



A likelihood framework analysis of an island radiation: phylogeography of the Lesser Antillean gecko *Sphaerodactylus vincenti*, in comparison with the anole *Anolis roquet*

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ABSTRACT

Aim The West Indies have hosted several spectacular radiations, including that of the litter geckos of the genus *Sphaerodactylus*. We analyse the phylogeography of the *Sphaerodactylus vincenti* complex and explore the possibility that there may be cryptic species to be revealed. Postulated colonization routes in this complex are estimated and compared with those of co-distributed lizards (the *Anolis roquet* complex).

Location Lesser Antilles.

Methods Phylogenetic relationships (gene trees) were estimated using maximum parsimony and Bayesian analysis of the cytochrome *b* sequence [mitochondrial DNA (mtDNA)] obtained from 53 individuals sampled in Dominica, Martinique, St Vincent, Bequia and Mustique. The Bayesian relaxed-clock method was used to estimate the time to the most recent common ancestor and a likelihood framework analysis was employed to probabilistically estimate the geographic origin of the main clades of the *S. vincenti* complex. These methods were repeated on the co-distributed species complex of *A. roquet*, and their timing and colonization routes were compared.

Results Phylogenetic analysis of mtDNA of the *S. vincenti* complex in the Lesser Antilles reveals a deep split between the northern (north Martinique and Dominica) and southern (south Martinique, St Vincent, Grenadines and possibly St Lucia) clades with about 22% mean divergence. Together with geological information, these results suggest that Martinique is occupied by populations that began evolving in allopatry 12.5 million years ago, and which came into secondary contact once precursor islands coalesced to produce present-day Martinique.

Main conclusions We regard the two main forms of *Sphaerodactylus* as separate species based on their substantial mtDNA divergence and largely diagnostic scapula ocelli (present in the north, but largely absent in the south). Although there are similarities in the precursor islands occupied by the *Anolis* and *Sphaerodactylus* species, their colonization sequence is different, probably due to the stochastic nature of the long-distance dispersal involved in island colonization.

Keywords

Ancestral range, *Anolis roquet*, island biogeography, Lesser Antilles, mtDNA, PhyloMapper, *Sphaerodactylus festus*, *Sphaerodactylus kirbyi*.

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INTRODUCTION

The West Indies have been the focus of considerable interest in the fields of ecology, biogeography and evolutionary biology (Hedges, 1996; Ricklefs & Bermingham, 2008), not least

because of their very high species diversity and endemism. There are several spectacular radiations in this archipelago, the most well studied being that of *Anolis* lizards (Roughgarden, 1995; Losos, 2009). Other less-studied groups in this region with impressive diversification include the extinct

megalonychid sloths (White & MacPhee, 2001), the largely extinct capromyid rodents (Woods, 1989), the eleutherodactyline frogs (Heinicke *et al.*, 2007) and the sphaerodactyline geckos (Gamble *et al.*, 2008).

The West Indies are generally considered as being composed of two major geographic and geological entities. The Greater Antilles are old fragments of continental crust, while the Lesser Antilles are of more recent origin, forming a double volcanic arc at the boundary between the Caribbean plate and the North Atlantic ocean floor (Maury *et al.*, 1990). The eastern outer arc was active from the Eocene to mid-Oligocene, while the western arc started its activity in the early Miocene and is still active today (Maury *et al.*, 1990). While the Greater Antilles may have been connected to Central America by land bridges, the Lesser Antilles never had such a connection with the continent. Moreover, most of these islands have never been connected to each other, which implies that over-water dispersal was, and is, the route for colonization of these islands (Hedges, 1996). The alternative hypothesis of the existence of a land bridge between South America and Cuba (the GAARlandia hypothesis; Iturralde-Vinent & MacPhee, 1999) is generally not supported by the timing of the diversification of Caribbean taxa (Hedges, 2006; Ali, 2012; but see Alonso *et al.*, 2011).

Geckos from the genus *Sphaerodactylus* comprise about 100 species distributed in the Caribbean Islands and adjacent continental areas. Most of this diversity, about 80 species, is in the West Indies, rendering this one of the most diverse vertebrate genera in the area (Schwartz & Henderson, 1991; Hedges, 1996). All species of *Sphaerodactylus* are typically very small, *Sphaerodactylus ariasae* being the smallest described terrestrial amniote (Hedges & Thomas, 2001). They generally inhabit leaf litter in a wide range of habitats. Phylogenetic relationships within West Indian species have been investigated using immunological and allozyme data (Hass, 1991) and mitochondrial DNA (mtDNA) sequences (Hass, 1996), but Lesser Antillean species (nine species) have been under-represented in these studies. Most species of *Sphaerodactylus* are endemic to one island, or even to a limited region within an island (Hass, 1996), but a few species of *Sphaerodactylus* from the Lesser Antilles are known to have a wider range and inhabit several adjacent islands. However, in these more widespread nominal species, high divergence suggests that they may contain forms worthy of recognition as distinct species (Thorpe *et al.*, 2008a). This high within-species divergence, allied to their extremely small size and secretive behaviour, may have led to an underestimation of the real number of species. Close investigation may therefore reveal cryptic diversity, as exemplified in a recent study of *Sphaerodactylus fantasticus*, where an extremely high molecular divergence between some of the islands of Les Saintes has led to the recognition of *Sphaerodactylus physacinus* as a distinct species (Thorpe *et al.*, 2008a).

