Molecular Ecology (2008) doi: 10.1111/j.1365-294X.2007.03686.x

Adaptive radiation in Lesser Antillean lizards: molecular phylogenetics and species recognition in the Lesser Antillean dwarf gecko complex, *Sphaerodactylus fantasticus*

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Abstract

The time associated with speciation varies dramatically among lower vertebrates. The nature and timing of divergence is investigated in the fantastic dwarf gecko *Sphaerodactylus fantasticus* complex, a nominal species that occurs on the central Lesser Antillean island of Guadeloupe and adjacent islands and islets. This is compared to the divergence in the sympatric anole clade from the *Anolis bimaculatus* group. A molecular phylogenetic analysis of numerous gecko populations from across these islands, based on three mitochondrial DNA genes, reveals several monophyletic groups occupying distinct geographical areas, these being Les Saintes, western Basse Terre plus Dominica, eastern Basse Terre, Grand Terre, and the northern and eastern islands (Montserrat, Marie Galante, Petite Terre, Desirade). Although part of the same nominal species, the molecular divergence within this species complex is extraordinarily high (27% patristic distance between the most divergent lineages) and is compatible with this group occupying the region long before the origin of the younger island arc. Tests show that several quantitative morphological traits are correlated with the phylogeny, but in general the lineages are not uniquely defined by these traits. The dwarf geckos show notably less nominal species-level adaptive radiation than that found in the sympatric southern clade of *Anolis bimculatus*, although both appear to have occupied the region for a broadly similar period of time. Nevertheless, the dwarf gecko populations on Les Saintes islets are the most morphologically distinct and are recognized as a full species (*Sphaerodactylus phyzacinus*), as are anoles on Les Saintes (*Anolis terraealtae*).

Keywords: adaptive radiation, Lesser Antilles, mtDNA, phylogeography, speciation

Received 28 June 2007; revision received 24 November 2007; accepted 16 December 2007

Introduction

The evolutionary timescale of divergence and speciation in small ectothermic vertebrates varies widely. At one extreme, African lake cichlid fishes may show species swarms evolving over a time period measured in hundreds or tens of thousands of years. For example, East African Haplochromini from the Lake Victoria catchment have evolved species flocks with 500–800 species in 89 000–120 000 years (Verheyen *et al*. 2003; Genner *et al*. 2007) requiring rapid speciation. In contrast, speciation in Caribbean lizards, such as anoles, may be measured in several millions of years (Creer *et al*. 2001; Thorpe & Stenson 2003; Thorpe *et al*. 2005a). Indeed, population genetic studies suggest that even 8 million years of divergence may be insufficient for allopatric speciation in Lesser Antillean anoles (Ogden & Thorpe 2002; Thorpe 2005). This is in spite of the fact that anoles do not appear to have a slower rate of molecular evolution than African lake fishes (Thorpe *et al*. 2005a; Genner *et al*. 2007), may be able to respond rapidly to selection pressures (Malhotra & Thorpe 1991; Thorpe & Malhotra 1992; Losos *et al*. 2004, 2006; Schoener *et al*. 2005; Thorpe *et al*. 2005b), and are among the most speciose genera of terrestrial vertebrates (Losos 2004).

Research into the adaptive radiation of lizards on small islands, across several taxa (geckos, lacertids, skinks and anoles) and biogeographical regions (Caribbean and Canary

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Islands), has shown the existence of both old phylogeographical lineages within nominal species and population ecotypes adapted by natural selection to environmental zonation within these islands (Brown *et al*. 1991; Thorpe *et al*. 1996; Malhotra & Thorpe 2000a; Thorpe & Richard 2001; Thorpe 2002; Gübitz *et al*. 2005). Natural selection experiments (Malhotra & Thorpe 1991; Thorpe *et al*. 2005b), parallel variation among independent islands (Brown *et al*. 1991; Thorpe *et al*. 1996, 2004) and correlations between traits and environmental factors (Thorpe *et al*. 1996; Thorpe & Malhotra 1996; Gübitz *et al*. 2000, 2005; Malhotra & Thorpe 2000a; Thorpe 2002; Thorpe & Stenson 2003) give a portrait of potentially rapid and widespread adaptation across numerous traits such as scalation, hue, colour pattern, body size and shape. As a generalization, little of this pronounced variation within small islands appears to be linked to the lineages, in spite of their considerable age. Hence, natural selection appears to be the dominant process in determining the current appearance of these animals, rather than deep-seated historical processes. Apart from its importance in elucidating the process of adaptation (Thorpe *et al*. 2004) and speciation (Thorpe & Richard 2001; Ogden & Thorpe 2002), this has implications for systematics, not least when a nominal species is distributed across several islands. Conventionally, such trait variation within nominal species (both within and among islands) has been dealt with by naming subspecies, but in many cases they do not reflect the lineages and they are an inadequate and inaccurate reflection of within-island selection regimes. Selection pressures on different traits may not be geographically congruent, and may vary gradually across space rather than categorically (Malhotra & Thorpe 2000a). The inappropriateness of subspecific nomenclature in these circumstances can be seen in numerous examples from Caribbean anoles (Malhotra & Thorpe 2000a; Thorpe & Stenson 2003) to Canary Island lacertids (Thorpe & Malhotra 1996; Thorpe *et al*. 1996a).

Leaf litter, or dwarf geckos *Sphaerodactylus* are crepuscular insectivores, and are among the smallest of all lizards. Lesser Antillean *Sphaerodactylus*, like the anoles, occupy both the young (Pliocene and late Miocene) and old (Eocene to Miocene) arc islands (Maury *et al*. 1990). Here, we attempt to elucidate the relationships of the fantastic dwarf gecko, *Sphaerodactylus fantasticus*, using molecular phylogenetic analysis of three mitochondrial DNA (mtDNA) genes and analysis of a broad suite of quantitative traits. This nominal species occupies the of islands of the Guadeloupe archipelago and adjacent islands in the central Lesser Antilles, that is Montserrat, Basse Terre, Grande Terre, La Desirade, Petite Terre, Marie Galante, Les Saintes, and Dominica (Fig. 1). This particular species has a sexually dimorphic colour pattern that shows considerable variation within and between islands, and not surprisingly a series of subspecies have been recognized (King 1962; Thomas 1965; Appendix I). This study aims to look at the molecular evolution and adaptive radiation in this group and compare it to that in the sympatric anoles in the *Anolis bimaculatus* group, a lineage of which occupies an almost identical range (Stenson *et al*. 2004).

Materials and methods

Molecular methods

For the DNA analysis, tail tips were taken from 10 gecko specimens from each of the 48 localities distributed across all islands known to be occupied (Fig. 1) and preserved in 80% ethanol. This is non-intrusive as tail tips are naturally autotomized and re-grown. Genomic DNA was extracted using GeneElute Mammalian Genomic DNA Miniprep kit (Sigma-Aldrich). Sections of three mtDNA genes [cytochrome *b (*cyt *b)*, ND4 and 12S] were sequenced. A 474-bp region of cyt *b* was available from Jones (1999) derived from manual sequencing using CYTb-702 and CYTb-703 primers (Malhotra & Thorpe 2000b) based on MVZ16 (Moritz *et al*. 1992) and L12841 (Kocher *et al*. 1989). A 401-bp region of ND4 was amplified using the primers in Arevalo *et al*. (1994), and about 400 bp of 12S were amplified using primers L1091 and H1557 (Knight & Mindell 1993). Sequencing of polymerase chain reaction (PCR) products was performed in both directions using a BigDye terminator cycle sequencing kit (Applied Biosystems) using manufacturer's instructions and sequences were run on and ABI PRISM 377 sequencer (Applied Biosystems), or were sent to Macrogen (www.macrogen.com). Alignment of cyt *b* and ND4 fragments was straightforward, but for the 12S gene, regions of ambiguous alignment (uncertain homology) were removed before analyses leaving a fragment of 381 bp.

