrated dating analysis, and all are from the Miocene. They are: _Pygopus hortulanus_ from northern Australia, several species of _Euleptes_ from Europe, and several amber-preserved _Sphaerodactylus_ from the Dominican Republic. The existence of fossil _Sphaerodactylus_ makes the sphaerodactyl clade an ideal group among geckos for dating techniques that utilize fossil calibrations.

Here we provide the first molecular genetic phylogenetic hypothesis of the sphaerodactyl geckos. Our objectives are to generate a phylogeny of the Sphaerodactyl geckos and their closest relatives, evaluate previous phylogenetic hypotheses of the sphaerodactyl geckos with regard to the other major gecko lineages, and use divergence date estimates to inform a biogeographical scenario regarding the possible Gondwanan relationships between the New World sphaerodactyl geckos and their closest Old World relatives. Specifically, we wish to test the hypothesis that the distribution of sphaerodactyl geckos was influenced by Gondwanan vicariance. Evidence in support of a vicariance hypothesis would be an estimated divergence date of the sphaerodactyl geckos from their closest Old World relative *c*. 100 Myr BP or greater. An estimated divergence date substantially less than 100 Myr BP would lead us to reject the vicariance hypothesis and a dispersal hypothesis would be favoured by default.

Materials and methods

Taxon sampling and DNA sequencing

We sampled representatives of each of the five genera of sphaerodactyl geckos, as well as genera previously hypothesized to be closely related to them –
Pristurus, *Cnemaspis*, *Narudasia*, *Saurodactylus* and *Quedenfeldtia* (**Kluge, 1995**). Representative taxa from the other major gekkotan clades were also included. The basal position of geckos in relation to other squamates (**Townsend *et al.*, 2004**; **Vidal & Hedges, 2005**) suggested that any non-gekkotan squamates would be appropriate outgroups. The skink, *Trachydosaurus rugosus*, and the amphisbaenid, *Rhineura floridana*, were therefore included as outgroups. Locality data, museum catalogue numbers or field numbers, and GenBank accession numbers for sampled taxa are listed in **Table 1**.

Table 1. Details of material examined.

Species	Specimen ID	Locality	GenBank accession numbers				
			RAG1	*RAG2*	*c-mos*	*ACM4*	*PDC*
Eublepharis macularius	TG 00081	Pakistan	–	EF534942	EF534900	EF534857	–
Eublepharis macularius	JS2	Pakistan	EF534776	–	–	–	EF534816
Coleonyx variegatus	CAS 205334	California, USA	EF534777	EF534943	EF534901	EF534858	EF534817
Rhacodactylus ciliatus	TG 00080	New Caledonia	–	EF534944	EF534902	EF534859	–
Rhacodactylus ciliatus	AMS R 146595	Rivière Bleue, New Caledonia	EF534778	–	–	–	EF534818
Oedura marmorata	AMS 143861	Queensland, Australia	EF534779	EF534945	EF534903	EF534860	EF534819
Nephrurus milii	AMB 499	Western Australia, Australia	EF534780	EF534946	EF534904	EF534861	EF534820
Carphodactylus laevis	AMS 143258	Queensland, Australia	EF534781	EF534947	EF534905	EF534862	EF534821
Lialis burtonis	TG 00078	Irian Jaya, Indonesia	EF534782	EF534948	EF534906	EF534863	EF534822
Pygopus nigriceps	AMB 53	Northern Territory, Australia	EF534783	EF534949	EF534907	EF534864	EF534823

Pseudogonatodes guianensis	KU 222142	Loreto, Peru	EF534784	EF534950	EF534908	EF534865	EF534824
Sphaerodactylus roosevelti	CAS 198428	Bahia de la Ballena, Puerto Rico	EF534785	EF534951	EF534909	EF534866	EF534825
Sphaerodactylus ocoae	CAS 198444	nr Santo Domingo, Dominican Republic	EF534786	EF534952	EF534910	EF534867	EF534826
Sphaeodactylus nigropunctatus	FLMNH 144010	Florida, USA	–	EF534953	EF534911	EF534868	EF534827
Sphaerodactylus elegans	YPM 14795	Florida, USA	EF534787	EF534954	EF534912	EF534869	EF534828
Sphaerodactylus torrei	JB 34	Cuba	EF534788	EF534955	EF534913	EF534870	EF534829
Lepidoblepharis sp.	KU 218367	Manabi, Ecuador	EF534789	EF534956	EF534914	EF534871	EF534830
Lepidoblepharis xanthostigma	MVZ 171438	Limon, Costa Rica	EF534790	EF534957	EF534915	EF534872	EF534831
Coleodactylus septentrionalis	LSUMZ H-12351	Roraima, Brazil	EF534791	EF534958	EF534916	EF534873	EF534832
Coleodactylus brachystoma	MZUSP 92569	Piauí, Brazil	EF534792	EF534959	EF534917	EF534874	EF534833
Gonatodes daudinii	JB 38	Union, St Vincent and Grenadines	EF534793	EF534960	EF534918	EF534875	EF534834
Gonatodes annularis	ROM 22961	Guyana	–	EF534961	EF534919	EF534876	–
Gonatodes annularis	No ID	French Guiana	EF534794	–	–	–	EF534835
Gonatodes caudiscutatus	KU 218359	Limon, Ecuador	EF534795	EF534962	EF534920	EF534877	EF534836
Gonatodes hasemani	UNIBAN 1649	Rondônia, Brazil	–	EF534963	EF534921	EF534878	EF534837
Gonatodes humeralis	MF 19492	Ecuador	EF534796	EF534964	EF534922	EF534879	EF534838
Gonatodes albogularis	MVZ 204073	Limon, Costa Rica	EF534797	–	–	–	EF534839
Gonatodes albogularis	KU 289808	San Salvador, El Salvador	–	EF534965	EF534923	EF534880	–
Gonatodes sp.	BPN 1303	Imbaimadai, Guyana	EF534798	EF534966	EF534924	EF534881	EF534840
Teratoscincus roborowskii	TG 00070	China	EF534799	EF534967	EF534925	EF534882	EF534841
Teratoscincus microlepis	TG 00074	Pakistan	EF534800	EF534968	EF534926	EF534883	EF534842
Teratoscincus scincus	JFBM 14252	Turkmenistan	–	EF534969	EF534927	EF534884	–
Teratoscincus keyserlingii	CAS 228808	Yazd Province, Iran	EF534801	–	–	–	EF534843
Saurodactylus brosseti	TG 00082	Morocco	EF534802	EF534970	EF534928	EF534885	EF534844
Pristurus carteri	TG 00083	Yemen	EF534803	EF534971	EF534929	EF534886	EF534845
Quedenfeldtia trachyblephara	MVZ 178121	Oukaimeden, Morocco	EF534804	EF534972	EF534930	EF534887	EF534846

Aristelliger lar	JB 01	Dominican Republic	EF534805	EF534973	EF534931	EF534888	EF534847
Euleptes europaea	No number	Liguria, Italy	EF534806	EF534974	EF534932	EF534889	EF534848
Phyllodactylus xanti	ROM 38490	Baja California Sur, Mexico	EF534807	EF534975	EF534933	EF534890	EF534849
Narudasia festiva	AMB 3243	Narudas, Namibia	EF534808	EF534976	EF534934	EF534891	EF534850
Cnemaspis limi	LLG 6267	Pulau Tioman, Malaysia	EF534809	EF534977	EF534935	EF534892	EF534851
Rhoptropus boultoni	CAS 214713	Twyfelfontein, Namibia	EF534810	EF534978	EF534936	EF534893	EF534852
Phelsuma madagascariensis	FG/MV 2002.797	Manongarivo, Madagascar	EF534811	EF534979	EF534937	EF534894	AB081507
Lepidodactylus lugubris	AMB 4111	Kirimati, Kiribati	EF534812	EF534980	EF534938	EF534895	EF534853
Gekko gecko	No ID	unknown	EF534813	–	–	–	EF534854
Gekko gecko	TG 00079	Indonesia	–	EF534981	EF534939	EF534896	–
Hemidactylus frenatus	TG 00088	Indonesia	–	EF534982	EF534940	EF534897	–
Hemidactylus frenatus	AMB 7411	Pidenipitiya, Sri Lanka	EF534814	–	–	–	EF534855
Trachydosaurus rugosus	JFBM 13685	New South Wales, Australia	EF534815	EF534983	EF534941	EF534898	EF534856
Rhineura floridana	FLMNH 141814	Florida, USA	AY662618	DQ119631	AY487347	EF534899	–

Museum abbreviations follow Leviton *et al.* (1985) except as follows: AMB, Aaron M. Bauer; TG, Tony Gamble; JB, Jon Boone; BPN, Brice Noonan; FG/MV, Frank Glaw/Miguel Vences; LLG, L. Lee Grismer; MF, Mike Forstner; JS, Jay Sommers; UNIBAN, Universidade Bandeirantes de São Paulo.

Genomic DNA was extracted from muscle, liver or tail clips using the DNeasy Blood and Tissue kit (Qiagen, Valencia, CA, USA). PCR was used 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*) and phosducin (*PDC*). Primers used are listed in **Table 2**. PCR products were purified using Exonuclease I and Shrimp Alkaline Phosphatase (**Hanke & Wink, 1994**), the QIAquick PCR Purification kit (Qiagen), or AMPure magnetic bead solution (Agencourt Bioscience, Beverly, MA, USA) following the manufacturer's recommendations. Sequencing was performed using Big Dye (Perkin Elmer, Waltham, MA, USA) or DYEnamicET Dye Terminator Kit (GE Healthcare, Fairfield, CT, USA) terminator cycle sequencing with CleanSeq magnetic bead solution purification (Agencourt Bioscience) on an ABI 3730 × l at the Advanced Genetic Analysis Center, University of Minnesota, MN, USA or an ABI 3700 automated sequencer at Villanova University, PA, USA. Sequences were checked for accuracy by incorporating negative controls and sequencing complementary strands and assembled using SEQUENCHER ver. 4.2 (Gene Codes, Ann Arbor, MI, USA).