In this study we investigate the phylogeny and biogeography of another widespread *Sphaerodactylus* species: *Sphaerodactylus vincenti* Boulenger, 1891. This relatively large-sized

sphaerodactyl gecko (snout–vent length up to 40 mm) is distributed in the central/southern Lesser Antilles on the islands of Dominica, Martinique, St Lucia and St Vincent. A phylogenetic study of the Lesser Antilles *Sphaerodactylus* species based on 430 bp of the cytochrome *b* suggested that its closest relatives are *Sphaerodactylus kirbyi* from the Grenadines, just south of St Vincent, and *Sphaerodactylus microlepis* from St Lucia (Ogden, 2002). The colour pattern is highly variable and nine subspecies have been described (see Appendix S1 in Supporting Information). This superficial morphological diversity is highest on Martinique, which has six subspecies (Schwartz, 1964). Schwartz (1964) hypothesized that this island is the centre of origin of the species and that St Lucia and St Vincent were colonized from southern Martinique populations, while Dominica was colonized from northern Martinique populations. The high colour-pattern diversity observed in Martinique may be the result of the complex geological history of this island, or adaptation to the pronounced environmental zonation on Martinique (Thorpe *et al.*, 2008b, 2010).

Martinique is composed of both younger and older arc elements. The Caravelle and Sainte Anne peninsulas have an older arc origin, whereas the rest of the island has a more recent origin. It is thought that the different parts of Martinique (Andreieff *et al.*, 1976; Maury *et al.*, 1990) were originally separate islands that merged through the uplifting of a central region in a scenario broadly compatible with that illustrated in Thorpe *et al.* (2008b). This complex history has had a profound impact on the molecular genetic diversity of another lizard, *Anolis roquet*, where very divergent lineages evolved in allopatry on distinct proto-islands before coming into secondary contact once the islands coalesced (Thorpe & Stenson, 2003; Thorpe *et al.*, 2008b, 2010). However, with this anole and other Lesser Antillean anoles, it is generally adaptation to the environmental zonation that determines its appearance (colour and pattern) and traditional subspecies (Thorpe & Stenson, 2003), rather than these geo-historical processes (Thorpe *et al.*, 2008b).

Here we construct a phylogeny of *S. vincenti* across most of its distribution range to elucidate the inter-island colonization sequence. Furthermore, we use the new statistical phylogeographic tool of likelihood framework analysis (LFA) to test probabilistically the location of the ancestors of the different lineages in relation to the proto-islands that formed present-day Martinique. We also compare this phylogeographic history on Martinique with that of the sympatric anole *A. roquet*.

MATERIALS AND METHODS

Samples

Fifty-three ingroup specimens from the *S. vincenti* complex were selected from all islands where this species is currently known to occur (Fig. 1, Appendix S2a). *Sphaerodactylus vincenti* was not sampled from St Lucia, where there was a

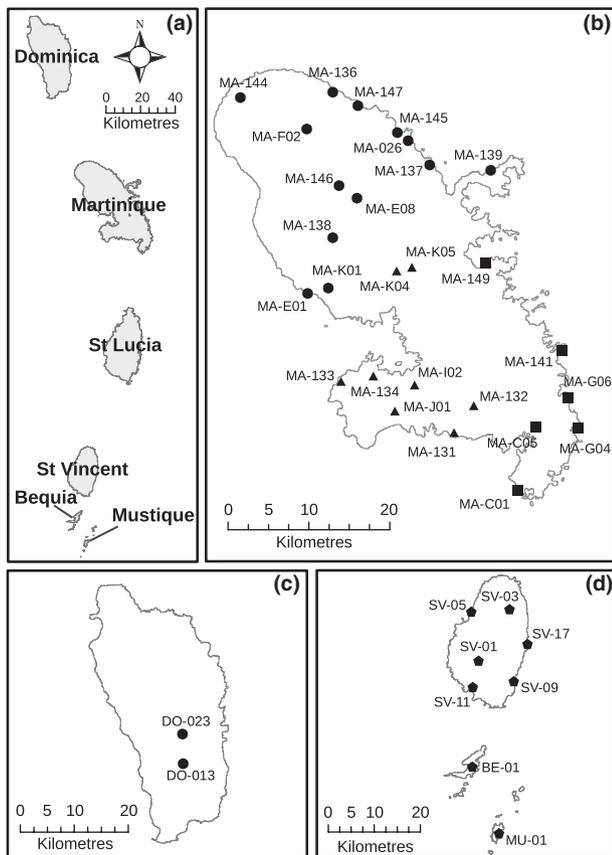


Figure 1 Map of the localities sampled for the *Sphaerodactylus vincenti* complex. (a) Overview of the study zone in the Lesser Antilles. (b) Detail of Martinique (MA) sampling. (c) Detail of Dominica (DO) sampling. (d) Detail of St Vincent (SV) and the Grenadines [Bequia (BE) and Mustique (MU)] sampling. Locality codes correspond to the sites described in Appendix S2 and the symbols used correspond to the four main clades as in Fig. 2.

report of its discovery at a single locality (Schwartz, 1964), but where we, and other herpetologists (S. B. Hedges, Pennsylvania State University, pers. comm.) have failed to find this species in spite of recent intensive, organized fieldwork. The locality on this island where *S. vincenti* was reported has been extensively developed in the following decades and its persistence is questionable; although as these geckos are cryptic, one cannot exclude this possibility. Preliminary analyses using a short cytochrome *b* sequence of *S. kirbyi* from the Grenadines (Bequia) showed that this sample was nested deeply within *S. vincenti* (Y.S.G., unpublished data). We therefore obtained two tissue samples of *S. kirbyi* from Grenadines (Mustique) for further investigation. We used *S. microlepis* from St Lucia and *S. fantasticus* from Guadeloupe as outgroups. Voucher specimens used in this study are deposited at the Molecular Ecology and Evolution of Reptiles Unit at Bangor University. The *A. roquet* sample localities are given in Thorpe & Stenson (2003) and Thorpe *et al.* (2005), with additional information in Thorpe *et al.* (2008b).