Phylogenetic analyses

Two phylogenetic analyses were performed with *Sphaerodactylus sabanus* and *S. sputator* as the outgroup. Analysis 1 (Fig. 2) was based on sequences from all three genes on samples illustrated in Fig. 1. Analysis 2 (Appendix II) was based only on cyt *b* sequences, but with a greater number of replicate specimens per locality and more localities as illustrated in Fig. 1. The Bayesian method (MRBAYES version 3.1) was used to reconstruct the tree (Huelsenbeck & Ronquist 2001) based on an optimized model of sequence evolution, determined for the specific data set by the Bayes information criterion (BIC) in MRAIC version 1.4.3 (Nylander 2004). Three independent runs of four simultaneous Markov chains (one cold and three heated) were run for 10 million generations, sampling the chains every 1000 generations. The first three million generations

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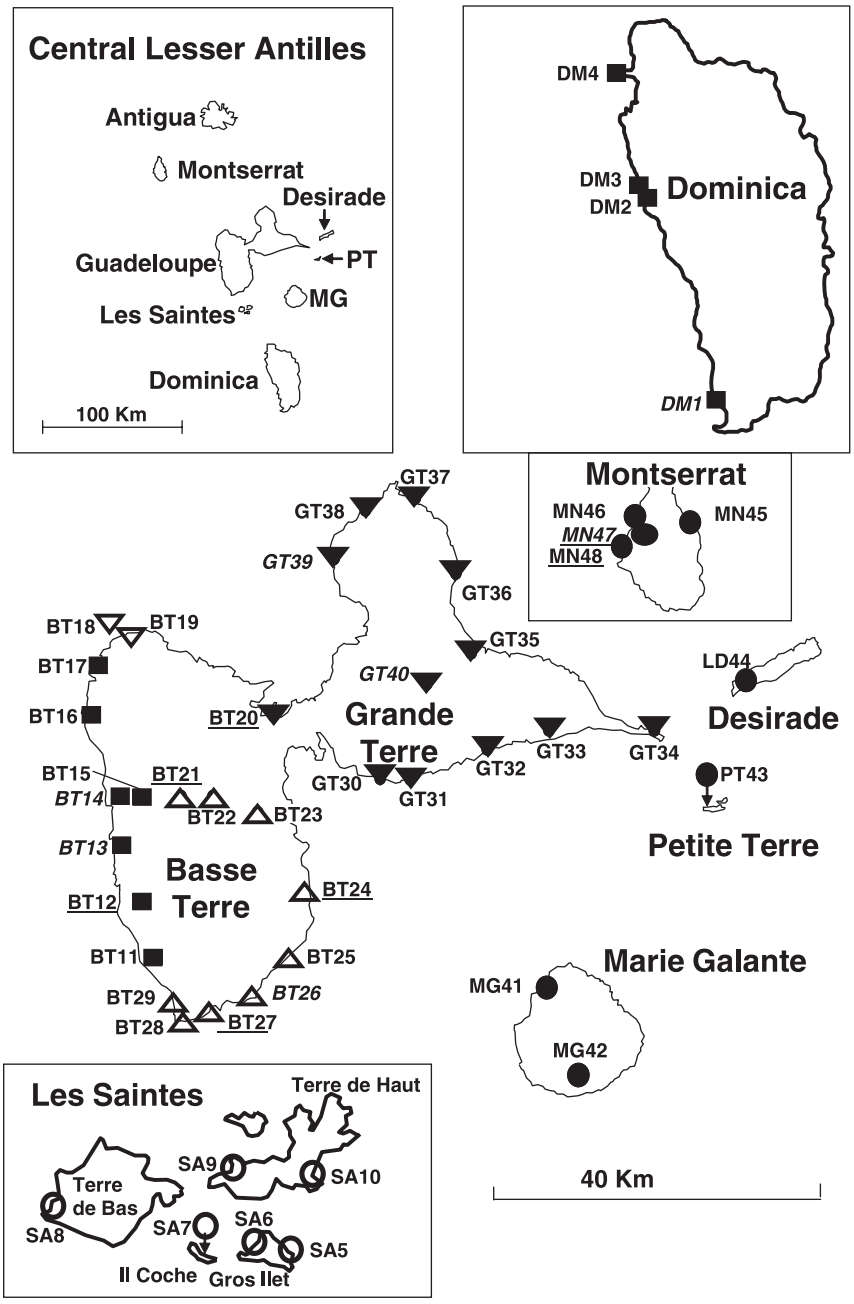

Fig. 1 Distribution of sampled localities of the *Sphaeradactylus fantasticus* complex. Symbols represent the main lineages (Fig. 2), italics indicate additional localities used in the cytochrome *b* tree (Appendix II), and underlined localities were not used in the analysis of quantitative traits.

(3000 trees) were discarded as the burn-in. Convergence was checked by plotting the parameters against generations, and using the diagnostic tools available in MRBAYES version 3.1. A 50% majority rule consensus tree ('Bayesian' tree) was constructed from the 7000 remaining trees. Node support was considered significant when more than 95% of the sampled trees recovered a particular clade (Huelsenbeck & Ronquist 2001). The hypothesis of a molecular clock was tested by running maximum-likelihood analyses on the model and data for Analysis 1 in PAUP* version 4.0b10 (Swofford 2003), both with, and without, the assumption of a molecular clock, and then comparing the trees with a likelihood-ratio test (Arbogast *et al*. 2002). In addition, the topography of the Bayesian tree from Analysis 1 was checked by a mixed-model Bayesian analyses performed with the sequence partitioned by gene, and the maximum likelihood (ML, both with and without a molecular clock) trees above.