Table 2. Primers used in this study.

Primer name	Primer sequence (5′–3′)	Source
RAG1		
G396	TCTGAATGGAAATTCAAGCTGTT	Groth & Barrowclough (1999)
G397	AAAGGTGGCCGACCGAGGCAGCATC	Groth & Barrowclough (1999)
F700	GGAGACATGGACACAATCCATCCTAC	Bauer *et al.* (2007)
R700	TTTGTACTGAGATGGATCTTTTTGCA	Bauer *et al.* (2007)
RAG2		
EM1-F	TGGAACAGAGTGATYGACTGCAT	This study

EM1-R	ATTTCCCATATCAYTCCCAAACC	This study
PY1-F	CCCTGAGTTTGGATGCTGTACTT	This study
PY1-R	AACTGCCTRTTGTCCCCTGGTAT	This study
c-mos		
G73	GCGGTAAAGCAGGTGAAGAAA	Saint *et al.* (1998)
G74	TGAGCATCCAAAGTCTCCAATC	Saint *et al.* (1998)
FU-F	TTTGGTTCKGTCTACAAGGCTAC	This study
FU-R	AGGGAACATCCAAAGTCTCCAAT	This study
ACM4		
tg-F	CAAGCCTGAGAGCAARAAGG	This study
tg-R	ACYTGACTCCTGGCAATGCT	This study
PDC		
PHOF2	AGATGAGCATGCAGGAGTATGA	Bauer *et al.* (2007)
PHOR1	TCCACATCCACAGCAAAAAACTCCT	Bauer *et al.* (2007)

Sequences were aligned using T-COFFEE (**Notredame *et al.*, 2000**). Although this method is computationally complex and time-consuming, it minimizes the 'local minimum' errors of CLUSTAL (e.g. misaligned base pairs or whole domains) by simultaneously finding the multiple alignment that is most consistent with a set of pairwise alignments between the sequences. This is accomplished through computations of global and pairwise 'libraries' that allow information from all of the sequences to be considered during each alignment step, not just those being aligned in one particular step (**Notredame *et al.*, 2000**; **Higgins, 2003**). All sequences were translated to amino acids using MACCLADE ver. 4.08 (**Maddison & Maddison, 1992**) to confirm alignment and gap placement.

Phylogenetic analyses

Maximum parsimony analysis was conducted using heuristic search algorithms in PAUP* ver. 4.0b10 (**Swofford, 2002**) with equally weighted and unordered characters and with tree bisection–reconnection branch swapping. Nonparametric bootstrapping (**Felsenstein, 1985**) using 100 pseudoreplicates was performed to assess nodal support.

Bayesian inference phylogenetic analyses were conducted using MRBAYES ver. 3.1.2 (**Huelsenbeck & Ronquist, 2001**). All analyses began with a random starting tree, were run for 2,000,000 generations and were sampled every 100 generations. Convergence was checked by importing the trace files (p files) from the MRBAYES output to the computer program TRACER ver. 1.3 (**http://beast.bio.ed.ac.uk**), which plots the likelihood values against generation number. 'Burn in' trees (2000) were discarded and the remaining samples were used to estimate the posterior probability values, branch lengths and topology. The Akaike information criterion (AIC) has been shown to have many advantages over the likelihood ratio test in selecting the best-fit model of nucleotide substitution (**Posada & Buckley, 2004**), and we used the AIC as implemented in MRMODELTEST ver. 2.2 (**Nylander, 2004**) to estimate the best-fit model of nucleotide substitution for each data partition.

Combining data sets, even heterogeneous data sets, into a single phylogenetic analysis can often increase phylogenetic accuracy (**Kluge, 1989**; **Rokas *et al.*, 2003**). That said, it is important to find the best model for each subset of data to minimize systematic error (**Bull *et al.*, 1993**; **Wilgenbusch & de Queiroz, 2000**; **Lemmon & Moriarty, 2004**; **Brandley *et al.*, 2005**). Proper phylogenetic analysis of partitioned data should fit an appropriate model of molecular evolution to each subset of the larger data set. The subset of data can be based on data type (morphological or molecular data), gene function (protein-coding or ribosomal genes), genomic affiliation (nuclear or organelle genome), or some structural or positional characteristic (codon position, intron or exon, or, in the case of ribosomal genes, secondary structure). Some method of evaluating alternative partitioning strategies should be used to ensure that the model is not over- or under-parameterized. We used Bayes factors to determine the most appropriate strategy for partitioning the data. Bayes factors are a way of summarizing the evidence provided by the data for one hypothesis, described by a model, over another hypothesis (**Kass & Raftery, 1995**). Bayes factors, like frequentist statistics, can reject one hypothesis over another but, unlike traditional hypothesis testing, where the focus is on rejecting the null hypothesis, Bayes

factors can also provide evidence in support of a hypothesis (**Kass & Raftery, 1995**). Bayes factors were computed as the difference between the harmonic mean likelihoods of the more complex partitioning strategy (T_0) and the simpler portioning strategy (T_1) (**Nylander *et al.*, 2004**; **Brandley *et al.*, 2005**). We considered hypotheses with 2 ln Bayes factors with a value > 10 as very strongly supported (**Kass & Raftery, 1995**). Four different data-partitioning strategies were examined: all data combined (one partition), partitioned by gene (five partitions), partitioned by codon across the entire data set (three partitions), and partitioned by codon for each gene individually (15 partitions).

Dating phylogenies

The Bayesian phylogeny was tested for departure from a molecular clock. The Bayes tree using the best-fit partitioning strategy was constrained to evolve in a clock-like manner in MRBAYES and compared with the unconstrained tree using Bayes factors.

Absolute ages of nodes can be estimated directly if a phylogeny is clock-like, but non-clock-like phylogenies require a relaxed clock approach to dating nodes. We estimated divergence times by using nonparametric rate smoothing (**Sanderson, 1997**) with the Powell algorithm and a cross-validation analysis as implemented in the program r8s (**Sanderson, 2003**). Sampling confidence intervals for inferred divergences were obtained by reanalysing 100 bootstrap replicates of the complete data set as described in the r8s manual.

Several calibration points were used in the r8s analysis. The fossils *Euleptes* sp. (**Mueller & Moedden, 2001**) and *Euleptes gallica* (**Mueller, 2001**) were used to constrain the node containing *Euleptes* and its sister clade to a minimum of 22.5 Myr BP (**Agustí *et al.*, 2001**). The amber-preserved *Sphaerodactylus* sp. (**Kluge, 1995**) and *Sphaerodactylus dommeli* (**Böhme, 1984**) were used to constrain the node containing *Sphaerodactylus elegans* and its sister clade to a minimum of 23 Myr BP (**Grimaldi, 1995**).

Two nodes were fixed using biogeographical data. First was the *Teratoscincus scincus–Teratoscincus roborowskii* split (**Macey *et al.*, 1999**) caused by the Tien Shan–Pamir uplift 10 Myr BP (**Tapponier *et al.*, 1981**; **Abdrakhmatov *et al.*, 1996**). Second was the split between *Teratoscincus microlepis* and the remaining *Teratoscincus* species (**Macey *et al.*, 2005**) fixed at 20 Myr BP with the rise of the Hindu Kush (**Searle, 1991**).

Hypothesis testing

Several prior phylogenetic analyses have included the sphaerodactyl clade and related taxa. We used Bayes factors, as described above, to evaluate four of these alternative topological hypotheses (**Fig. 1**). Constrained trees were generated in MRBAYES under the best-fit partition strategy and the same parameters as stated previously. The first alternative hypothesis (H_1) tested whether the genus *Pristurus* was the sister group to the sphaerodactyl clade (**Kluge, 1987, 1995**). The second alternative hypothesis (H_2) tested the phylogenetic position of the genus *Teratoscincus*. **Kluge (1987)** suggested that *Teratoscincus* was the sister group to the remaining Gekkonidae, and erected the subfamily Teratoscincinae to reflect this relationship. The third alternative hypothesis (H_3) examined the relationship of the genus *Gonatodes* in relation to the remaining members of the sphaerodactyl clade. Several authors have suggested that *Gonatodes* is the most basal member of the sphaerodactyl clade due to the lack of an ungual sheath, a series of scales that cover the claw on the digits of sphaerodactyl geckos (**Vanzolini, 1968**; **Russell, 1972**; **Kluge, 1995**). The fourth alternative hypothesis (H_4) looked at the relationship between the sphaerodactyl clade and several genera that have been hypothesized as closely related and that were used by **Kluge (1995)** as outgroups. These allied genera included the previously mentioned *Pristurus* (**Kluge, 1987, 1995**). We also included the North African genera *Quedenfeldtia* and *Saurodactylus* and the Southern African genus *Narudasia*, which, along with *Pristurus* and the sphaerodactyl clade, lack cloacal bones and sacs (**Kluge, 1982**; **Kluge & Nussbaum, 1995**).

Finally, we included the genus *Cnemapsis*, which occurs in central and east Africa, India, Sri Lanka and Southeast Asia. *Cnemaspis* was at one time synonymized with the sphaerodactyl genus *Gonatodes* (**Boulenger, 1885**), and **Russell (1972)** asserted that the two genera were closely related.
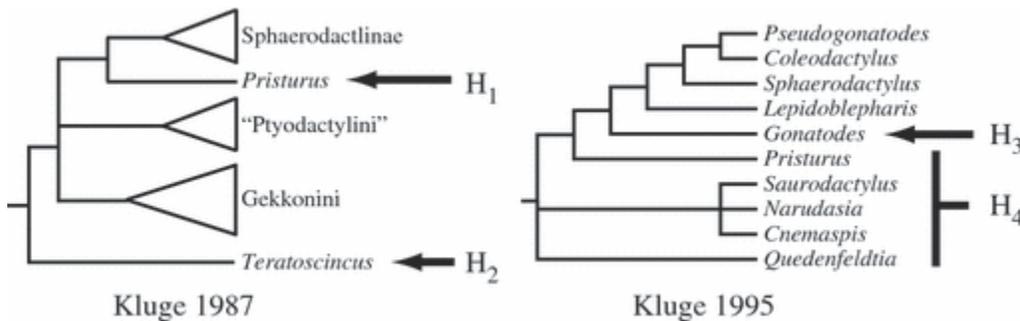

Figure 1 Previous phylogenetic hypotheses of Gekkotan lizards with special emphasis on the Sphaerodactylinae and allied taxa. Modified from **Kluge (1987, 1995)**. Alternative phylogenetic hypotheses tested in this paper are indicated with arrows.