Molecular methods

Genomic DNA was extracted using a Chelex procedure (Estoup *et al.*, 1996) from autotomized tail tissue that was fixed in ethanol. A fragment of mtDNA that included the complete cytochrome *b* gene was amplified using primers rGlu-1L (Kumazawa & Endo, 2004) and rPro-1H3 (TWA AAATKCTAGTTTTGGG). We used 10 μ L reactions with 3 mM MgCl₂, 0.3 mM of each nucleotide, 0.8 μ M of each primer, 0.5 units of GoTaq[®] Hot Start Polymerase with 2 μ L of 5 \times Colorless Flexi Buffer (Promega, Madison, WI, USA). Cycling conditions were a first denaturation and Taq activation step at 95 $^{\circ}$ C for 5 min, followed by 35 cycles (20 s for 95 $^{\circ}$ C, 30 s at 48 $^{\circ}$ C, and 45 s at 72 $^{\circ}$ C) and a final elongation step at 72 $^{\circ}$ C for 5 min. Polymerase chain reaction (PCR) products were then purified with Exonuclease I and Shrimp Alkaline Phosphatase and sequenced using internal primers cytb2F-2 (ACAACGCCACCCTAACACGATT) and cytb3R-2 (GGTGGGAATGTGATTTTATCTG) by MacroGen (<http://www.macrogen.com>). Sequences were edited and aligned with Codoncode Aligner (Codoncode Corporation, Dedham, MA, USA) and deposited in GenBank (see Appendix S2a for accession numbers). For the *A. roquet* complex, we used previously published sequences (Thorpe *et al.*, 2008b).

Phylogenetic analyses: *S. vincenti* complex

Phylogenetic analyses were performed using both maximum parsimony (MP) and Bayesian analysis (BA). For MP, PAUP* 4.0b10 (Swofford, 1999) was used to perform a heuristic search with tree bisection–reconnection (TBR) branch swapping and 1000 random sequence addition replicates. All characters were equally weighted and gaps were treated as missing data. Node support was estimated using nonparametric bootstrapping (Felsenstein, 1985) with 1000 replicates. For BA, the Bayesian information criterion (BIC) was used to select the best-fit model of nucleotide substitution using MRBIC 1.4.3 (Nylander, 2004). Two independent runs of eight chains (one cold and seven incrementally heated) were performed for 20 million generations with trees sampled every 1000th generation using MRBAYES 3.1 (Huelsenbeck & Ronquist, 2001). Convergence and stationarity were detected using TRACER 1.4 (Rambaut & Drummond, 2007) and the diagnostic statistics included in MRBAYES. The first 10 million generations were discarded as burn-in and the remaining trees were combined in a 50% majority rule consensus tree.

Divergence time between lineages

As we wished to compare lineage divergence with the geological times of island origin, we did not use geological dates of origin as calibration points. Instead we used a mean substitution rate calculated from other studies of squamates, including geckos (Brown & Pestano, 1998; Macey *et al.*, 1998; Gubitz *et al.*, 2000; Brown *et al.*, 2001; Zarza *et al.*, 2008) as

well as the rates estimated using multiple geological calibration points and corrected genetic distances with another Lesser Antillean species of *Sphaerodactylus* (Thorpe *et al.*, 2008a). We used a Bayesian relaxed-clock method implemented in BEAST 1.7 (Drummond & Rambaut, 2007) to estimate the age of the most recent common ancestor (MRCA) of the different clades. We used the same substitution model as for the BA above, used an informative prior for the ucl. mean parameter (0.0075 ± 0.0025 per site per million years) and selected an uncorrelated lognormal relaxed molecular clock model (Drummond *et al.*, 2006). Three runs of 20 million generations were executed, with a sampling every 1000 generations. Convergence and stationarity were checked using TRACER 1.4, and the first 5 million generations were discarded as burn-in. We first checked that the results of the three independent runs were similar, then we combined them and extracted the mean MRCA age and its 95% confidence interval with TRACER 1.4 (Rambaut & Drummond, 2007). For comparison, we repeated this process for the *A. roquet* tree featured in Thorpe *et al.* (2008b). Because of the larger number of sequences, we ran three runs of 100 million generations each, and discarded the first 25 million as burn-in.

Phylogeographic structure and lineage history: likelihood framework analysis

For both species complexes we used the software PHYLOMAPPER 1b1 (Lemmon & Lemmon, 2008) to estimate the phylogeographic history of the different lineages within Martinique. This software provides a statistical framework that allows both an estimate of phylogeographic history (and its statistical confidence) without *a priori* hypotheses, and for testing alternative hypotheses. Based on a gene tree with known topology and branch lengths (the Bayesian tree here), and a spatially explicit random walk migration model, this method allows the maximum likelihood estimation of the ancestral geographic coordinates, given the observed current coordinates, using an iterative optimization approach (Lemmon & Lemmon, 2008). Here we assume that each lineage evolved on a separate proto-island and thus we do not try to estimate the location of the ancestor of the species. We used this method to: (1) test for a phylogeographic association in the different lineages identified (null distribution generated by permuting the geographic locations of the tips of the genealogy 10,000 times); and (2) locate the geographic position of the ancestor of these lineages. We estimated the 95% confidence envelope of this position (i.e. the surface including all the positions that are not significantly different from the estimated maximum likelihood location) by sampling all the putative range every 0.05° of longitude and latitude, and comparing these sampled locations with the maximum likelihood one using a likelihood ratio test with one degree of freedom. We then compared these spatial confidence envelopes with a range of potential precursor islands (i.e. Caravelle, Pitons du Carbet, Morne Jacob, Piton Mont Conil, Morne

Pavillon, Montagne du Vauclin and Sainte Anne) to determine on which island each lineage most likely originated. Finally, because this method assumes that the gene tree is known, we investigated the effect of phylogenetic uncertainty on the estimation of ancestors' locations according to the method proposed by Lemmon & Lemmon (2008). To do that, we randomly sampled 1000 trees from the Bayesian posterior distribution and estimated the location of ancestors using each of these 1000 trees.

In order to compare the phylogeographic structure and lineage history of the *S. vincenti* complex with that of another Martinique species complex we selected the *A. roquet* complex. For this we used the populations and the Bayesian tree described in Thorpe *et al.* (2008b). We first investigated the four main clades: the north-west, south-west, south and central lineages. We also investigated the two sublineages on the north-west clade, but not those of the south-west clade, due to insufficient sample sites for the latter. All PHYLOMAPPER analyses were conducted using 1000 iterations.