The relationship between phylogeny and geography for a given lineage within an island is tested by matrix correspondence (Mantel test) (program by B. F. J. Manly, modified by R.S.T.; Manly 1986; Thorpe 2002) where the

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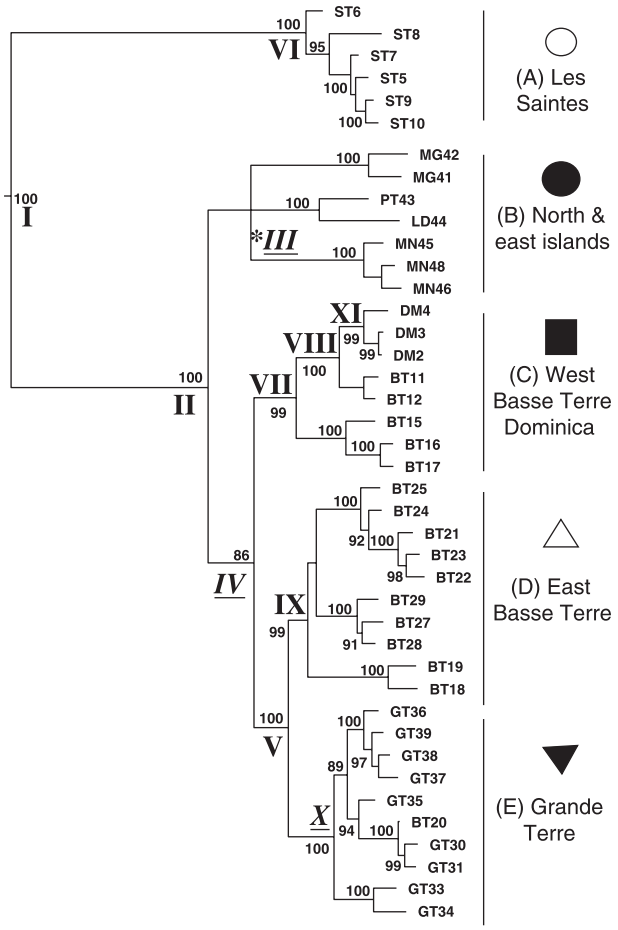

Fig. 2 Tree derived from Bayesian inference using three mitochondrial genes of the *Sphaeradactylus fantasticus* complex. Terminal nodes are localities in Fig. 1, nodes of interest are labelled I-X, those in italics are used in time calibration, and symbols represent the five main lineages geographically distributed as in Fig. 1. The posterior probabilities are given for the main nodes.

phylogeny is represented by the corrected patristic distances among sites (Analysis 1) and the geographical proximity is the simple linear distance over-land among sites, with the probability derived from 10 000 randomizations.

Timing

Timing phylogenies is fraught with difficulties. Here, we attempt to limit the impact of these by using geological timings for multiple calibration points within the phylogeny (Analysis 1) and using a range of timing methods. Sanderson 2002, 2003) penalized likelihood (PL) is used to time nodes using a semiparametric approach that allows for different substitution rates on branches. The age of three nodes (calibration points) were fixed and the age of the remaining nodes were estimated with the truncated Newton algorithm in the program r8s version 1.71 (Sanderson 2003). In addition, the mean patristic (tree) distances (PD) between lineages in Analysis 1 were computed for calibration purposes and subsequent timing. The mean rate for the patristic distances across the calibration points was used to estimate an approximate time of divergence at nodes of particular interest. These are supported by mean uncorrected genetic distance (UGD) between lineages (with standard errors) and corrected genetic distances (CGD) computed in mega 3 (Kumar *et al*. 2004).

The use of multiple geological calibrations within the phylogeny can result in the timings from more complex timing methods and the timing from simple mean patristic distances being very similar (Thorpe *et al*. 2005a). Here, we use three internal calibration points, the earliest origin of Basse Terre [*c*. 5 million years ago (Ma)] (Maury *et al*. 1990) and Montserrat (5 Ma) (Bouysse *et al*. 1983), and the emergence of Grant Terre in the Pleistocene (i.e. up to 2 Ma) (Maury *et al*. 1990). The former two calibration points allow timing of divergence between islands (and lineages) where polymorphism in the ancestral population may result in an over-estimation of the divergence times (Arbogast *et al*. 2002). However, the extent to which this is likely to be a problem can be revealed by comparing the rates suggested by the former two calibration points with the rate suggested by the latter point. If possible, the advantage of multiple calibrations makes their inclusion worthwhile.

Quantitative traits

For the analysis of quantitative traits, characters were recorded from 10 males and 10 females (from the subset of localities in Fig. 1), and technical photographs taken before release at point of capture. After excluding traits which did not show significant among-group variation for either sex by anova, 27 traits were studied. These were comprised of two body dimensions, nine scalation characters, nine measures of hue [with the RGB (red, green, blue) hue of specific areas interpreted with Adobe Photoshop], and seven of colour pattern. These characters were snout-vent length (SVL), size-adjusted head length (HL), mid-body scale rows (AB), number of mid-dorsal granular scales (MDR), number of ventral scales vent to snout (SVS), number of scales between the snout and fore-leg (NAS), number of scales between the fore-leg axis and cloaca (AVS), the number of lamellae on the fourth toes of the right hind leg (LAM), percentage of ventral scales that are keeled (KEEL), escutcheon depth in males (ESCD), escutcheon length in males (ESCL), number of dorsal stripes (LIN), length of dorsal stripe (LEN), percentage red (BR), green (BG) and blue (BB) hue of the trunk dorsum, intensity of pigmentation of the trunk dorsum (BCL), contrast in the percentage of red (RHC), green (GHC) and blue (BHC) hue in minimum

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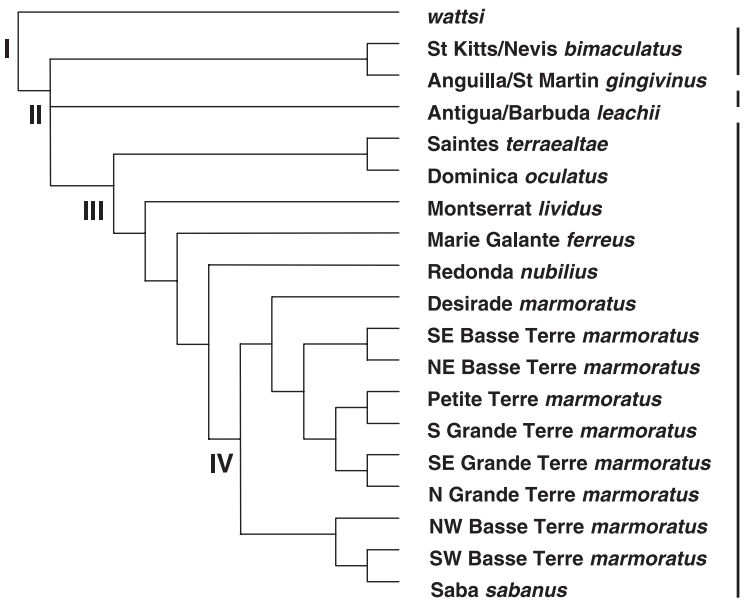

Fig. 3 Gene tree of the southern lineage of the *Anolis bimaculatus* group derived from Stenson *et al*. (2004) with the relationship between the main lineages (northwest, northeast and southern) shown as unresolved.

and maximum pigmented dorsal scales, contrast in the intensity of pigmentation of dorsal scales (THC), degree of dorsal pebbling (PEB), percentage red (HR), green (HG) and blue (HB) hue of the head, intensity of pigmentation of the head (HCL), proportion of the head covered by dark pigmentation (HP). Detailed descriptions of these characters appear in Jones (1999). As well as analysis of individual characters, multivariate generalizations of scalation, hue and pattern were used employing the construction of taxonomic distance (dissimilarity) from normalized characters. Scalation distances were based on AB, MDR, SVS, NAS, AVS, LAM, KEEL (together with ESCD and ESCL for males), hue distances were based on BR, BG, BB, RHC, GHC, BHC, HR, HG and HB, and colour pattern distances were based LIN, LEN, BCL, THC, PEB, HCL and HP.

To summarize the generalized divergence in quantitative traits, principal component analyses (PCA) of locality means were carried out, keeping sexes separate and using normalized data and the programs and procedures in Thorpe (1980). PCA were run on both the total character set and the subset of characters that were shown by the procedures below to be phylogenetically informative for that sex.