Biogeography

We examined the biogeography of the sphaerodactyl geckos and their closest relatives using dispersal/vicariance analysis (DIVA ver. 1.1; **Ronquist, 1996, 1997**). DIVA assigns a cost to possible biogeographical events such as vicariance (cost = 0), dispersal (cost = 1) and extinction (cost = 1), and optimizes the area distributions on a phylogeny. Because DIVA requires fully bifurcated trees, we ran analyses on all possible fully bifurcated trees individually and summarized the results. Species were placed in one of three biogeographical areas: the sphaerodactyl geckos and *Aristelliger* in the Western Hemisphere; *Quedenfeldtia, Pristurus, Euleptes* and *Saurodactylus* in an area representing North Africa, the Mediterranean region and the Arabian Peninsula; and *Teratoscincus* in central and south Asia.

There are limitations surrounding DIVA analyses, such as decreased reliability in ancestral area reconstructions as you reach the root of the tree, and the general trend to find widespread ancestors (**Sanmartín, 2003**) and we are aware there are many other methods of analysing species distributions (reviewed by **Posadas *et al.*, 2006**). Given our data, using a method that excluded phylogenetic information or either vicariance or dispersal would be biologically unrealistic. Event-based analyses, such as DIVA, which are modelled on biogeographical processes such as vicariance, dispersal and extinction, require no *a posteriori* explanations and have been shown to be biologically reasonable under a variety of circumstances (**Zink *et al.*, 2000**; **Sanmartín *et al.*, 2001**; **Xiang & Soltis, 2001**; **Wiens *et al.*, 2006a).**

Results

Phylogenetic analyses

We obtained sequence data for all taxa and genes except *PDC* for the amphisbaenid outgroup *R. floridana* and *RAG1* for *Sphaerodactylus nigropunctatus* and *Gonatodes hasemani*. *Post hoc* identification of the *Teratoscincus* specimen CAS 228808 indicated that it was *T. keyserlingii*, resulting in a chimeric sequence for what we have labelled *T. scincus* on our phylogenies. This should not affect the results presented here, given that *T. scincus* and *T. keyserlingii* are sister species (**Macey *et al.*, 2004**) and that phylogenetic and molecular dating methods appear to retain their accuracy when chimeric sequences are used (**Scally *et al.*, 2002**; **Van Rheede *et al.*, 2006**). There were 2637 characters, which consisted of 1502 variable sites, and 1045 parsimony-informative characters. Sequence length and model parameters for each partition are listed in **Table 3**. While sequence alignment was unambiguous, there were insertion/deletion (indel) events in several genes (summarized in **Table 4**). Some of the indel events for the *c-mos* and *RAG1* genes have been commented on by

others (**Han *et al.*, 2004**; **Townsend *et al.*, 2004**), but additional, novel indel events are reported here for the first time from newly sequenced taxa. The 12-bp deletion in *c-mos* in *Gonatodes annularis*, *Gonatodes hasemani*, and *Gonatodes* sp. is of particular interest, as it appears to be a synapomorphy for that clade within the genus *Gonatodes*.

Table 3. Estimated models of sequence evolution and total number of characters for each data partition used in the Bayesian phylogenetic analyses.

Partition	Model	Number of characters in partition
All data	GTR+I+Γ	2637
RAG2	GTR+I+Γ	365
c-mos	GTR+I+Γ	383
ACM4	GTR+I+Γ	444
RAG1	GTR+I+Γ	1050
PDC	GTR+I+Γ	395
1st codon	GTR+Γ	879
2nd codon	GTR+I+Γ	879
3rd codon	GTR+Γ	879
RAG2 1st codon	GTR+Γ	121
RAG2 2nd codon	GTR+I	122
RAG2 3rd codon	HKY+Γ	122
c-mos 1st codon	GTR+Γ	127
c-mos 2nd codon	GTR+Γ	128
c-mos 3rd codon	GTR+Γ	128
ACM4 1st codon	GTR+Γ	148
ACM4 2nd codon	GTR+Γ	148
ACM4 3rd codon	GTR+Γ	148
RAG1 1st codon	HKY+Γ	350
RAG1 2nd codon	GTR+Γ	350
RAG1 3rd codon	HKY+Γ	350
PDC 1st codon	GTR+Γ	132
PDC 2nd codon	GTR+I	132
PDC 3rd codon	HKY+Γ	131

Table 4. Insertion and deletion (indel) events for each data set.

Gene	Taxon	Event	Size (bp)	Position
c-mos	*Oedura marmorata*	Deletion	12	189
	Hemidactylus frenatus	Insertion	9	213
	Cnemaspis limi	Insertion	3	219
	Coleodactylus brachystoma	Deletion	3	231
	Gonatodes annularis	Deletion	12	231
	Gonatodes hasemani	Deletion	12	231
	Gonatodes sp.	Deletion	12	231
	Hemidactylus frenatus	Deletion	21	231
	Rhineura floridana	Deletion	21	231
ACM4	*Gonatodes albogularis*	Insertion	3	150
RAG1	Eublepharidae	Deletion	12	75
	Gekkonidae	Deletion	12	75
	Coleodactylus brachystoma	Deletion	6	90
	Diplodactylidae	Deletion	3	105
	Carphodactylidae	Deletion	3	105
	Pygopodidae	Deletion	3	105
	Coleodactylus brachystoma	Deletion	18	171
	Pristurus carteri	Insertion	3	708
PDC	*Phyllodactylus xanti*	Deletion	3	151

Position indicates distance of the indel, in bases, from the first base of each gene. Higher taxonomic categories follow Han *et al.* (2004).

Partitioning data greatly improved harmonic mean likelihood scores, and Bayes factors showed clear differences between the different partitioning strategies (**Table 5**). Partitions that involved codon position provided the greatest improvement of likelihood scores, and the best-fit partitioning strategy divided the data by gene and codon. Tree topologies across the different partitioning strategies were consistent with only minor differences occurring at poorly supported nodes.

Table 5. Bayes factor comparisons of all partitioning strategies.

Partition	P1	P2	P3	P4
P1 – all data	−24332.52			
P2 – by gene	64.74	−24300.15		
P3 – by codon	351.46	286.72	−24156.79	
P4 – by gene and codon	436.96	372.22	85.5	−24114.04

Bold values along the diagonal are the harmonic mean likelihood values for each partitioning strategy. Values below the diagonal are 2 ln Bayes factors with rows representing the H_0 and columns the H_A. All comparisons show strong support for the more complex H_0.

The maximum parsimony analysis produced two equally parsimonious trees (tree length = 4365). Parsimony trees were consistent with the partitioned Bayesian analysis. Topological variation within the ingroups occurred only at poorly supported nodes. Overall, clades with strong bootstrap support also had significant Bayesian posterior probabilities.

The monophyly of the Gekkota was well supported in relation to the outgroups (**Fig. 2**). The placement of the Eublepharidae as sister to the Gekkonidae and the basal position of the Diplodactylidae/Carphodactylidae/Pygopodidae are consistent with other recent molecular gekkotan phylogenies (**Donnellan et al., 1999**; **Han et al., 2004**; **Townsend et al., 2004**). A well supported clade containing the sphaerodactyl geckos *Saurodactylus*, *Teratoscincus*, *Quedenfeldtia*, *Aristelliger*, *Euleptes* and *Pristurus* was the sister group to the remaining Gekkonidae. Within this novel clade there was a polytomy, with one branch leading to the genus *Pristurus*, one branch leading to a poorly supported clade containing *Teratoscincus*, *Quedenfeldtia*, *Aristelliger* and *Euleptes*, and a third branch leading to a strongly supported clade containing *Saurodactylus* as the sister group to a monophyletic, well supported clade of sphaerodactyl geckos. Within the sphaerodactyl geckos there were two major clades, one consisting of *Pseudogonatodes*, *Coleodactylus* and *Sphaerodactylus*, and another clade containing *Lepidoblepharis* and *Gonatodes*.
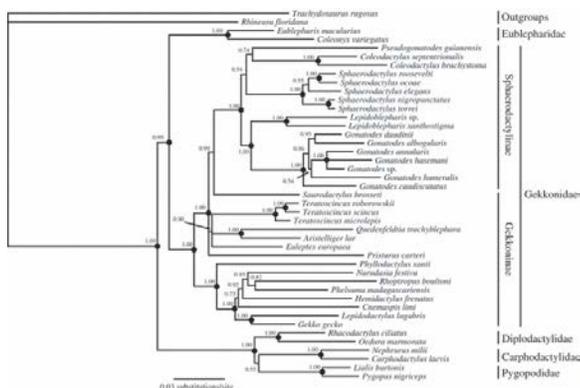

Figure 2 Bayesian phylogram using the best-fit partition strategy, with data partitioned by gene and codon. Labels above nodes represent the posterior probabilities. Black circles indicate nodes with parsimony bootstrap values > 70. Higher-level taxonomy follows **Han et al. (2004)**.

Dating phylogenies

The Bayesian phylogeny did not fit a molecular clock. The log likelihood of the constrained tree was −24197.14, and the 2 ln Bayes factor comparing constrained (clock) and unconstrained (non-clock) trees was 166.2, which indicates strong support for the null hypothesis (unconstrained tree, non-clock).