RESULTS

Phylogenetic analysis: *S. vincenti* complex

A total of 1251 bp were aligned between all taxa. The alignment was straightforward with no gaps within the cytochrome *b* coding sequence and just a 3 bp deletion after the end of this gene for the ingroup. No stop codons were detected within the coding sequence, suggesting that we did not amplify a pseudogene. Forty-seven unique haplotypes were identified from the 53 ingroup individuals sequenced. The best fit model selected was a general time reversible with rate heterogeneity (GTR + G).

Maximum parsimony gave 380 trees with 917 steps (retention index = 0.8982, rescaled consistency index = 0.5495). The strict consensus of these trees is almost identical to the Bayesian tree (Fig. 2), differing at just a few weakly supported terminal nodes. All the principal nodes are strongly supported by both methods [Bayesian posterior probabilities (PP) > 0.97 and bootstrap support (BS) > 83%] and four main lineages can be distinguished. The first is composed of haplotypes from northern Martinique and Dominica (C1: PP = 1.00, BS = 100%), the second of haplotypes from south Martinique (C2: Sainte Anne Peninsula, PP = 1.00, BS = 99%), the third of haplotypes from south-western Martinique (C3: Trois-Îlets Peninsula, PP = 1.00, BS = 100%) and the fourth of haplotypes from St Vincent and Grenadines, including *S. kirbyi* (C4: PP = 0.97, BS = 83%). Haplotypes from *S. kirbyi* do not form a monophyletic group. Within the first clade, the two haplotypes from Dominica are monophyletic (PP = 1.00, BS = 100%) and cluster together with haplotypes from the Caribbean coast of Martinique, but this last relationship is weakly supported (PP = 0.86, BS = 69%). Within the St Vincent–Grenadines clade, the first dichotomy is found between haplotypes from Mustique and the rest, followed by a division between Bequia and St Vincent.



Figure 2 Bayesian tree showing the phylogenetic relationships among the studied samples of the *Sphaerodactylus vincenti* complex from the Lesser Antilles. Numbers above branches are the bootstrap support from the maximum parsimony tree and the node posterior probabilities. The ages of the nodes discussed in the text (indicated by a black dot on the tree) are indicated below the corresponding branch (mean and 95% highest posterior density interval, in million years ago). Sample codes correspond to those given in Appendix S2. Four main clades can be distinguished whose geographic distribution is represented in Fig. 1.

Haplotypes from St Vincent are monophyletic, but this is weakly supported (PP = 0.64, BS = 69%).

Phylogeographic structure and divergence times: *S. vincenti* complex

There was a significant phylogeographic structure in the three lineages from Martinique (PHYLOMAPPER $P < 0.001$ for each clade). The locations of the ancestor of the different lineages and their 95% confidence envelope are indicated in Fig. 3a, and the effect of phylogenetic uncertainty on this estimation is depicted in Fig. 3b. The former indicates that the ancestor of the northern clade could be associated with either Morne Jacob or Pitons du Carbet, the ancestor of the south-eastern clade could be associated with either Montagne du Vauclin or the Sainte Anne Peninsula and the ancestor of the south-western clade could be associated with Morne Pavillon or Montagne du Vauclin (Fig. 3a). The old-arc proto-island of the Caravelle Peninsula and the young Piton Mont Conil were not associated with any lineage ancestor. The age

of the MRCA of the main lineages ranges from 12.5 Ma for the ancestor of all *S. vincenti* haplotypes to 1.5 Ma for the ancestor of clade C3 occupying south-west Martinique (Fig. 2). The age of the MRCA is estimated to be 1.6 Ma for the Dominican haplotypes and 1.6 Ma for the St Vincent haplotypes.

Phylogeographic structure and divergence times: *A. roquet* complex

Like *S. vincenti*, *A. roquet* shows deep phylogenetic lineages that are most likely the result of allopatric differentiation on different proto-islands (Thorpe & Stenson, 2003; Thorpe *et al.*, 2008b). However, there are more lineages distinguishable in *A. roquet*, and some of the main lineages can be further divided in two (Fig. 4a). The ancestor of the central lineage is located in the central region of Martinique (Fig. 4b) as are the centres from all the 1000 randomly selected trees. However, the 95% confidence envelope overlaps the Caravelle Peninsula so we cannot entirely exclude