Association of quantitative traits to the phylogeny

The extent of the association between the quantitative traits and the mtDNA lineages was investigated employing two methods. Primarily, Mantel (matrix correspondence) tests were used. Here, the matrix of patristic distances (or tree distances; Page & Holmes 1998) were compared to a matrix representing the dissimilarity (taxonomic distance) among localities based on quantitative traits. These were either single traits, or multivariate sets (based on normalized characters from scalation, hue and pattern). The probability of the null hypothesis of no association was tested comparing the original value (standardized regression or correlation) to the values obtained from 10 000 randomizations (Thorpe 2002). The patristic distance matrix was computed as the average patristic distance between localities (across the replicate individuals at a locality) derived from Analysis 2 (Appendix II). Those single characters where the null hypothesis on no association could be rejected at $P < 0.05$ after sequential Bonferroni correction (independently for each sex) were then additionally tested for phylogenetic independence using Abouheif (1999) test for serial independence (TFSI) of continuous data in Reeve and Abouheif's program PHYLOGENETIC INDEPENDENCE 2.0 (http://www2.mcgill.ca/biology/faculty/abouheif/index.html). This randomization test (1000 randomizations) allows a phylogeny with polytomies and, unlike the previous procedure, ignores branch lengths. Hence, these two approaches allow a contrast of methods.

Comparison with sympatric anoles

The islands occupied by *Sphaerodactylus fantasticus* are also occupied by the southern lineage (Fig. 3) of the *Anolis bimaculatus* group (Stenson *et al*. 2004), the only difference being that the anole lineage also occupies the small islands of Redonda and Saba to the north. The molecular phylogenetic analysis defining this lineage was based on 1005 bp of cyt *b* and cytochrome oxidase (Stenson *et al*. 2004). The associated uncorrected *p* distances which are used in this study are derived from Stenson (2000) and given in

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Appendix III and the molecular and phylogenetic methods are given in Stenson *et al*. (2004). The extent of within-island sampling in this anole study does not lend itself so well to using geological events to obtain multiple calibration points within the tree. However, the divergence between the western and eastern Basse Terre lineages can be timed at the earliest date of Basse Terre, as in case of the dwarf gecko. The mean divergence between lineages was calculated using a phylogeny derived from Stenson *et al*. (2004), in which their second and third nodes *bimaculatus* group nodes were collapsed as they vary among reconstruction algorithms (Fig. 3).

Results

Phylogeny

The sequences used in this study have GenBank Accession nos EU191623–756. The Bayesian trees (Fig. 2) for Analysis 1 are effectively the same whether or not mixed models are used, and this is supported by both ML trees, which also have congruent topologies. The model selected was the general time reversible (GTR) model with a proportion of invariable sites and variable rates across sites simulated by a gamma distribution (GTR + I + G). Moreover, Analysis 1 and 2 give trees with effectively the same basic topology and with the same focally important nodes, although there may be trivial differences with shallow nodes (Fig. 2; Appendix II). The likelihood-ratio test for a molecular clock revealed no significant difference between the ML trees (with and without the assumption of a clock) so the hypothesis of a molecular clock cannot be rejected (chi-square = 54.45, d.f. = 41, $P = 0.08$).

The three-gene analysis (Fig. 2) shows a series of well-defined lineages with distinct geographical origins. The primary node (I) is well supported and splits the haplotypes on Les Saintes from other groups. The next node (II) is also well supported and splits the north and eastern islands (Marie Galante, Petite Terre, Desirade, Montserrat) from other groups. Node IV is less well supported, but gives a clear geographical split within Guadeloupe between western Basse Terre and eastern Basse Terre plus Grande Terre. Node V is well supported and splits eastern Basse Terre from Grande Terre. This gives five major groups, Les Saintes (A), north and eastern islands (B), western Basse Terre (C), eastern Basse Terre (D), and Grande Terre (E). There is generally considerable phylogeographical structuring within these major groups. In group A, there is little geographical structuring within Les Saintes, but in group B the small islands of Petite Terre and Desirade have closely related haplotypes and both the Montserrat and Marie Galante haplotypes are monophyletic. In Group C, the Dominica haplotypes are nested within the western Basse Terre haplotypes where there is latitudinal structure and a strong correlation between phylogeny and geography (Mantel test $r = 0.96$, $P < 0.0102$). In group D, there is also strong phylogeographical structure (Mantel test $r = 0.73$, $P < 0.0006$) because of a clear latitudinal differentiation within eastern Basse Terre. In group E, there is clear phylogeographical structure (Mantel test $r = 0.78$, $P < 0.0001$) within the Grande Terre group (which includes a single adjacent locality in Basse Terre) into northern, south/central and eastern areas.

Timing

The approximate time of origin of Montserrat is used to time the divergence between Montserrat and the Desirade/Petite Terre lineage (Fig. 2, node III), the approximate origin of Basse Terre is used to time the divergence between west Basse Terre and the lineage including east Basse Terre (Fig. 2, node IV), and the emergence of Grande Terre is used to time the divergence within the Grande Terre lineage (Fig. 2, node X). The former two calibration points (nodes III, IV), which may be compromised by ancestral polymorphism, in fact both consistently suggest slower rates than suggested by node X (Table 1) so this does not appear to be a major problem. The patristic distances are derived using the GTR model selected for the phylogeny, while MEGA 3 employed the closest available Tamura–Nei model for correcting the genetic distances as GTR model was not available. Penalized likelihood times are given in Table 1 together with patristic distances, corrected genetic distances and uncorrected genetic distances, and their associated calibration rates and subsequent node timings. The rates suggested by these calibrations points do not vary much within each metric (distance type) and subsequent node timing are comparable among metrics, although, as expected the uncorrected distance gives an underestimate for the deepest node compared to corrected distances.

Quantitative traits

The link between the phylogeny and the quantitative traits (Tables 2 and 3) is not strong. This is notable in males where the variation in only one colour character (THC), two individual scalation characters, multivariate scalation, and SVL have a phylogenetic component. In females, hue has a strong phylogenetic component, two individual pattern characters and multivariate pattern are associated with the phylogeny, but only one scalation character. Even with multivariate analysis, the PCA scatter diagrams do not generally show very well separated morphologically distinct lineages, with either the subset of phylogenetically informative characters (Fig. 4), or total character set (Appendix IV). The Les Saintes lineage (Fig. 2 lineage A) is, however, the most distinct (Fig. 4).