Because the phylogeny departed from a molecular clock, we used the nonparametric rate-smoothing method with the Powell algorithm to estimate dates of divergence (**Table 6**; **Fig. 3**). The dates provided by this analysis are concordant with divergence dates from other studies. The split between the Carphodactylidae and Diplodactylidae was estimated to be approximately 66 Myr BP using immunological data (**King, 1987**) and our data suggest a similar divergence date of 69.9 Myr BP. Another immunological study estimated the *Rhoptropus/Phelsuma* split to have occurred about 70 Myr BP (**Joger, 1985**) and our estimate was 66.8 Myr BP. The estimates by **Wiens _et al._ (2006a,b)**, on the other hand, produced divergence dates quite different from those presented here. **Wiens _et al._ (2006a,b)** dated the *Teratoscincus/Gekko* split to 63.7 ± 7.7 Myr BP, based on ages derived from a penalized-likelihood analysis of *RAG1* data vs. 113.2 ± 47.6 Myr BP in our analyses. Possible reasons for these differences could include the different data sets used and different methods of estimating branch lengths, as well as the different calibrations used between our two studies. Further, the **Wiens _et al._ (2006a,b)** study uses only a single gene to estimate divergence dates, which is typically less accurate than multi-gene estimates (**Bell & Donoghue, 2005**).

Table 6. Estimated ages (in Myr) and the corresponding 95% CI for all nodes, obtained using nonparametric rate smoothing (node labels shown in Fig. 3).

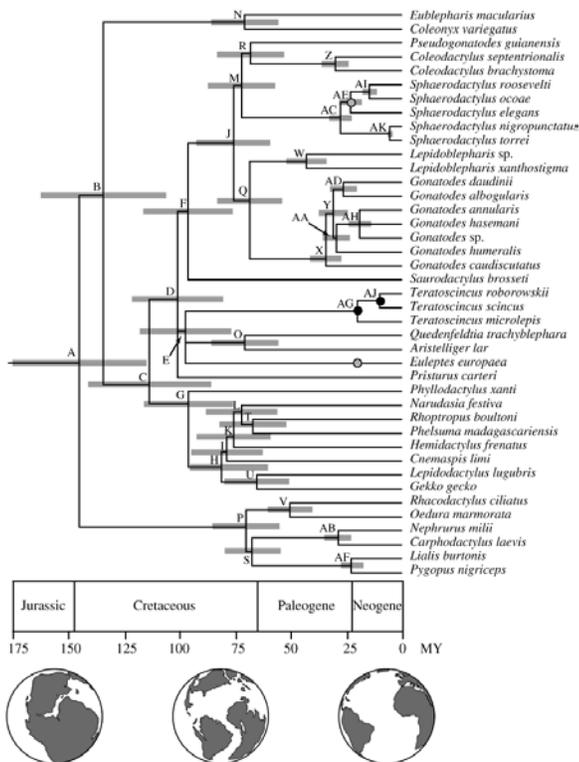| Node	Date	CI	Node	Date	CI	Node	Date	CI
A	144.6	61.6	N	70.5	30.5	AA	29.4	13.6
B	133.9	56.8	O	70.5	30.5	AB	28.6	12.5
C	113.2	47.6	P	69.9	30.5	AC	27.6	10.9
D	100.6	42.2	Q	68.2	28.4	AD	26.3	11.8
E	97.1	42.0	R	67.9	28.5	AE	23.1	9.6
F	95.9	40.4	S	67.2	25.8	AF	22.8	10.5
G	95.7	40.6	T	66.8	29.4	AG	20.0	0.0
H	80.9	34.5	U	65.1	28.5	AH	19.0	9.2
I	78.6	35.3	V	50.3	22.3	AI	14.6	6.4
J	75.5	31.4	W	42.8	18.7	AJ	10.0	0.0
K	75.4	33.9	X	34.1	14.8	AK	5.6	2.3
L	71.8	32.4	Y	30.8	13.4			
M	71.8	30.6	Z	29.8	12.8			

Figure 3 Chronogram of the partitioned Bayesian phylogeny generated using nonparametric rate smoothing. Approximate divergence dates are indicated along the *x*-axis. Grey bars indicate 95% confidence intervals calculated from bootstrap analysis. Actual dates and confidence intervals are listed in **Table 6**. Black circles represent fixed-age nodes; grey circles, minimum-age constraint nodes. Globes illustrate the break-up of Gondwana and the opening of the Atlantic Ocean shown at 200 Myr BP, 90 Myr BP and the present (modified from PALEOMAP website, **http://www.scotese.com**).

Hypothesis testing

Bayes factor comparisons between the unconstrained phylogeny and alternative hypotheses are summarized in **Table 7**. The harmonic mean likelihood of the unconstrained topology (H_0, our default Bayes tree from **Fig. 2**) had a much larger value than the alternative constrained topologies (H_1–H_4; **Fig. 1**) and was strongly preferred (*sensu***Kass & Raftery, 1995**) in every comparison.

Table 7. Bayes factor comparisons of alternative topological hypotheses (H_A, summarized in Fig. 1) to the optimal, unconstrained Bayesian topology (H_0, Fig. 2) (all comparisons show strong support for the unconstrained topology).

Alternative hypothesis (H_A)	−l Ln	2 ln Bayes factor	Evidence for H_0
H_1	−24122.18	16.28	Strongly supported
H_2	−24150.04	72.00	Strongly supported
H_3	−24124.00	19.92	Strongly supported
H_4	−24371.17	514.26	Strongly supported

Biogeography

Our primary biogeographical interest was in the clade containing the sphaerodactyl geckos, *Saurodactylus*, *Teratoscincus*, *Quedenfeldtia*, *Aristelliger*, *Euleptes* and *Pristurus*. There was slight variation in DIVA analyses among the multiple fully bifurcated trees, but all scenarios indicated that the ancestral area for the entire clade was North Africa, the Mediterranean and the Arabian Peninsula. All analyses also required three dispersal events. The first dispersal event was to the Western Hemisphere in the ancestor to the *Saurodactylus* + sphaerodactyl clade. Another dispersal to the Western Hemisphere was required for the genus *Aristelliger* and was placed at several different nodes depending on which fully bifurcated tree was

analysed. The final dispersal event was to central and south Asia for the genus *Teratoscincus* and, like *Aristelliger*, was placed at several different nodes depending on which fully bifurcated tree was analysed.

Discussion

Phylogeny

The content of the novel, expanded sphaerodactyl clade recovered in the analysis is surprising. Although the inclusion of *Saurodactylus*, *Quedenfeldtia* and *Pristurus* in this group has been proposed previously and supported by morphological characters (**Kluge, 1995**), the genera *Teratoscincus*, *Euleptes* and *Aristelliger* have never before been associated with one another. The exclusion of *Cnemaspis* and *Narudasia* from this clade, as well as the lack of support for a sister group relationship of *Pristurus* to the New World sphaerodactyls or to *Quedenfeldtia*, is at odds with previous hypotheses based on morphology (**Arnold, 1990a,b, 1993**; **Kluge, 1995**). We suggest that certain shared features (e.g. small size and diurnality) may have yielded extensive homoplasy in a diversity of characters, particularly those of the head, which would be most affected by miniaturization and large eye size.

The highly autapomorphic *Teratoscincus* is monophyletic, as has been demonstrated by previous workers (**Macey *et al.*, 1999**). However, *Teratoscincus*'s distinctive position as the sister group to the remaining Gekkonidae (**Kluge, 1987**) is rejected. **Han *et al.* (2004)** also rejected this relationship, but found no evidence to support particularly close relationships with any other genera based on partial *c-mos* sequence data alone. Our results likewise provide no strong support for affinities within the expanded sphaerodactyl clade.

The West Indian *Aristelliger* was considered to be enigmatic by **Underwood (1954)**, who regarded it as a basal gekkonid because of its retention of oil droplets in the eyes and its amphicoelous vertebrae. **Hecht (1952)** suggested on the basis of external digital structure that it might be related to *Tarentola* or *Phyllopezus*. **Russell (1976, 1979)** demonstrated that the internal architecture of the digits was relatively simple in *Aristelliger*, but found nothing to link it closely to other gekkonid genera (**Russell & Bauer, 2002**). Its inclusion in the same large clade as sphaerodactyls is not entirely unexpected. Immunological distances between *Sphaerodactylus* and *Aristelliger* were found to be lower than between the former and other genera of gekkonine geckos (**Hass, 1991**; **Hedges, 1996**). We found strong support for its sister group relationship with the North African *Quedenfeldtia*, although this divergence seems to be ancient (**Fig. 3**). Interestingly, a putative synapomorphy linking *Aristelliger* and *Teratoscincus* was identified nearly 20 years ago (**Bauer & Russell, 1989**), but was ignored and regarded as convergence because any close relationship between these two taxa was considered implausible. Both taxa possess parafrontal bones (**Fig. 4**), structures apparently uniquely derived within the Gekkota. These structures may be evidence of a sister group relationship between these genera, or they may be more widespread within the clade to which these taxa belong. Alternatively, these structures may not be ossified in other members of the clade, all of which are much smaller in size than either *Teratoscincus* or *Aristelliger*.
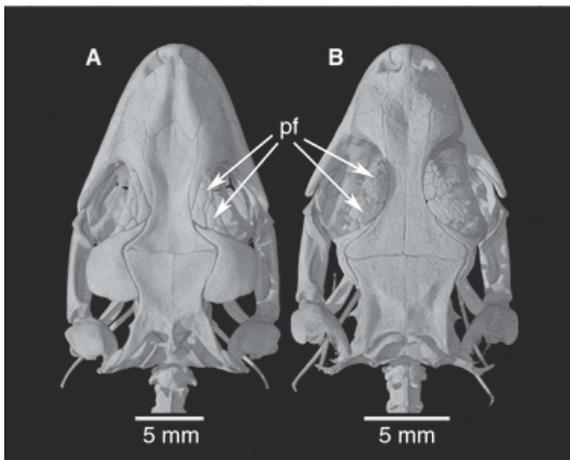
Figure 4 Dorsal views of skulls of (a) *Aristelliger georgeensis* (CAS 176485); (b) *Teratoscincus przewalskii* (CAS 171013) showing the position of the parafrontal bones (pf), a putative synapomorphy of the clade subtended by node E (**Fig. 3**). Skulls were imaged from intact specimens using high-resolution X-ray computed tomography.