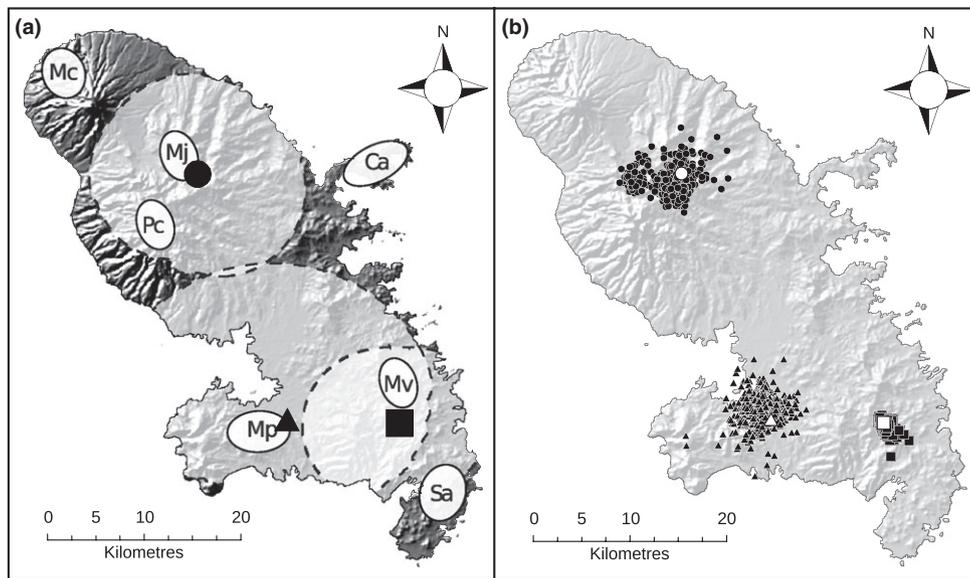


Figure 3 Maximum likelihood estimates of the location of the ancestor of the northern, south-eastern and south-western clades of the *Sphaerodactylus vincenti* complex from the Lesser Antilles. (a) Confidence envelopes (95%) with the locations used to represent the position of the proto-islands on the proto-island test: Ca, Caravelle Peninsula; Mc, Piton Mont Conil; Mj, Morne Jacob; Mp, Morne Pavillon; Pc, Pitons du Carbet; Mv, Montagne du Vauclin; Sa, Sainte Anne peninsula. (b) Effect of the genealogy on the estimated location of the clade ancestors for *S. vincenti*. The white symbols represent the location of the ancestors estimated from the tree shown in Fig. 2 while the black symbols represent the locations of the ancestors estimated using 1000 trees sampled randomly from the Bayesian posterior distribution.

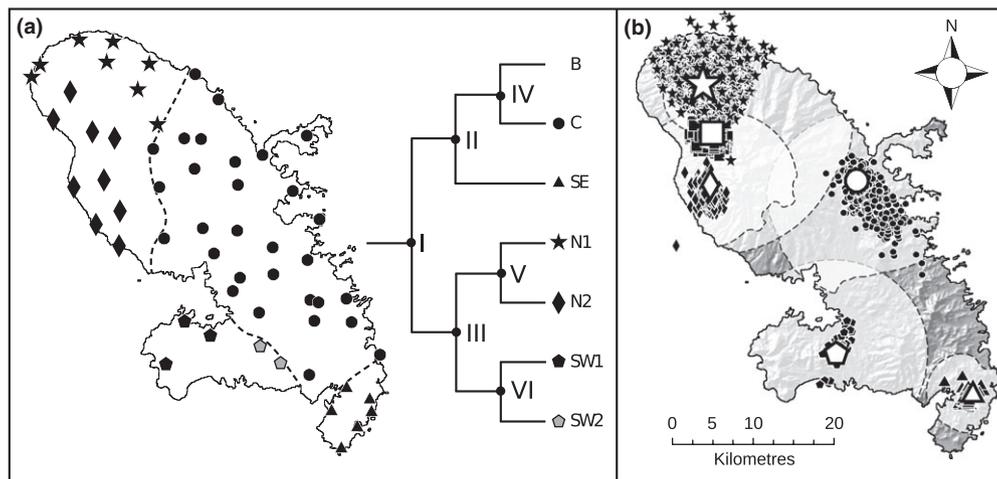


Figure 4 Phylogeography of the *Anolis roquet* complex. (a) Schematic tree representing the phylogenetic relationships among *A. roquet* main lineages and the geographic distribution of these lineages (after Thorpe *et al.*, 2008b). Codes are: B, Barbados; C, central Martinique; S, south Martinique; NW, north-west Martinique; SW, south-west Martinique. Roman numerals correspond to nodes discussed in the text and in Table 1. (b) Maximum likelihood estimates of the location of the ancestor of the main lineages of *A. roquet* and their associated 95% confidence envelopes.

an origin in this area, although the central area is the most likely area of origin. The sister group of this central clade is the southern lineage that is centred on the Sainte Anne Peninsula. The undivided south-western lineage is associated with the Trois-Îlets Peninsula. The north-western clade is associated with the north-west precursor island from the

younger arc. Two subclades can be distinguished within this north-west lineage, the first one (NW1) being associated with the Pitons du Carbet and the second one (NW2) with the Piton Mont Conil–Montagne Pelée complex. Age estimates for nodes in Fig. 4a are given in Table 1 and Appendix S3.

Table 1 Node ages for the *Anolis roquet* complex (in million years ago, Ma). The node names correspond to those given in Fig. 4 and Appendix S3.

Node	Mean age (Ma)	95% HPD
I	8.37	3.35–15.45
II	6.74	2.67–12.32
III	5.57	2.03–10.38
IV	5.39	2.16–9.85
V	3.43	1.13–6.67
VI	2.82	0.75–5.68
C	3.27	1.14–6.16
SE	3.00	0.82–5.99
N1	1.76	0.48–3.54
N2	1.38	0.33–2.90
SW1	0.59	0.00–1.53
SW2	1.23	0.20–2.72
B	4.41	1.74–8.06

HPD, highest posterior density.

DISCUSSION

Phylogenetic relationships and species status: *S. vincenti* complex

The primary division in our gene tree separates the lineages occupying northern Martinique and Dominica (northern clade) from those occupying the southern half of Martinique and islands to the south, St Vincent and the Grenadines (southern clade). Individuals from the area occupied by the northern mtDNA lineage can readily be distinguished from the region occupied by the southern lineage as they have a pair of black ocelli with white spots on the shoulder (above the anterior limb). These ocelli are generally absent in southern individuals (Appendix S2b). The only previous *Sphaerodactylus* species complex to be investigated in depth (*S. fantasticus*), shows no such clear link between morphology and mtDNA lineage (Thorpe *et al.*, 2008a). In fact, in lizards from environmentally heterogeneous Lesser Antillean islands, quantitative traits, including colour pattern traits, generally vary spatially in response to the environmental zonation rather than reflect the relatively deep phylogeographic divisions. This is overwhelmingly so with the various anoles species which have been investigated (Thorpe, 2002; Thorpe & Stenson, 2003; Losos, 2009). Consequently, the link between a diagnostic trait and a lineage is unusual in these organisms, and the deep division in the gene tree (21.7% corrected divergence) and largely diagnostic trait raises the issue as to whether these two lineages should be recognized as distinct species. Two specimens with a southern haplotype (MA-141 and MA-149) had ocelli. This could simply mean that this single character is not perfectly 100% diagnostic, or it could reveal some genetic exchange between these largely parapatric forms. Neither precludes their recognition as separate species, but better sampling in critical areas and detailed work using nuclear genetic markers is necessary for a more rigorous test of their species status. Never-

theless, with the information currently available we regard them as separate species. We recognize the northern form, showing the diagnostic dark ocelli with light centres, as *S. festus*. This form was described in Schwartz (1964) as *S. vincenti festus*, and was originally described as a species (*S. festus*) by Barbour (1915). The holotype (MCZ10622) is from 1 km north-west of Schoelcher on the Caribbean coast of northern Martinique. The range of this species is northern Martinique (approximately north of a line from Schoelcher to the Caravelle Peninsula) and Dominica. The range of this species includes the conventional subspecies *monolifer* and *pheristus* and some of the range of *ronaldi*.