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Table 1 Distances, rates and times. Nodes are as in Fig. 2 with their calibration date (Calib) or penalized likelihood times (PL), both million years ago. Mean pairwise patristic distance (PD), associated rate (PDR) and time (PDT); corrected genetic distance (CGD), associated rate (CGDR) and time (CGDT); together with uncorrected genetic distance (UGD), associated rate (UGDR) and time (UGDT) are given for each node (distances × 100, with standard error bracketed where appropriate, times in million years ago, and rate per million years). The distances, and subsequent rates and times for Node III are based on the divergence between Montserrat and the Petite Terre/Desirade lineage

Node	Calib	PL	PD	CGD	UGD	PDR	CGDR	UGDR	PDT	CGDT	UGDT
I	—	13.4	27.4	14.2 (1.2)	11.4 (0.8)	—	—	—	13.0	10.2	9.1
II	—	6.6	13.9	7.7 (0.5)	6.7 (0.4)	—	—	—	6.5	5.6	5.4
III	5	—	10.3	7.1 (0.8)	6.3 (0.6)	2.07	1.42	1.26	—	—	—
IV	5	—	10.2	6.2 (0.6)	5.5 (0.4)	2.03	1.25	1.10	—	—	—
V	—	3.8	8.2	5.0 (0.5)	4.5 (0.4)	—	—	—	3.8	3.6	3.6
VI	—	1.8	3.0	1.9 (0.3)	1.8 (0.3)	—	—	—	1.4	1.4	1.5
VII	—	3.4	6.6	4.4 (0.5)	3.8 (0.4)	—	—	—	3.1	3.2	3.0
VIII	—	1.6	3.1	1.9 (0.4)	1.8 (0.3)	—	—	—	1.4	1.0	1.5
IX	—	3.2	7.3	5.1 (0.6)	4.6 (0.5)	—	—	—	3.4	2.7	3.7
X	2	—	4.7	3.0 (0.4)	2.8 (0.4)	2.36	1.5	1.40	—	—	—
XI	—	0.8	1.7	1.1 (0.3)	1.0 (0.3)	—	—	—	0.8	0.6	0.8
Mean	—	—	—	—	—	2.15	1.39	1.25	—	—	—

Table 2 Mantel and TFSI tests for association between quantitative traits and phylogeny. Character codes are given in the methods, bold indicates a significant association by Mantel test after sequential Bonferroni correction and an * indicates a significance association at $P < 0.05$ only before sequential Bonferroni correction. TFSI probabilities are given only for those univariate characters that show a significant association (after Bonferroni correction) using a Mantel test

Character	Character type	Female Mantel r (P)	Female TFSI P	Male Mantel r (P)	Male TFSI P
SVL		0.10 (> 0.05)	—	**0.17 (0.0090)**	< 0.003
HL	scalation	0.09 (> 0.05)	—	0.07 (> 0.05)	—
AB	scalation	0.02 (> 0.05)	—	0.03 (> 0.05)	—
MDR	scalation	0.02 (> 0.05)	—	0.21 (< 0.05*)	—
SVS	scalation	0.03 (> 0.05)	—	0.08 (> 0.05)	—
NAS	scalation	0.06 (> 0.05)	—	0.02 (< 0.05*)	—
AVS	scalation	0.07 (> 0.05)	—	0.09 (> 0.05)	—
LAM	scalation	0.14 (< 0.05*)	—	**0.20 (0.0002)**	< 0.001
KEEL	scalation	**0.26 (0.0022)**	< 0.001	**0.18 (0.0035)**	< 0.001
ESCD	scalation	—	—	0.08 (> 0.05)	—
ESCL	scalation	—	—	0.06 (> 0.05)	—
multivariate	scalation	0.11 (> 0.05)	—	**0.24 (0.0015)**	—
LIN	pattern	**0.35 (0.0022)**	< 0.001	0.07 (> 0.05)	—
LEN	pattern	0.18 (< 0.05*)	—	0.06 (> 0.05)	—
BCL	pattern	0.18 (< 0.05*)	—	0.03 (> 0.05)	—
THC	pattern	0.03 (> 0.05)	—	**0.20 (0.0027)**	< 0.001
PEB	pattern	0.10 (> 0.05)	—	0.07 (> 0.05)	—
HCL	pattern	**0.36 (0.0000)**	< 0.001	0.02 (> 0.05)	—
HP	pattern	0.09 (> 0.05)	—	0.07 (> 0.05)	—
multivariate	pattern	**0.41 (0.0000)**	—	0.03 (> 0.05)	—
BR	hue	0.09 (> 0.05)	—	0.05 (> 0.05)	—
BG	hue	**0.21 (0.0030)**	< 0.014	0.11 (> 0.05)	—
BB	hue	**0.21 (0.0018)**	< 0.002	0.09 (> 0.05)	—
RHC	hue	**0.30 (0.0010)**	< 0.004	0.02 (> 0.05)	—
GHC	hue	0.12 (< 0.05*)	—	0.02 (> 0.05)	—
BHC	hue	**0.29 (0.0003)**	< 0.001	0.02 (> 0.05)	—
HR	hue	**0.34 (0.0000)**	< 0.001	0.02 (> 0.05)	—
HG	hue	**0.43 (0.0000)**	< 0.001	0.05 (> 0.05)	—
HB	hue	**0.47 (0.0000)**	< 0.001	0.02 (> 0.05)	—
multivariate	hue	**0.42 (0.0000)**	—	0.05 (> 0.05)	—

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Table 3 Ranges of locality means for characters with a significant association with phylogeny (Table 2). Character abbreviations are in the text, with M for males and F for females, the lineage code is as in Fig. 2, the island codes and localities numbers are from Fig. 1 and are SA (Les Saintes), GI (Gros Ilet: 5, 6), CO (Coche: 7), TB (Terre d Bas: 8), TH (Terre d Haut: 9, 10), MG (Marie Galante: 41, 42), LD-PT (Desirade & Petite Terre: 43, 44), MN (Montserrat: 45, 46), W BT (West Basse Terre: 11, 13–17 and includes Dominica 1–4), E BT (East Basse Terre: 18, 19, 22, 23, 25, 26, 28, 29), and GT (Grande Terre: 30–40)

Lineage	(A)	(A)	(A)	(A)	(B)	(B)	(B)	(C)	(D)	(E)
Island	SA-GI	SA-CO	SA-TB	SA-TH	MG	LD-PT	MN	W BT	E BT	GT
M SVL	21.3–22.0	21.0	23.6	22.6	21.6–22.0	22.5–23.4	22.1–24.3	23.5–26.4	22.7–26.6	22.3–25.6
M LAM	8.8–9.0	9.0	9.0	9.0–9.2	9.8	9.6–10.2	9.0	9.0–10.2	9.6–10.0	9.2–10.2
M KEEL	2.2–2.6	2.0	2.6	2.4–2.8	2.2–2.8	2.8	3.8	2.0–3.6	2.0–5.0	2.8–4.6
M THC	25–26	24	29	13–19	5–8	15–22	0–6	0–24	7–25	11–26
F KEEL	2.8–3.0	2.2	2.4	2.8–3.0	2.4–2.8	3.2–4.0	2.0–2.2	2.0–4.2	2.4–5.0	4.4–5.0
F LIN	0.0	0.0	0.2	0.0	0.4–2.6	0.4–3.6	2.8–3.0	0.4–1.6	1.2–4.0	0.0–3.2
F HCL	21–23	19	21	22–24	15–16	14–18	17–18	15–21	12–22	14–17
F BG	42–43	35	41	42–43	38–39	33–35	35–36	32–43	35–42	33–40
F BB	7–10	5	14	9–11	8–9	23–28	20–26	4–27	7–20	16–24
F RHC	41–42	39	42	36–38	30–36	28–29	32–34	17–47	29–39	22–29
F BHC	13–15	18	17	16–23	18–35	38	25–31	11–48	15–31	28–48
F HR	36–38	42	38	37–38	52	44–54	42–47	42–57	37–54	42–53
F HG	36–38	40	38	34–36	48	42–46	41–47	41–49	37–46	39–47
F HB	24–29	19	21	27–28	0	0–13	6–17	0–18	0–26	0–18