The subject of clutch size presents another potential synapomorphy for the Spaherodactylidae. Most geckos possess a fixed clutch size of two eggs (**Kluge, 1987**) although several lineages will lay only one egg per clutch. Geckos that lay single egg clutches are typically smaller species, and the reduction in clutch size has been associated with small body size, for example in sphaerodactyl geckos and *Saurodactylus* (**Kluge, 1995**; **Schleich *et al.*, 1996**). Several medium- to large-size geckos, such as *Quedenfeldtia, Pristurus* and *Aristelliger*(**Hecht, 1952**; **Kluge, 1995**), also posses single egg clutches, a hitherto unexplained feature. With the exception of *Teratoscincus*, which lays two eggs per clutch (**Szczerbak & Golubev, 1986**), and *Euleptes,* which lays one or two eggs per clutch (**Rieppel & Schneider, 1981**), all other members of the Sphaerodactylidae lay single egg clutches.

Euleptes was resurrected from the synonymy of *Phyllodactylus* by **Bauer *et al.* (1997)** to accommodate the single living species of Mediterranean leaf-toed gecko. **Bauer *et al.* (1997)**, however, suggested no particularly close relationships with other genera, but rather emphasized that a suite of derived morphological characters supported the recognition of *Euleptes europaea* as a lineage distinct from all other leaf-toed taxa. Some authors have suggested close affinities of *Euleptes* with leaf-toed geckos of Africa and/or Australia, but our broader phylogenetic analysis of all gekkotan genera strongly supports these taxa, exclusive of *Euleptes*, as part of a large, chiefly Afro–Malagasy radiation (unpublished data) represented in this study by *Rhoptropus* and *Phelsuma*.

Not surprisingly, we find strong support for the Sphaerodactylinae as traditionally construed, and for the monophyly of each of the constituent genera for which we had multiple samples. We retrieved the same pattern of relationships among *Pseudogonatodes*, *Coleodactylus* and *Sphaerodactylus* as **Kluge (1995)**, albeit with poor nodal support. Our results differ, however, from the morphologically derived phylogeny, as well as all pre-cladistic hypotheses of relationship (**Noble, 1921**; **Parker, 1926**; **Vanzolini, 1968**) in finding strong support for the sister-group status of *Gonatodes* and *Lepidoblepharis*. All previous hypotheses have considered *Gonatodes* as the sister group to the remaining genera, in part on the basis of its absence of an ungual sheath.

Taxonomy
Our data strongly support the content of, if not the generic interrelationships within, the basalmost clade in the Gekkonidae (*sensu***Han *et al.*, 2004**). We find strong support for the Sphaerodactylinae (*sensu***Underwood, 1954**; **Kluge, 1967**), but reject **Kluge's (1987)** Teratoscincinae and Sphaerodactylini (inclusive of *Pristurus*). In

order to maintain a classification that is isomorphic with respect to our retrieved phylogeny, we propose a new classification for this portion of the Gekkota (**Fig. 5**; **Table 8**). The entire expanded sphaerodactyl clade is accorded familial rank as the Sphaerodactylidae (**Fig. 5**). Within this group, the well supported *Saurodactylus* + New World sphaerodactyl clade is defined as the Sphaerodactylinae, and the five New World genera that originally constituted **Underwood's (1954)** Sphaerodactylidae comprise the Sphaerodactylini. All other members of the Sphaerodactylidae (*Pristurus*, *Teratoscincus*, *Euleptes*, *Aristelliger*, *Quedenfeldtia*) are considered *incertae sedis* within the family. The name Teratoscincinae remains available for a clade including *Teratoscincus* should future research clarify relationships among these genera.
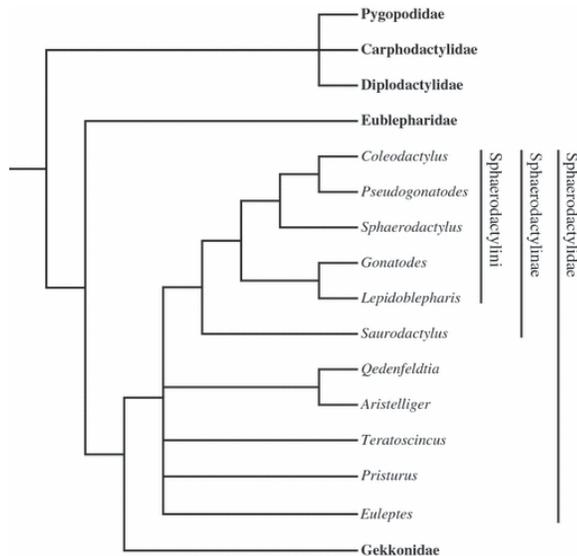

Figure 5 Summary of the phylogenetic relationships and higher level taxonomy of the spaherodactyl geckos and related genera, as presented in this paper.

Table 8. Previous and current higher order classification of extant Gekkota.

Underwood (1954)
Gekkonoidea
Eublepharidae
Sphaerodactylidae: *Coleodactylus,*
Gonatodes, Lepidoblepharis,
Pseudogonatodes, Sphaerodactylus
Gekkonidae
Diplodactylinae: *Aristelliger,*
Saurodactylus, Teratoscincus
Gekkoninae: *Euleptes*
incertae sedis: Pristurus, Quedenfeldtia
Kluge (1967, 1976)
Gekkonidae
Eublepharinae
Gekkoninae: *Aristelliger, Euleptes,*
Pristurus, Quedenfeldtia,
Saurodactylus, Teratoscincus
Spaherodactylinae: *Coleodactylus,*
Gonatodes, Lepidoblepharis,
Pseudogonatodes, Sphaerodactylus

Diplodactylinae
Diplodactylini
Carphodactylini
Pygopodidae
Pygopodinae
Lialisinae
Kluge (1987)
Gekkota
Eublepharoidea
Eublepharidae
Gekkonoidea
Gekkonidae
Gekkoninae
'Ptyodactylini': *Euleptes, Quedenfeldtia, Saurodactylus*
Gekkonini: *Aristelliger*
Sphaerodactylini: *Pristurus, Coleodactylus, Gonatodes, Lepidoblepharis, Pseudogonatodes, Sphaerodactylus*
Teratoscincinae: *Teratoscincus*
Pygopodidae
Diplodactylinae
Carphodactylini
Diplodactylini
Pygopodinae
Han *et al* (2004)
Gekkota
Eublepharidae
Gekkonidae
Gekkoninae: *Aristelliger, Euleptes, Pristurus, Quedenfeldtia, Saurodactylus, Teratoscincus*
Sphaerodactylinae: *Coleodactylus, Gonatodes, Lepidoblepharis, Pseudogonatodes, Sphaerodactylus*
Diplodactylidae
Carphodactylidae
Pygopodidae
This paper
Gekkota
Eublepharidae
Gekkonidae
Sphaerodactylidae: *Coleodactylus, Gonatodes, Lepidoblepharis, Pseudogonatodes, Euleptes, Sphaerodactylus, Aristelliger, Pristurus, Quedenfeldtia, Saurodactylus, Teratoscincus*
Diplodactylidae
Carphodactylidae
Pygopodidae

Biogeography

The combination of a robust, multi-gene phylogeny, divergence date estimation using both fossils and biogeographical events, and dispersal–vicariance analysis provided a clear hypothesis regarding the biogeography of the sphaerodactyl geckos and their closest relatives. DIVA analysis shows that the

Sphaerodactylidae probably had its origins in a region containing what is now northern Africa, the Mediterranean and the Arabian peninsula during the mid-Cretaceous.

Our data strongly support a Cretaceous divergence between the New World sphaerodactyls and *Saurodactylus*, and that cladogenesis was associated with the opening of the Atlantic Ocean *c.* 100–120 Myr BP (**Parrish, 1993**; **Hay *et al.*, 1999**) and supports the vicariance hypothesis. The opening of the South Atlantic has also been proposed to be responsible for major divergences within the Amphisbaenidae (**Macey *et al.*, 2004**).

Within the Western Hemisphere, the presumed centre of origin of sphaerodactyl geckos is northern South America, including Colombia and Venezuela (**Vanzolini, 1968**). This region still contains the greatest diversity of species of *Lepidoblepharis*, *Pseudogonatodes* and *Gonatodes*. *Coleodactylus* has its greatest diversity within the Amazon basin and Brazilian Cerrado. Most *Sphaerodactylus* species occur in the Caribbean, where the genus reaches its greatest diversity. The diversification of *Sphaerodactylus* seems to have coincided with the period of increased connectivity of the Greater Antilles and the Caribbean to South America at the beginning of the Oligocene (**Crawford & Smith, 2005**).

The colonization of the New World by geckos is clearly complex. Our analyses indicate that the Sphaerodactylidae is of Gondwanan origin and that vicariance alone is sufficient to explain the presence of *Gonatodes*, *Sphaerodactylus*, *Lepidoblepharis*, *Pseudogonatodes* and *Coleodactylus* in the Americas. It may also explain the divergence of *Aristelliger* from *Quedenfeldtia*. On the other hand, the endemic Neotropical members of the genera *Tarentola* (**Carranza *et al.*, 2000, 2002**), *Hemidactylus* (**Carranza & Arnold, 2006**) and *Lygodactylus* (M. Vences, personal communication) appear to be the result of post-Gondwanan dispersal from the Old World. The origin of the remaining Neotropical genera of geckos (*Homonota*, *Bogertia*, *Phyllodactylus*, *Phyllopezus*, *Gymnodactylus*, *Thecadactylus*) remains uncertain, but our results suggest that the New World *Phyllodactylus*, at least, is representative of another ancient lineage that may be of Gondwanan origin.