The southern clade occupies the southern half of Martinique (approximately south of a line from Fort de France to just south of the Caravelle Peninsula), St Vincent and the Grenadines. The Grenadine litter gecko, *S. kirbyi*, does not appear to warrant species status. This species was described from the Grenadines by Lazell (1994), but our results show that this taxon is not monophyletic and is nested deeply within *S. vincenti*. We therefore consider that *S. kirbyi* is a junior synonym of *S. vincenti*. Hence, *S. vincenti sensu stricto* generally lacks scapula ocelli and is distributed across the southern half of Martinique, St Vincent, the Grenadines and possibly St Lucia. The range of this species includes the conventional subspecies *vincenti*, *josephinae*, *psammius* and part of the range of *ronaldi*, and also probably *adamus* from Martinique islet of Rocher du Diamant.

In the northern clade (C1) the Dominican haplotypes are a weakly supported sister group to the Martinique northern Caribbean coastal haplotypes (north of Schoelcher, close to the type locality of this northern species). Other than the tendency for spatially close haplotypes to group together there is little other pronounced phylogeographic structure in the northern clade. In the southern clade phylogeographic structure is more apparent, and there are three well-supported main subclades; C2 occupies the Sainte Anne Peninsula in the south and the south-east coast of Martinique (corresponding to the conventional subspecies *psammius* and part of *ronaldi*), C3 occupies the south-west (Trois-Îlets) peninsula and some central regions of Martinique (conventional subspecies *josephinae* and *adamus*), and C4 occupies St Vincent and the Grenadines (ex *S. kirbyi* and conventional subspecies *S. v. vincenti*). The Grenadine/St Vincent (C4) clade is a sister group to the south-west/central Martinique (C3) clade. None of these southern clades (C2, C3, C4) have notable phylogeographic structure within them and the Grenadines do not form a monophyletic group with the C4 clade. This lack of substructure within the four main clades (C1–C4) is not typical of phylogeographic structure in Lesser Antillean island lizards or those from other archipelagos such as the Canary Islands. Many show progressive substructure, such as the Martinique anole (Thorpe & Stenson, 2003), the fantastic litter gecko (Thorpe *et al.*, 2008a) and Canary Island geckos (Gubitz *et al.*, 2000). The lack of progressive substructure may well be the result of bottlenecking within these four main clades.

Historical biogeography: *S. vincenti* complex

The phylogenetic evidence suggests that the species complex originated in Martinique and then colonized the other islands as hypothesized by Schwartz (1964), and the pattern of intra-island variation on Martinique suggests that the different lineages are a result of the complex geological history of this island. Likelihood framework analysis indicates that the estimated location of the different lineage ancestors on Martinique can be associated with several precursor areas.

The ancestor of the northern clade is located very close to Morne Jacob, and the 1000 tree estimates (Fig. 3b) are tightly clustered around this area. The likelihood framework confidence envelope does not allow us to reject the hypothesis that the ancestral location was on the more recently formed Pitons du Carbet, but this appears less likely. The rejection of an ancestral location for this clade on the very recent Piton Mont Conil is not surprising, but the rejection of the ancient Caravelle Peninsula is surprising given the age of the primary split. This suggests that even if Caravelle may have been colonized early by a lineage of *S. vincenti*, it went extinct and was replaced by the lineage that evolved later in the Morne Jacob/Pitons du Carbet area. With just the one sample from the Caravelle Peninsula, firm conclusions cannot be drawn. Hence more extensive sampling of this area may bring a different perspective on the importance of this peninsula for the observed genetic diversity of *S. vincenti*. The ancestor of the south-eastern lineage is located close to Montagne du Vauclin and the 1000 tree estimates are tightly clustered around this area. However, the confidence envelope overlaps the older precursors of Sainte Anne, which cannot therefore be excluded as the ancestral site of this lineage. The 95% confidence envelope for the location of the ancestor of the south-western clade overlaps with two proto-islands, the Montagne du Vauclin and the Morne Pavillon, but this lineage is more likely to have originated on the latter, as the 1000 tree estimates (Fig. 3b) are all clustered to a greater or lesser extent around this area and not Vauclin.

Colonization timing and sequence: *S. vincenti* complex

Between-island divergence times can be exaggerated by subsequent loss of, or failure to sample, haplotypes, and this is proportionally more influential with recent events. Bearing in mind that the actual separation of two populations is always younger than the age of their MRCA (Arbogast *et al.*, 2002), it is possible to infer the inter-island colonization sequence of this species employing the estimated location of the intra-island lineage ancestors together with the divergence times between lineages.

The first split occurred around 12.5 Ma (95% confidence interval 5.1–22.4) between populations in southern and northern Martinique. At the time of divergence, the inner arc had not yet started its activity and the only emerged

islands were the Sainte Anne Peninsula in the south and the Caravelle Peninsula in the north (Westercamp *et al.*, 1989), which generates complications in interpreting the LFA results. The LFA suggests the ancestor of the northern lineage was located on Morne Jacob, and not on ancient Caravelle, but Morne Jacob emerged only 4 Ma (Westercamp *et al.*, 1989), so it can only have been colonized considerably later than the initial north–south split. The most likely situation is that Caravelle was the original site of the northern clade (*c.* 12.5 Ma) and this colonized Morne Jacob when it emerged (*c.* 4 Ma), but subsequently the Caravelle-specific haplotypes were lost before, or when, the area was invaded by the Morne Jacob population when the islands coalesced. The age of the MRCA of the northern clade is 4.6 (1.8–8.4) Ma, which is compatible with the age of Morne Jacob and this scenario.