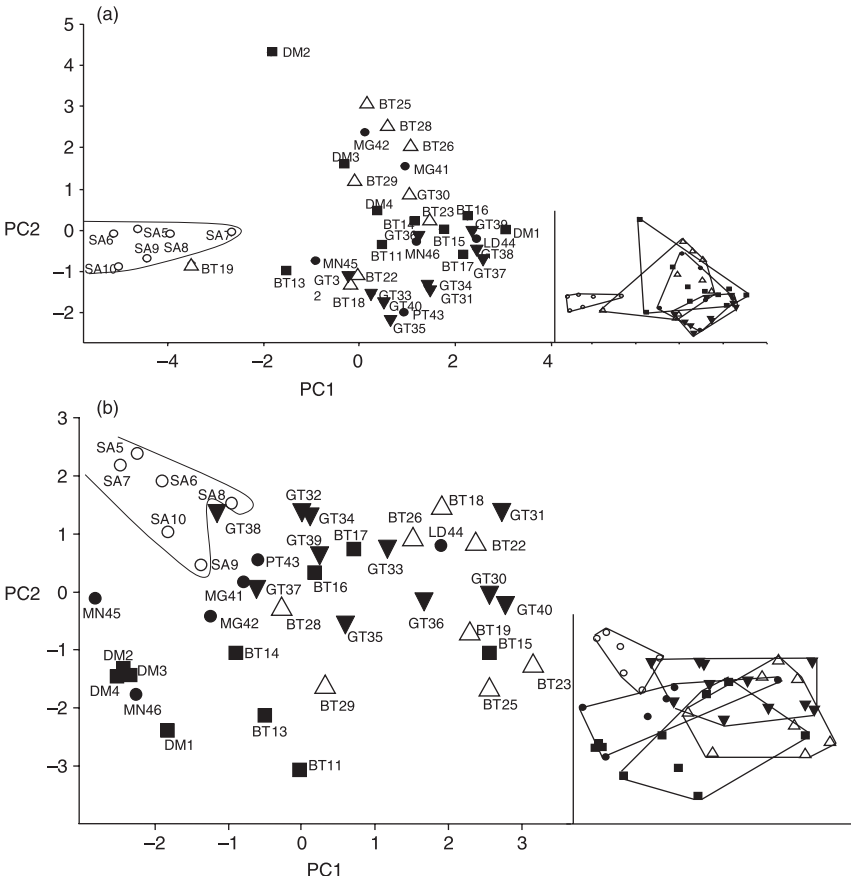

Fig. 4 Principal component analysis of female (a) and male (b) samples using those quantitative traits that have an association with phylogeny. Locality labels and lineage symbols are as in Figs 1 and 2. The inset figure shows the samples from a given lineage in enclosed in a convex polygon, which illustrates how all but Les Saintes lineage are not morphologically distinct.

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Comparison with sympatric anoles

The average divergence between the western and eastern Basse Terre anole samples is 8.33% which implies a rate of 1.67% per million years for these uncorrected genetic distances, based on cyt *b* and cytochrome oxidase genes (Stenson 2000).

Discussion

The primary phylogenetic split in the *Sphaerodactylus fantasticus* complex is between the Les Saintes lineage and the other lineages. There are phylogenetic parallels with the sympatric southern lineage of the *Anolis bimaculatus* group anoles insofar as *Anolis* from Les Saintes are also phylogenetically distinct from the other populations of *Anolis marmoratus* in the Guadeloupe archipelago (Creer *et al*. 2001; Stenson *et al*. 2004). Have these gecko and anole clades radiated since the origin of the young arc of island or do they predate this and originate in the old arc before the origin of the young arc? While the timing of phylogenetic splits is problematic, the use of multiple internal geological calibrations points has, in similar circumstances, resulted in notable agreement among sophisticated and simpler approaches (Thorpe *et al*. 2005a). In this study, there is also very close agreement in timing between the penalized likelihood methods and the average patristic distance (Table 1). Moreover, the additional use of less sophisticated approaches (such as average uncorrected genetic distances) makes cross-study comparison feasible as they are more widely used in the literature. Molecular clocks for anoles (Thorpe *et al*. 2005b), and similar squamates (Brown & Pestano 1998; Macey *et al*. 1998; Gubitz *et al*. 2000; Brown *et al*. 2001) over a variety of mitochondrial genes suggest broadly comparable rates for uncorrected genetic distances computed across the three genes of *Sphaerodactylus* using multiple geological calibrations.

Apart from Desirade, which is ancient, the current distribution of the *S. fantasticus* complex is on the young arc, or on submerged older island that have emerged since the origin of the young arc (e.g. Marie Galante). The split between Les Saintes and other lineages is deep (corrected patristic distance 27.4, uncorrected genetic distance 11.4%) across the three genes which implies a time of divergence of 13.4 Ma using penalized likelihood (down to 9.1 Ma UGD) (Table 1). This is well before the origin of the young arc in this area, which in this region is thought to date from *c*. 4–6 Ma (Maury *et al*. 1990). Hence, the *S. fantasticus* complex in total is generally older than the islands it currently inhabits (except Desirade). In particular, Les Saintes are not thought to be older than 4.7 million years (Maury *et al*. 1990) which suggests that representatives of this lineage were living on old arc islands before the origin, and subsequent colonization, of Les Saintes. As these representatives are no longer extant and *in situ* on the older islands, this suggests their extinction and replacement with more recently evolved lineages. This is compatible with the lack of comparably high levels of divergence at the next youngest node within either Les Saintes (node VI, PL 1.8 Ma to PD 1.4 Ma), or its sister lineage (node II, PL 6.6 Ma to UGD 5.4 Ma). Within Les Saintes at least, bottlenecking, perhaps multiple bottlenecking over time, may explain the loss of haplotypes and the relatively low level divergence among these very small islets.

In the sympatric southern lineage of the *A. bimaculatus* group, the deepest node (Fig. 3, node III) is the split between Les Saintes/Dominica and the other groups which has 13.1% corrected genetic distance and is timed at 7.9 Ma, which is comparable with the equivalent time for the comparable node in the *S. fantasticus* complex (Node I, 11.4% uncorrected genetic distance, *c*. 9.1 Ma) (Table 3). The divergence between the *bimaculatus* group and its sister group (*wattsi* complex), and between the major *bimaculatus* clades (northwest, northeast and south), time at 9.7 Ma and 8.9 Ma, respectively (Table 3). Consequently, both the gecko and sympatric anoles appear to have originated and diverged before the origin of the young arc in this area.

There are other phylogenetic comparisons between the gecko and sympatric anoles. Eastern and western Basse Terre populations are divergent in both groups, with relative similar levels of uncorrected genetic distance (gecko node II 6.3%, anole node IV 8.3%). In the *S. fantasticus* complex, this suggests a divergence of the western and eastern groups either side of the central mountains as Basse Terre arose in the north and progressively developed towards the south, with subsequent colonization of Grande Terre from adjacent eastern Basse Terre. The oldest split within the eastern Basse Terre lineage is between the northern (18, 19) localities and those further south, which is compatible with an origin in the north for the Basse Terre populations and subsequent expansion and differentiation southwards. A similar process is feasible for *A. marmoratus*, but with the islands adjacent to Grande Terre (i.e. Desirade and Petite Terre) being relatively recently colonized from Grande Terre rather than having a very distinct origin as in the geckos. The relationships between the gecko populations on the northern and eastern islands (Marie Galante, Montserrat, Desirade and Petite Terre) are not fully resolved but there is no evidence that they have been recently colonized from Basse Terre or Grande Terre and given the small size and low elevation of Petite Terre it is likely to have been colonized from Desirade rather than the reverse.