There is ambiguity in the dispersal–vicariance analysis regarding where on our phylogeny the dispersal to central Asia occurred. The additional information provided by the fossil and biogeographical calibrated dating can provide some insight. There is strong evidence for an extensive faunal exchange between Africa and Asia throughout the Paleogene (**Ducrocq, 2001**; **Antoine *et al.*, 2003**; **Marivaux *et al.*, 2005**). A possible scenario for the dispersal of the *Teratoscincus* lineage from north Africa/Arabia to central Asia was during the middle Eocene via an eastern trans-Tethys dispersal route, the so-called 'Iranian route', linking the faunas of northern Africa and Arabia to south-west Asia (**Gheerbrant & Rage, 2006**). Such a scenario puts *Teratoscincus* in south Asia at the time of the Indian collision with Asia, 40–50 Ma, and subsequent vicariant events (**Macey *et al.*, 1999**).

The apparent switch in historical biogeography from a vicariance-dominated paradigm back to a dispersalist paradigm, while welcome, must be tempered.
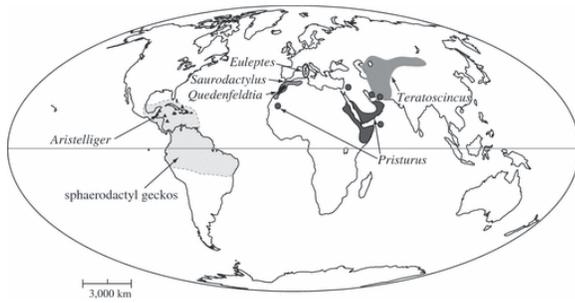
6 [Geographical distributions of the Sphaerodactylidae. The 'sphaerodactyl geckos' include the genera *Coleodactylus*, *Gonatodes*, *Lepidoblepharis*, *Pseudogonatodes* and *Sphaerodactylus*. Sources include *Aristelliger* (**Powell *et al.*, 1996**; **Köhler, 2003**); *Euleptes* (**Bauer *et al.*, 1997**); *Pristurus* (**Geniez & Arnold, 2006**); *Quedenfenldtia* and *Saurodactylus* (**Bons & Geniez, 1996**; **Schleich *et al.*, 1996**); sphaerodactyl geckos (**Kluge, 1995**); and *Teratoscincus* (**Macey *et al.*, 2005**). The map uses an equal-area, Mollweide projection.]

There is no doubt that a vicariance-only viewpoint (**Nelson, 1979**) is short-sighted and biologically unrealistic. Similarly, the recent dispersalist trend (**Cook & Crisp, 2005**; **McGlone, 2005**; **de Queiroz, 2005**) should not be allowed to overshadow the reality and importance of vicariance in shaping species' distributions. This study and others (**Noonan & Chippindale, 2006**) have shown that vicariance is still a viable hypothesis for many Gondwanan taxa. The biological reality of animal and plant distributions is often more complicated than the simplistic biogeographical models at our disposal, and biogeographers must consider that vicariance, dispersal and extinction are each important processes in shaping species' distributions (**Zink *et al.*, 2000**; **Sanmartín & Ronquist, 2004**; **Cook & Crisp, 2005**; **Halas *et al.*, 2005**; **McGlone, 2005**).

Acknowledgements

References

Abdrakhmatov, K.Y., Aldazhanov, S.A., Hager, B.H., Hamburger, M.W., Herring, T.A., Kalabaev, K.B., Makarov, V.I., Molnar, P., Panasyuk, S.V., Prilepin, M.T., Reilinger, R.E., Sadybakasov, I.S., Souter, B.J., Trapeznikov, Y.A., Tsurkov, V.Y. & Zubovich, A.V. (1996) Relatively recent construction of the Tien Shan inferred from GPS measurements of present-day crustal deformation rates. *Nature*, **384**, 450– 453.

Agustí, J., Cabrera, L., Garcés, M., Krijgsman, W., Oms, O. & Parés, J.M. (2001) A calibrated mammal scale for the Neogene of Western Europe. State of the art. *Earth Science Review*, **52**, 247– 260.

Alifanov, V.R. (1989) The oldest gecko (Lacertilia, Gekkonidae) from the lower Cretaceous of Mongolia. *Paleontologicheskii Zhurnal*, **1**, 124– 126 (in Russian).

Antoine, P., Welcomme, J., Marivaux, L., Baloch, I., Benammi, M. & Tassy, P. (2003) First record of Paleogene Elephantoidea (Mammalia, Proboscidea) from the Bugti hills of Pakistan. *Journal of Vertebrate Paleontology*, **23**, 977– 980.

Arnold, E.N. (1990a) Why do morphological phylogenies vary in quality? An investigation based on the comparative history of lizard clades *Proceedings of the Royal Society of London Series B, Biological Sciences*, **240**, 135– 172.

Arnold, E.N. (1990b) The two species of Moroccan day-geckoes, *Quedenfeldtia* (Reptilia: Gekkonidae). *Journal of Natural History*, **24**, 757– 762.

Arnold, E.N. (1993) Historical changes in the ecology and behaviour of semaphore geckos (*Pristurus*, Gekkonidae) and their relatives. *Journal of Zoology*, **229**, 353– 384.

Austin, J.J., Arnold, E.N. & Jones, C.G. (2004) Reconstructing an island radiation using ancient and recent DNA: the extinct and living day geckos (*Phelsuma*) of the Mascarene islands. *Molecular Phylogenetics and Evolution*, **31**, 109– 122.

Bauer, A.M. (1990) Phylogenetic systematics and biogeography of the Carphodactylini (Reptilia: Gekkonidae). *Bonner Zoologische Monographien*, **30**, 1– 218.

Bauer, A.M. (1993) African-South American relationships: a perspective from the Reptilia. *Biological relationships between Africa and South America* (ed. by P. Goldblatt), pp. 244– 288. Yale University Press, New Haven, CT.

Bauer, A.M. & Russell, A.P. (1989) Supraorbital ossifications in geckos (Reptilia: Gekkonidae). *Canadian Journal of Zoology*, **67**, 678– 684.

Bauer, A.M., Good, D.A. & Branch, W.R. (1997) The taxonomy of the southern African leaf-toed geckos (Squamata: Gekkonidae), with a review of Old World '*Phyllodactylus*' and the description of five new genera. *Proceedings of the California Academy of Sciences*, **49**, 447– 497.

Bauer, A.M., Böhme, W. & Weitschat, W. (2004) An Early Eocene gecko from Baltic amber and its implications for the evolution of gecko adhesion. *Journal of Zoology*, **265**, 327– 332.

Bauer, A.M., DeSilva, A., Greenbaum, E. & Jackman, T.R. (2007) 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*. **83**, 22– 32.

Bell, C.D. & Donoghue, M.J. (2005) Dating the Dipsacales: comparing models, genes, and evolutionary implications. *American Journal of Botany*, **92**, 284– 296.

Böhme, W. (1984) Erstfund eines fossilen Kugelfingergeckos (Sauria: Gekkonidae: Sphaerodactylinae) aus Dominikanischem Bernstein (Oligozan von Hispaniola, Antillen). *Salamandra*, **20**, 212– 220.

Bons, J. & Geniez, P. (1996) *Amphibiens et reptiles du Maroc (Sahara Occidental compris) atlas biogéographique*. Asociación Herpetológica Española, Barcelona, Spain.

Borsuk-Bialynicka, M. (1990) *Gobekko cretacicus gen. et sp. n.*, a new gekkonid lizard from the Cretaceous of the Gobi Desert. *Acta Palaeontologia Polonica*, **35**, 67– 76.

Boulenger, G.A. (1885) *Catalogue of the lizards in the British Museum (Natural History)*, Vol. 1. Taylor & Francis, London.

Brandley, M.C., Schmitz, A. & Reeder, T.W. (2005) Partitioned Bayesian analyses, partition choice, and the phylogenetic relationships of scincid lizards. *Systematic Biology*, **54**, 373– 390.

Brown, W.C. & Alcala, A.C. (1957) Viability of lizard eggs exposed to sea water. *Copeia*, **1957**, 39– 41.

Bull, J.J., Huelsenbeck, J.P., Cunningham, C.W., Swofford, D.L. & Waddell, P.J. (1993) Partitioning and combining data in phylogenetic analysis. *Systematic Biology*, **42**, 384– 397.

Carranza, S. & Arnold, E.N. (2006) Systematics, biogeography, and evolution of *Hemidactylus* geckos (Reptilia: Gekkonidae) elucidated using mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution*, **38**, 531– 545.

Carranza, S., Arnold, E.N., Mateo, J.A. & Lopez-Jurado, L.F. (2000) Long-distance colonization and radiation in gekkonid lizards, *Tarentola* (Reptilia: Gekkonidae), revealed by mitochondrial DNA sequences. *Proceedings of the Royal Society B: Biological Sciences*, **267**, 637– 649.

Carranza, S., Arnold, E.N., Mateo, J.A. & Geniez, P. (2002) Relationships and evolution of the North African geckos, *Geckonia* and *Tarentola* (Reptilia: Gekkonidae), based on mitochondrial and nuclear DNA sequences. *Molecular Phylogenetics and Evolution*, **23**, 244– 256.

Conrad, J.L. & Norell, M.A. (2006) High resolution X-ray computed tomography of an Early Cretaceous gekkonomorph (Squamata) from Öösh (Övörkhangai; Mongolia). *Historical Biology*, **18**, 405– 431.

Cook, L.G. & Crisp, M.D. (2005) Directional asymmetry of long-distance dispersal and colonization could mislead reconstructions of biogeography. *Journal of Biogeography*, **32**, 741– 754.

Cracraft, J. (1974) Continental drift and vertebrate distribution. *Annual Review of Ecology and Systematics*, **5**, 215– 261.

Crawford, A.J. & Smith, E.N. (2005) Cenozoic biogeography and evolution in direct-developing frogs of Central America (Leptodactylidae: Eleutherodactylus) as inferred from a phylogenetic analysis of nuclear and mitochondrial genes. *Molecular Phylogenetics and Evolution*, **35**, 536– 555.

Donnellan, S.C., Hutchinson, M.N. & Saint, K.M. (1999) Molecular evidence for the phylogeny of Australian gekkonoid lizards. *Biological Journal of the Linnean Society*, **67**, 97– 118.