The LFA suggests Montagne du Vauclin to be the most likely ancestral site for the south-east lineage. The age of this proto-island is 9.5 Ma (Westercamp *et al.*, 1989) which is more recent than the mean age of the first split (12.5 Ma), but is included in its confidence interval. Bearing in mind the caveats regarding the relationship between the MRCA and actual time of separation of populations, this could be the site of the ancestral population. On the other hand, the 95% confidence envelope of the LFA overlaps slightly with the ancient Sainte Anne Peninsula, so the alternative hypothesis of an ancestral population on this peninsula cannot be excluded, although it is less likely than an origin on Montagne du Vauclin (Fig. 5a, step I).

Subsequent to the north–south split the south-western populations split from the south-eastern populations at *c.* 8.1 (3.3–14.3) Ma, which is broadly compatible with the geological age of Morne Pavillon and surrounding areas (9–6.8 Ma, Westercamp *et al.*, 1989), the location of the ancestral population suggested by LFA. The Morne Pavillon area could have been colonized from Vauclin, or even directly from Sainte Anne, depending on the interpretation above (Fig. 5a, step II).

These south-western populations are the origin of the colonization of the islands further south, including the Grenadines and St Vincent and possibly St Lucia. These appear to have split from the south-west population at 5.1 Ma (2.1–9.3). The Grenadines haplotypes are basal to the St Vincent haplotypes, suggesting that St Vincent may have been colonized from the Grenadines (Fig. 5a, step III). However, the absence of St Lucian samples may compromise this interpretation.

Finally, Dominica was colonized from north Martinique, perhaps from the north Caribbean coast, which has sister haplotypes to Dominica (Fig. 5a, step III). The age of the MRCA for the samples from Dominica is 1.6 (0.4–3.1) Ma, but the estimate may be somewhat unreliable because only two samples were available for this island.

Comparison with sympatric anoles

The complex geological history of Martinique is likely to have had a profound impact on the genetic diversity of the