Southwest Basse Terre may have been the source of relatively recent colonizations of other islands for both the geckos and anoles. The Dominican *S. fantasticus* populations are paraphyletic to the west Basse Terre populations and are nested with those from SW Basse Terre suggesting that Dominica has recently been colonized from this area

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of Basse Terre. The alternative of anthropogenic transfer is unlikely, because the latitudinal phylogeographical divergence within the monophyletic Dominica lineage (node XI, PL time 0.8 Ma, 1.7% patristic distance to 1.0% uncorrected genetic distance) suggests *in situ* differentiation and the divergence between Dominica and the sister lineage in SW Basse Terre is also rather too large (node VIII, 3.1 patristic distance to 1.8% uncorrected genetic distance) to be readily explained away by missing haplotypes. Moreover, the distribution of *S. fantasticus* within Dominica is not restricted to pertinent areas of human activity such as ports, as it is with other introduced forms such as *Anolis cristatellus* and *Eleutherodactylus johnstonei* (Malhotra *et al*. 2007). Consequently, at the extreme southern end of the range Dominica appears to have been the major island most recently colonized by the gecko, perhaps between 1 Ma and 1.6 Ma if timed by the gross divergence from SW Basse Terre, or 0.6–0.8 Ma if timed by divergence within Dominica. The Saban anole is paraphyletic, nested within SW Basse Terre so this area is likely to have provided the colonizers for Saba, once again relatively recently, but too early to be due to human intervention.

Patterns of divergence and taxonomic recognition

As expected, the conventional subspecies (Schwartz & Henderson 1991), whose distribution is illustrated in Appendix I, do not generally map well to the primary lineages of the phylogeny and are not discussed further. However, the question remains as to whether any of the distinct lineages, with their distinct geographical distribution, should have taxonomic recognition. The extent of divergence of the populations from Les Saintes (27.4%) is so outstanding that they are a candidate for full species recognition. As simple mtDNA divergence is not generally used on its own as a criterion for species recognition, it is important to note that they are morphologically the most divergent when considered multivariately (Fig. 4) and are generally distinct in morpho-space. Compared to other populations in the *S. fantasticus* complex, the males tend to be smaller, have fewer lamellae, and tend not to have pronounced keeling of the scales. Compared to other populations, the females tend to have no dorsal stripes, they tend not to be heavily keeled, and they tend to have an intensely pigmented head with little red hue, a high green and low blue hue to the trunk, a strong contrast between the amount of red on some trunk scales compared to others and a weak contrast in blue (Table 2).

Although there is a phylogenetic signal in many of the quantitative traits, these characters may also be influenced by natural selection for current ecological conditions. This is certainly pronounced, irrespective of distinct phylogeographical lineages, in many lizards from environmentally heterogeneous islands (Thorpe & Malhotra 1996; Thorpe *et al*. 1996a, 2004; Malhotra & Thorpe 2000a; Thorpe & Richard 2000). The rest of the complex, outside Les Saintes, covers a large geographical range with a range of environmental conditions, and even within lineages covering large geographical ranges there may be environmental heterogeneity. It is then unsurprising to find that that the range of variation among and between the other clades is so great that it overlaps the range of variation found in Les Saintes. Hence, Table 2 reveals no truly diagnostic univariate morphological characters even though Les Saintes populations tend to be morphologically divergent (Fig. 4) and are generally distinct in multivariate morpho-space. Here, we raise the taxonomic status of Les Saintes populations from subspecies to full species, that is *Sphaerodactylus phyzacinus* (Thomas 1965).

There may be instances where primary lineages meet, and the extent to which they interbreed may illuminate their specific status. In Basse Terre, the western Basse Terre (C) lineage may meet the eastern Basse Terre lineage (D) in the northern and southern extremities of the island and perhaps elsewhere. At a lower level of phylogenetic divergence, the eastern Basse Terre lineage may also meet the Grande Terre lineage (E) in eastern Basse Terre. Further population level work needs to be undertaken to establish the status of these parapatric forms. However, given the lack of diagnostic characters for these other primary lineages, we refrain from naming any further full species in this complex, at least until further study reveals their reproductive relationships where they make contact. Hence, the name *S. fantasticus* applies to populations in its previous nominal range (Dominica, Basse Terre, Grande Terre, Montserrat, Petite Terre, Desirade, Marie Galante) except Les Saintes. Consequently, for these dwarf geckos *c*. 13 million years (PL and patristic distance times) of evolution has produced just two nominal species (Fig. 5).

In the southern lineage of the *bimaculatus* group anole, the population from Les Saintes was recognized as a subspecies of the largely Guadeloupean *A. marmoratus*. However, it is clearly not monophyletic with the *A. marmoratus* clade, but is a sister taxa to the phylogenetically distant, but geographically adjacent, Dominican *Anolis oculatus*. Consequently, we support raising the status of Les Saintes anoles to that of a full species, *Anolis terraealtae* as in Barbour (1915) and Roughgarden & Pacala (1989). The adaptive radiation of the southern *bimaculatus* lineage encompasses seven nominal species implying six speciation events (Fig. 5), which is notably more than the single event giving two nominal species of the *S. fantasticus* complex in the same time frame. It is difficult to know whether this tell us more about the differences in the arbitrary nature of species recognition in the two groups than about differences in their evolutionary biology. For example, anoles may have more nominal species because, being ubiquitous and larger, they have been more inten-

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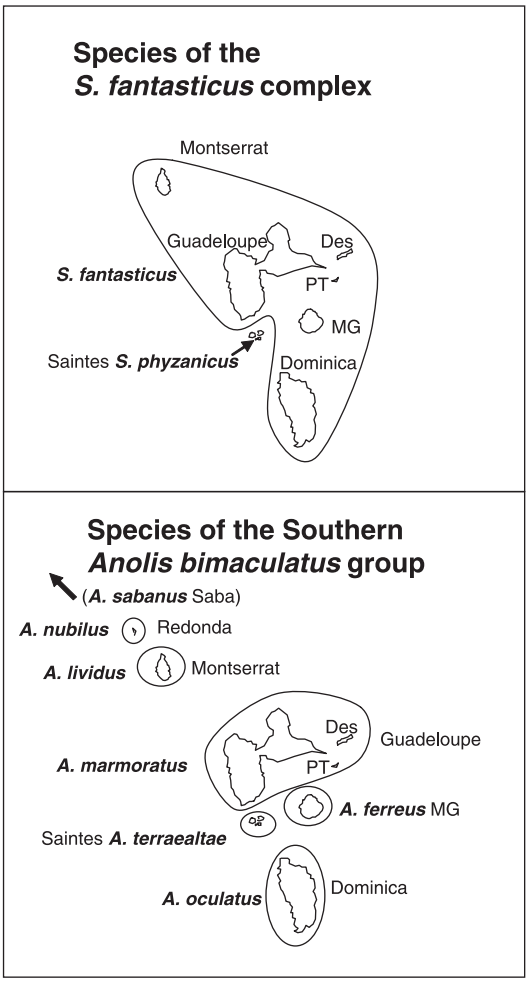

Fig. 5 Adaptive radiation of the *Sphaerodactylus fantasticus* complex (a) showing the distribution of two nominal species, and of the southern lineage of the *Anolis bimaculatus* group (b) showing the distribution of seven nominal species, five of which are sympatric with the *S. fantasticus* complex.

sively studied. However, investigating the population genetics and interbreeding where previously allopatric populations of these groups meet should help to resolve these issues (Ogden & Thorpe 2002; Thorpe 2005).