Ducrocq, S. (2001) Palaeogene anthropoid primates from Africa and Asia: new phylogenetical evidences. *Comptes Rendus de l'Academie des Sciences Serie II a Sciences de la Terre et des Planetes*, **332**, 351– 356.

Estes, R. (1983) The fossil record and early distribution of lizards. *Advances in herpetology and evolutionary biology* (ed. by A.G.J. Rhodin and K. Miyata), pp. 365– 398. Museum of Comparative Zoology, Cambridge, MA.

Evans, S.E. (2003) At the feet of the dinosaurs: the early history and radiation of lizards. *Biological Reviews of the Cambridge Philosophical Society*, **78**, 513– 551.

Felsenstein, J. (1985) Confidence limits on phylogenies: an approach using the bootstrap. *Evolution*, **39**, 783– 791.

Geniez, P. & Arnold, E.N. (2006) A new species of Semaphore geckos *Pristurus* (Squamata: Gekkonidae) from Mauretania, represents a 4700 km range extension for genus. *Zootaxa*, **1317**, 57– 68.

Gheerbrant, E. & Rage, J.C. (2006) Paleobiogeography of Africa: how distinct from Gondwana and Laurasia? *Palaeogeography, Palaeoclimatology, Palaeoecology*, **241**, 224– 246.

Grimaldi, D. (1995) On the age of Dominican amber. *Amber, resinite, and fossil resins* (ed. by K.B. Anderson and J.C. Crelling), pp. 203– 217. American Chemical Society, Washington, DC.

Groth, J.G. & Barrowclough, G.F. (1999) Basal divergences in birds and the phylogenetic utility of the nuclear *RAG-1* gene. *Molecular Phylogenetics and Evolution*, **12**, 115– 123.

Halas, D., Zamparo, D. & Brooks, D.R. (2005) A historical biogeographical protocol for studying biotic diversification by taxon pulses. *Journal of Biogeography*, **32**, 249– 260.

Han, D., Zhou, K. & Bauer, A.M. (2004) 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*, **83**, 353– 368.

Hanke, M. & Wink, M. (1994) Direct DNA sequencing of PCR amplified vector inserts following enzymatic degradation of primer and dNTPs. *Biotechniques*, **17**, 858– 860.

Hass, C.A. (1991) Evolution and biogeography of West Indian *Sphaerodactylus* (Sauria: Gekkonidae): a molecular approach. *Journal of Zoology*, **225**, 525– 561.

Hay, W.W., DeConto, R.M., Wold, C.N., Wilson, K.M., Voigt, S., Schulz, M., Wold, A.R., Dullo, W., Ronov, A.B., Balukhovsky, A.N. & Söding, E. (1999) Alternative global Cretaceous paleogeography. *Evolution of the Cretaceous ocean–climate system* (ed. by E. Barrera and C. Johnson), pp. 1– 47. Special Paper 332. Geological Society of America, Boulder, CO.

Hecht, M.K. (1952) Natural selection in the lizard genus *Aristelliger*. *Evolution*, **6**, 112– 124.

Hedges, S.B. (1996) The origin of West Indian amphibians and reptiles. *Contributions to West Indian herpetology: a tribute to Albert Schwartz* (ed. by R. Powell and R.W. Henderson), pp. 95– 128. Society for the Study of Amphibians and Reptiles, Ithaca, NY.

Hedges, S.B. & Thomas, R. (2001) At the lower size limit in Amniote Vertebrates: a new diminutive lizard from the West Indies. *Caribbean Journal of Science*, **37**, 168– 173.

Higgins, D. (2003) Multiple alignment: theory. *The phylogenetic handbook: a practical approach to DNA and protein phylogeny* (ed. by M. Salemi and A.M. Vandamme), pp. 45– 60. Cambridge University Press, Cambridge, UK.

Hoffstetter, R. (1946) Sur les gekkonida et fossiles. *Bulletin du Museum d'Histoire Naturelle, Paris*, **18**, 195– 203.

Huelsenbeck, J.P. & Ronquist, F. (2001) MrBayes: Bayesian inference of phylogeny. *Bioinformatics*, **17**, 754– 755.

Joger, U. (1985) The African Gekkonine radiation – preliminary phylogenetic results, based on quantitative immunological comparisons of serum albumins. *African vertebrates: systematics, phylogeny and evolutionary ecology* (ed. by K.L. Schuchmann), pp. 479– 494. Zoologisches Forschungsinstitut und Museum A. Koenig, Bonn, Germany.

Kass, R.E. & Raftery, A.E. (1995) Bayes factors. *Journal of the American Statistical Association*, **90**, 773– 795.

King, M. (1987) Origin of the Gekkonidae: chromosomal and albumin evolution suggests Gondwanaland. *Search*, **18**, 252– 254.

Kluge, A.G. (1967) Higher taxonomic categories of gekkonid lizards and their evolution. *Bulletin of the American Museum of Natural History*, **135**, 1– 60.

Kluge, A.G. (1969) The evolution and geographical origin of the New World *Hemidactylus mabouia-brookii* complex (Gekkonidae, Sauria). *Miscellaneous Publications of the Museum of Zoology, University of Michigan*, **138**, 1– 78.

Kluge, A.G. (1976) Phylogenetic relationships in the lizard family Pygopodidae: an evaluation of theory, methods, and data. *Miscellaneous Publications of the Museum of Zoology, University of Michigan*, **152**, 1– 72.

Kluge, A.G. (1982) Cloacal bones and sacs as evidence of gekkonid lizard relationships. *Herpetologica*, **38**, 348– 355.

Kluge, A.G. (1983) Epidermal gland evolution in gekkonoid lizards. *Journal of Herpetology*, **17**, 89– 90.

Kluge, A.G. (1987) Cladistic relationships in the Gekkonidae (Squamata, Sauria). *Miscellaneous Publications of the Museum of Zoology, University of Michigan*, **173**, 1– 54.

Kluge, A.G. (1989) A concern for evidence and a phylogenetic hypothesis of relationships among *Epicrates* (Boidae, Serpentes). *Systematic Zoology*, **38**, 7– 25.

Kluge, A.G. (1995) Cladistic relationships of sphaerodactyl lizards. *American Museum Novitates*, **3139**, 1– 23.

Kluge, A.G. & Nussbaum, R.A. (1995) A review of African–Madagascan gekkonid lizard phylogeny and biogeography (Squamata). *Miscellaneous Publications of the Museum of Zoology, University of Michigan*, **183**, 1– 20.

Köhler, G. (2003) *Reptiles of Central America*. Herpeton Verlag, Offenbach, Germany.

Lemmon, A.R. & Moriarty, E.C. (2004) The importance of proper model assumption in Bayesian phylogenetics. *Systematic Biology*, **53**, 265– 277.

Leviton, A.E., Gibbs, R.H., Heal, E. & Dawson, C.E. (1985) Standards in herpetology and ichthyology: part 1. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. *Copeia*, **1985**, 802– 832.

Lundberg, J.G. (1993) African–South American fish clades and continental drift: problems with a paradigm. *Biological relationships between Africa and South America* (ed. by P. Goldblatt), pp. 157– 199. Yale University Press, New Haven, CT.

Macey, J.R., Wang, Y., Ananjeva, N.B., Larson, A. & Papenfuss, T.J. (1999) 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*, **12**, 320– 332.

Macey, J.R., Papenfuss, T.J., Kuehl, J.V., Fourcade, H.M. & Boore, J.L. (2004) Phylogenetic relationships among amphisbaenian reptiles based on complete mitochondrial genomic sequences. *Molecular Phylogenetics and Evolution*, **33**, 22– 31.

Macey, J.R., Fong, J.J., Kuehla, J.V., Shafei, S., Ananjeva, N.B., Papenfuss, T.J. & Boore, J.L. (2005) The complete mitochondrial genome of a gecko and the phylogenetic position of the Middle Eastern *Teratoscincus keyserlingii*. *Molecular Phylogenetics and Evolution*, **36**, 188– 193.

Maddison, W.P. & Maddison, D.R. (1992) *MacClade, analysis of phylogeny and character evolution, version 3.0*. Sinauer, Sunderland, MA.

Marivaux, L., Ducrocq, S., Jaeger, J., Marandat, B., Sudre, J., Chaimanee, Y., Tun, S.T., Htoon, W. & Soe, A.N. (2005) New remains of *Pondaungimys anomaluropsis* (Rodentia, Anomaluroidea) from the latest middle Eocene pondaung formation of central Myanmar. *Journal of Vertebrate Paleontology*, **25**, 214– 227.

McGlone, M.S. (2005) Goodbye Gondwana. *Journal of Biogeography*, **32**, 739– 740.

Moritz, C., Case, T.J., Bolger, D.T. & Donnellan, S. (1993) Genetic diversity and the history of Pacific island house geckos (*Hemidactylus* and *Lepidodactylus*). *Biological Journal of the Linnean Society*, **48**, 113– 133.

Mueller, J. (2001) A new fossil species of *Euleptes* from the early Miocene of Montaigu, France (Reptilia, Gekkonidae). *Amphibia–Reptilia*, **22**, 341– 348.

Mueller, J. & Moedden, C. (2001) A fossil leaf-toed gecko from the Oppenheim/Nierstein Quarry (Lower Miocene, Germany). *Journal of Herpetology*, **35**, 529– 532.

Nagy, Z.T., Joger, U., Wink, M., Glaw, F. & Vences, M. (2003) Multiple colonization of Madagascar and Socotra by colubrid snakes: evidence from nuclear and mitochondrial gene phylogenies. *Proceedings of the Royal Society B: Biological Sciences*, **270**, 2613– 2621.

Nelson, G. (1979) From Candolle to Croizat: comments on the history of biogeography. *Journal of the History of Biology*, **11**, 269– 305.

Noble, G.K. (1921) The bony structure and phyletic relations of *Sphaerodactylus* and allied lacertilian genera, with the description of a new genus. *American Museum Novitates*, **4**, 1– 16.