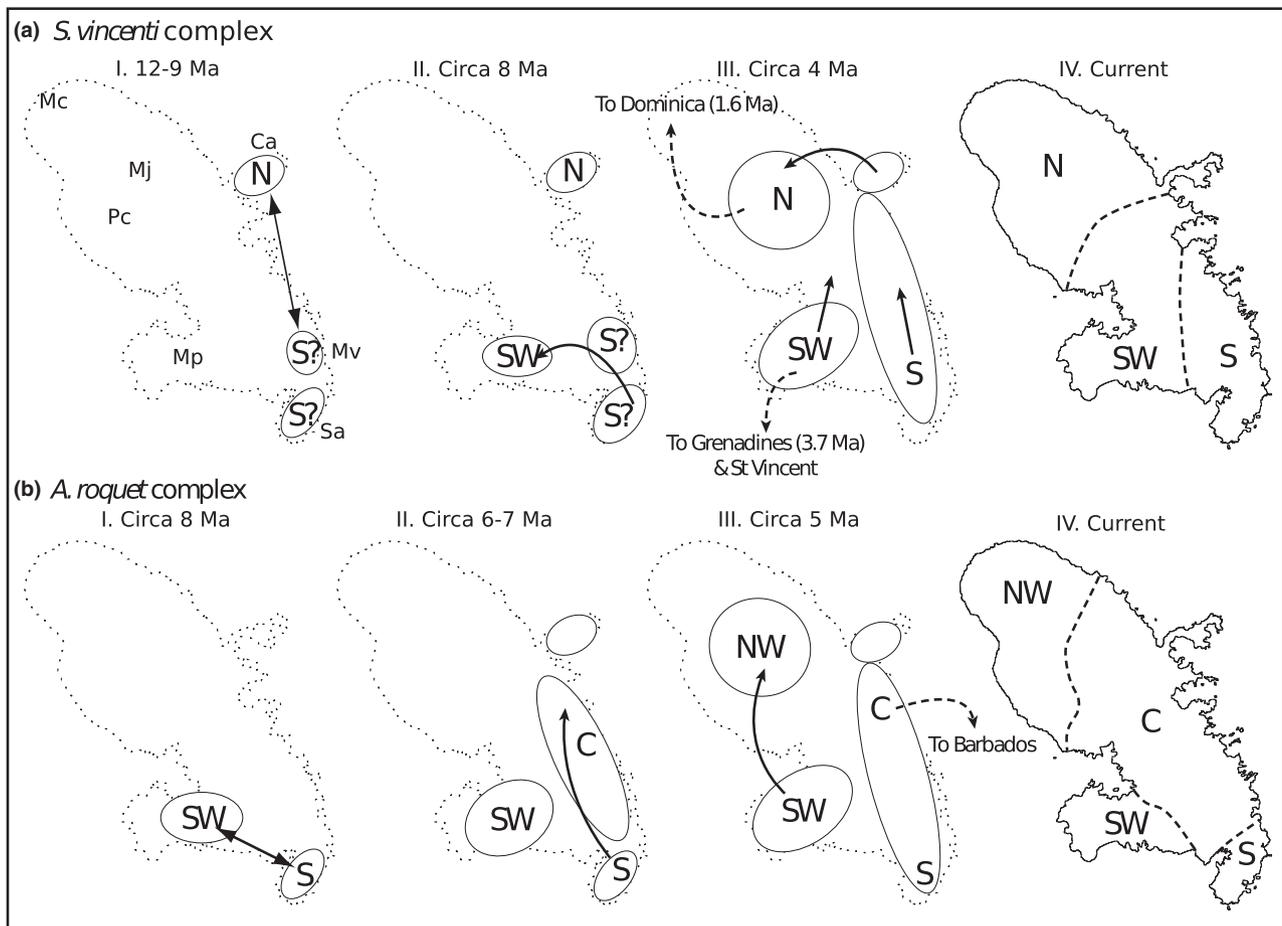


Figure 5 Colonization sequence for the *Sphaerodactylus vincenti* and *Anolis roquet* complexes on the Martinique precursors and associated islands. (a) The *S. vincenti* complex. (I) The first divergence is between Sainte Anne (Sa) in the south and probably Caravelle (Ca) in the north, with (II) subsequent colonization of the Morne Pavillon (Pa) in the south-west peninsula either directly from Sainte Anne or via Vauclin (Va), and the colonization of the northern younger arc areas of Morne Jacob (Mj) and Pitons du Carbet (Pc) with subsequent loss of Caravelle haplotypes. (III) Dominica was then colonized from the north and then the Grenadines from the south-west, and subsequently St Vincent from the Grenadines, the occupation and role of St Lucia being unknown. (b) *A. roquet* complex. (I) The first divergence is between Sainte Anne and the Morne Pavillon in the south-west peninsula, (II) then the south colonized either the Vauclin or Caravelle areas with subsequent colonization of Barbados, and the south-west colonized the north-west (Piton du Carbet and associated area). (III) The central region was then colonized from either the Caravelle or Vauclin areas with subsequent loss of original haplotypes, and there was secondary divergence within both the south-west and north-west regions with the Montagne Pelée area being colonized recently (see text for further explanation).

terrestrial fauna of the island. However, despite this interesting history, the only other terrestrial species that has been studied in detail on this island is the lizard *A. roquet* (Thorpe & Stenson, 2003; Thorpe *et al.*, 2008b). Here the dates of the earlier nodes estimated by BEAST assuming a 'lizard' clock are very close to those estimated from using geological calibration points, particularly for deeper nodes (Thorpe *et al.*, 2005). In *A. roquet* more lineages can be distinguished than in *S. vincenti*, and the divergence starts rather later, but these lineages occupied some of the same proto-islands. The first split in this species separates a central + south group (clades C and S) from a western group (clades SW and NW) with an age of the MRCA of 8.4 Ma (node I; 3.3–15.4 Ma). The LFA indicates a precursor population on the SW peninsula at Morne Pavillon/Ducos (the same as for

the *S. vincenti* complex), and another on the ancient Sainte Anne Peninsula (one of the several possibilities for the *S. vincenti* complex). Hence the first step for this complex is a divergence between a Sainte Anne population and a SW peninsula (Morne Pavillon) population early on in the geological origin of the latter (Fig. 5b, step I). Chronologically, the next phylogenetic division is between the southern (Sainte Anne) population and the central Martinique/Barbados group lineage *c.* 6.7 Ma (node II; 2.7–12.3 Ma). The LFA suggests an origin in the northern central region. At this period, the underwater mountain chain of Vauclin-Pitault had been uplifted, and this whole central region was at least partly emerged, and maybe already connected to the Caravelle area (Fig. 5b, step II; Westercamp *et al.*, 1989). The low diversity of this central clade (Thorpe *et al.*, 2008b)

compared with its considerable age (Table 1) also suggests a severe bottleneck and haplotype loss. At a slightly later stage, c. 5.6 Ma (node III; 2.0–10.4 Ma) the SW and NW lineages split, and the LFA suggests a north-west origin. Both Pitons du Carbet and Morne Jacob are located within the probability contour of the LFA. Although these precursor islands were not emerged at the earliest times suggested by the confidence interval for this split, they were emerged by the later times, and so the timing is compatible with an origin on either Morne Jacob or the Pitons du Carbet (Fig. 5b, step III). The NW lineage subsequently split, suggesting a colonization of the more northerly Mt Conil/Montagne Pelée area once it had emerged.

The *S. vincenti* complex is somewhat older than the *A. roquet* complex, but a comparison of the two species complexes suggests a similar history of divergence in allopatry on precursor islands and subsequent secondary contact when the precursor islands coalesced into present-day Martinique. They share some precursor islands, and a combination of dating and LFA suggests that early populations of both complexes may have occupied the ancient precursor of Caravelle, but have been subsequently lost. Nevertheless, aspects of their colonization history differ and this is to be expected. Although in some co-distributed species vicariance events may result in similar phylogeographic patterns (Schneider *et al.*, 1998), the stochastic nature of the long-distance dispersal involved in island colonization means that many will not (Crandall *et al.*, 2008; Parent *et al.*, 2008).

The centres of origin indicated by LFA clearly depend on the arbitrarily selected phylogenetic level. This may be because violations of the assumptions of the model are more likely when the lineage is older. The analyses of the *A. roquet* NW lineage illustrated this situation. By selecting the whole NW clade for the analysis, we included two sublineages that evolved on separate islands, thus violating the assumption of dispersal across a continuous landscape. By analysing the two subclades separately, we were able to have a more reliable result, with smaller confidence envelopes. However, we notice that the inferred ancestor of the NW clade is situated between the inferred ancestors of the N1 and N2 lineages and its 95% confidence envelope contains both ancestors of its two sublineages. Hence, it appears that working at a phylogenetic level that violates some of the assumptions of the method does not lead to false results, but just limits the precision of the ancestral locality. Although we did not have enough samples to perform a similar analysis within the SW lineage, we expect a similar situation in this case.

The resolution of the likelihood framework analysis is limited if a lineage has a limited geographic distribution and few haplotypically discrete terminal nodes. Nevertheless, when combined with both molecular and geological dates, it offers a useful insight into colonization sequence. Here it has proved particularly useful in making explicit the possible role of the ancient Caravelle area, even though original Caravelle haplotypes no longer exist among those sampled.

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SUPPORTING INFORMATION

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

Appendix S1 Conventional subspecies of the *Sphaerodactylus vincenti/kirbyi* complex.

Appendix S2 (a) List of specimens used in this study with locality and GenBank accession numbers. (b) Images of males and females of *Sphaerodactylus vincenti* and *S. festus*.

Appendix S3 BEAST tree for the *Anolis roquet* complex.

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