Noonan, B.P. & Chippindale, P.T. (2006) Vicariant origin of Malagasy reptiles supports Late Cretaceous Antarctic landbridge. *The American Naturalist*, **168**, 730– 741.

Notredame, C., Higgins, D.G. & Heringa, J. (2000) t-coffee: a novel method for fast and accurate multiple sequence alignment. *Journal of Molecular Biology*, **302**, 205– 217.

Nylander, J.A.A. (2004) *MrModeltest v2*. Program distributed by the author. Evolutionary Biology Centre, Uppsala University, Uppsala, Sweden.

Nylander, J.A.A., Ronquist, F., Huelsenbeck, J.P. & Nieves-Aldrey, J.L. (2004) Bayesian phylogenetic analysis of combined data. *Systematic Biology*, **53**, 47– 67.

Parker, H.W. (1926) The Neotropical lizards of the genera *Lepidoblepharis*, *Pseudogonatodes*, *Lathrogecko*, and *Sphaerodactylus*, with the description of a new genus. *Annals and Magazine of Natural History*, **17**, 291– 301.

Parrish, J.T. (1993) The palaeogeography of the opening South Atlantic. *The Africa–South America connection* (ed. by W. George and R. Lavocat), pp. 8– 27. Clarendon Press, Oxford, UK.

Posada, D. & Buckley, T.R. (2004) Model selection and model averaging in phylogenetics: advantages of the AIC and Bayesian approaches over likelihood ratio tests. *Systematic Biology*, **53**, 793– 808.

Posadas, P., Crisci, J.V. & Katinas, L. (2006) Historical biogeography: a review of its basic concepts and critical issues. *Journal of Arid Environments*, **66**, 389– 403.

Powell, R., Henderson, R.W., Adler, K. & Dundee, H.A. (1996) An annotated checklist of West Indian amphibians and reptiles. *Contributions to West Indian herpetology: a tribute to Albert Schwartz* (ed. by R. Powell and R.W. Henderson), pp. 51– 93. Society for the Study of Amphibians and Reptiles, Ithaca, NY.

De Queiroz, A. (2005) The resurrection of oceanic dispersal in historical biogeography. *Trends in Ecology and Evolution*, **20**, 68– 73.

Raxworthy, C.J., Forstner, M.R.J. & Nussbaum, R.A. (2002) Chameleon radiation by oceanic dispersal. *Nature*, **415**, 784– 787.

Rieppel, O. & Schneider, B. (1981) *Phyllodactylus europaeus* Gené 1838 – Europäischer Blattfingergecko. *Handbuch der reptilien und amphibien Europas* (ed. by W. Böhme), pp. 108– 118. Akademische Verlagsgesellschaft, Wiesbaden, Germany.

Rokas, A., Williams, B.L., King, N. & Carroll, S.B. (2003) Genome-scale approaches to resolving incongruence in molecular phylogenies. *Nature*, **425**, 798– 804.

Ronquist, F. (1996) *diva version 1.1*. Computer program and manual available by anonymous FTP from Uppsala University (ftp://uu.se or ftp://systbot.uu.se).

Ronquist, F. (1997) Dispersal–vicariance analysis: a new approach to the quantification of historical biogeography. *Systematic Biology*, **46**, 195– 203.

Russell, A.P. (1972) *The foot of Gekkonid lizards: a study in comparative and functional anatomy*. PhD thesis, University of London.

Russell, A.P. (1976) Some comments concerning interrelationships amongst gekkonine geckos. *Morphology and biology of reptiles. Linnean Society Symposium Series 3* (ed. by A.d'A. Bellairs and C.B. Cox), pp. 217– 244. Academic Press, London.

Russell, A.P. (1979) Parallelism and integrated design in the foot structure of gekkonine and diplodactyline geckos. *Copeia*, **1979**, 1– 21.

Russell, A.P. (2002) Integrative functional morphology of the gekkotan adhesive system (Reptilia: Gekkota). *Integrative and Comparative Biology*, **42**, 1154– 1163.

Russell, A.P. & Bauer, A.M. (2002) Underwood's classification of the geckos: a 21st century appreciation. *Bulletin of the Natural History Museum (Zoology)*, **68**, 113– 121.

Saint, K.M., Austin, C.C., Donnellan, S.C. & Hutchinson, M.N. (1998) C-mos, a nuclear marker useful for squamate phylogenetic analysis. *Molecular Phylogenetics and Evolution*, **10**, 259– 263.

Sanderson, M. (1997) A nonparametric approach to estimating divergence times in the absence of rate constancy. *Molecular Biology and Evolution*, **14**, 1218– 1231.

Sanderson, M. (2003) r8s: inferring absolute rates of molecular evolution and divergence times in the absence of a molecular clock. *Bioinformatics*, **19**, 301– 302.

Sanmartín, I. (2003) Dispersal vs. vicariance in the Mediterranean: historical biogeography of the Palearctic Pachydeminae (Coleoptera, Scarabaeoidea). *Journal of Biogeography*, **30**, 1883– 1897.

Sanmartín, I. & Ronquist, F. (2004) Southern hemisphere biogeography inferred by event-based models: plant versus animal patterns. *Systematic Biology*, **53**, 216– 243.

Sanmartín, I., Enghoff, E. & Ronquist, F. (2001) Patterns of animal dispersal, vicariance and diversification in the Holarctic. *Biological Journal of the Linnean Society*, **73**, 345– 390.

Scally, M., Madsen, O., Douady, C.J., De Jong, W.W., Stanhope, M.J. & Springer, M.S. (2002) Molecular evidence for the major clades of placental mammals. *Journal of Mammalian Evolution*, **8**, 239– 277.

Schleich, H.H., Kästle, W. & Kabisch, K. (1996) *Amphibians and reptiles of North Africa*. Koeltz Scientific, Koenigstein, Germany.

Searle, M.P. (1991) *Geology and tectonics of the Karakorum Mountains*. John Wiley, New York.

Swofford, D.L. (2002) *paup*. Phylogenetic analysis using parsimony (*and other methods)*. Version 4. Sinauer Associates, Sunderland, MA.

Szczerbak, N.N. & Golubev, M.L. (1986) *Gecko fauna of the USSR and contiguous regions*. Naukova Dumka, Kiev, Ukraine (in Russian).

Tapponier, P., Mattauer, M., Proust, F. & Cassaigneau, C. (1981) Mesozoic ophiolites, sutures, and large-scale tectonic movements in Afghanistan. *Earth and Planetary Science Letters*, **52**, 355– 371.

Townsend, T., Larson, A., Louis, E. & Macey, J.R. (2004) Molecular phylogenetics of Squamata: The position of snakes, amphisbaenians, and dibamids, and the root of the squamate tree. *Systematic Biology*, **53**, 735– 758.

Underwood, G. (1954) On the classification and evolution of geckos. *Proceedings of the Zoological Society of London*, **124**, 469– 492.

Van Rheede, T., Bastiaans, T., Boone, D.N., Hedges, S.B., De Jong, W.W. & Madsen, O. (2006) The platypus in its place: nuclear genes and indels confirm the sister group relation of Monotremes and Therians. *Molecular Biology and Evolution*, **23**, 587– 597.

Vanhooydonck, B., Andronescu, A., Herrel, A. & Irschick, D.J. (2005) Effects of substrate structure on speed and acceleration capacity in climbing geckos. *Biological Journal of the Linnean Society*, **85**, 385– 393.

Vanzolini, P.E. (1968) Geography of the South American Gekkonidae (Sauria). *Arquivos de Zoologia*, **17**, 85– 112.

Vences, M., Kousch, J., Rödel, M.O., Lötters, S., Channing, A., Glaw, F. & Böhme, W. (2004) Phylogeography of *Ptychadena mascareniensis* suggests transoceanic dispersal in a widespread African-Malagasy frog. *Journal of Biogeography*, **31**, 593– 601.

Vidal, N. & Hedges, S.B. (2005) The phylogeny of squamate reptiles (lizards, snakes, and amphisbaenians) inferred from nine nuclear protein-coding genes. *Comptes Rendus Biologies*, **328**, 1000– 1008.

Vitt, L.J., Sartorius, S.S., Avila-Pires, T.C.S., Zani, P.A. & Espósito, M.C. (2005) Small in a big world: ecology of leaf-litter geckos in New World tropical forests. *Herpetological Monographs*, **19**, 137– 152.

Werner, Y.L. (1969) Eye size in geckos of various ecological types (Reptilia: Gekkonidae and Sphaerodactylidae). *Israel Journal of Zoology*, **18**, 291– 316.

Whiting, A.S., Sites, J.W., Pellegrino, K.C.M. & Rodrigues, M.T. (2006) Comparing alignment methods for inferring the history of the new world lizard genus *Mabuya* (Squamata: Scincidae). *Molecular Phylogenetics and Evolution*, **38**, 719– 730.

Wiens, J.J., Graham, C.H., Moen, D.S., Smith, S.A. & Reeder, T.W. (2006a) Evolutionary and ecological causes of the latitudinal diversity gradient in hylid frogs: treefrog trees unearth the roots of high tropical diversity. *The American Naturalist*, **168**, 579– 596.

Wiens, J.J., Brandley, M.C. & Reeder, T.W. (2006b) Why does a trait evolve multiple times within a clade?. Repeated evolution of snakelike body form in squamate reptiles *Evolution*, **60**, 123– 141.

Wilgenbusch, J. & De Queiroz, K. (2000) Phylogenetic relationships among the phrynosomatid sand lizards inferred from mitochondrial DNA sequences generated by heterogeneous evolutionary processes. *Systematic Biology*, **49**, 592– 612.

Xiang, Q.Y. & Soltis, D.E. (2001) Dispersal–vicariance analyses of intercontinental disjuncts: historical biogeographical implications for angiosperms in the northern hemisphere. *International Journal of Plant Sciences*, **162**, S29– S39.

Zink, R.M., Blackwell-Rago, R.C. & Ronquist, F. (2000) The shifting roles of dispersal and vicariance in biogeography. *Proceedings of the Royal Society B: Biological Sciences*, **267**, 497– 503.