Acknowledgements

A.G.J. wishes to thank the authorities in Dominica, Guadeloupe and Montserrat for permission to work and the BBSRC for a studentship. We wish to thank C. Ercolani for laboratory work and the anonymous referees for their comments.

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This work was derived from several sources, most notably Alex Jones' PhD thesis (supervised by A.M. and R.S.T.) on the molecular phylogeny, phylogeography and adaptation of Lesser Antillean dwarf geckos. Yann Surget-Groba is interested in the molecular ecology of Lizards, including the evolution of viviparity and speciation. Roger S. Thorpe and Anita Malhotra have investigated natural selection, population genetics, molecular phylogeography and speciation in island lizards as part of their broader research activities of the Molecular Ecology and Evolution of Reptile Unit in Bangor. The other focus of interest in this unit is the evolution of venomous snakes and their venoms.

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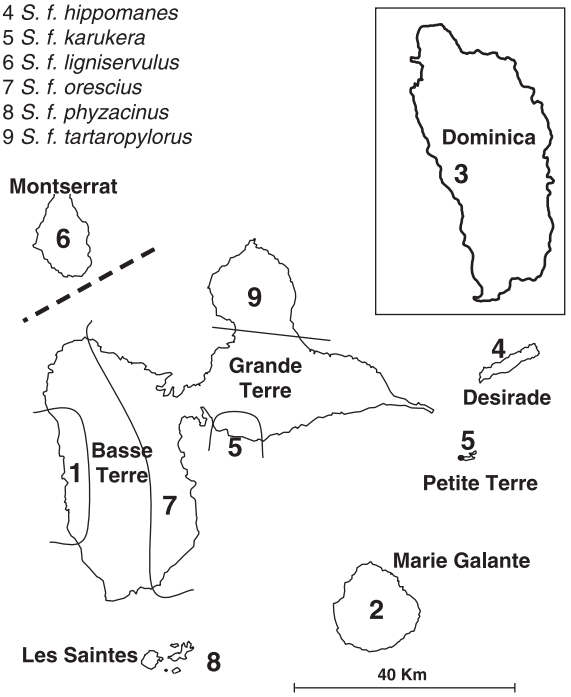
Appendix I

Conventional subspecies of the *Sphaerodactylus fantasticus* complex
Adapted from Schwartz and Henderson (1991)
1 *S. f. fantasticus*
2 *S. f. anidrotus*
3 *S. f. fuga*
4 *S. f. hippomanes*
5 *S. f. karukera*
6 *S. f. ligniservulus*
7 *S. f. orescius*
8 *S. f. phyzacinus*
9 *S. f. tartaropylorus*



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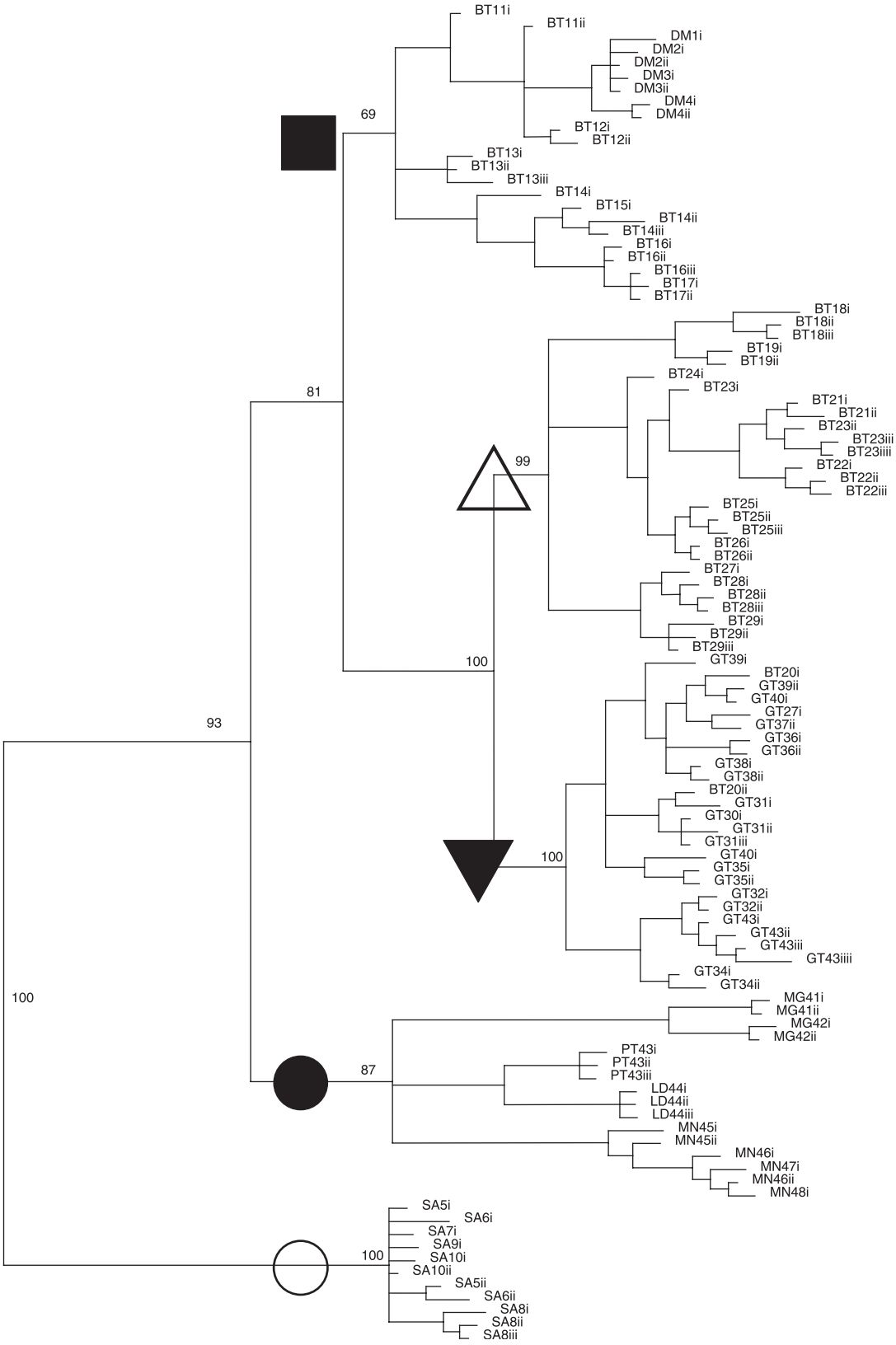
Appendix II

Cytochrome *b* gene tree. Legend is as for Fig. 2 except i–v which indicates the individual replicate sample at that locality.



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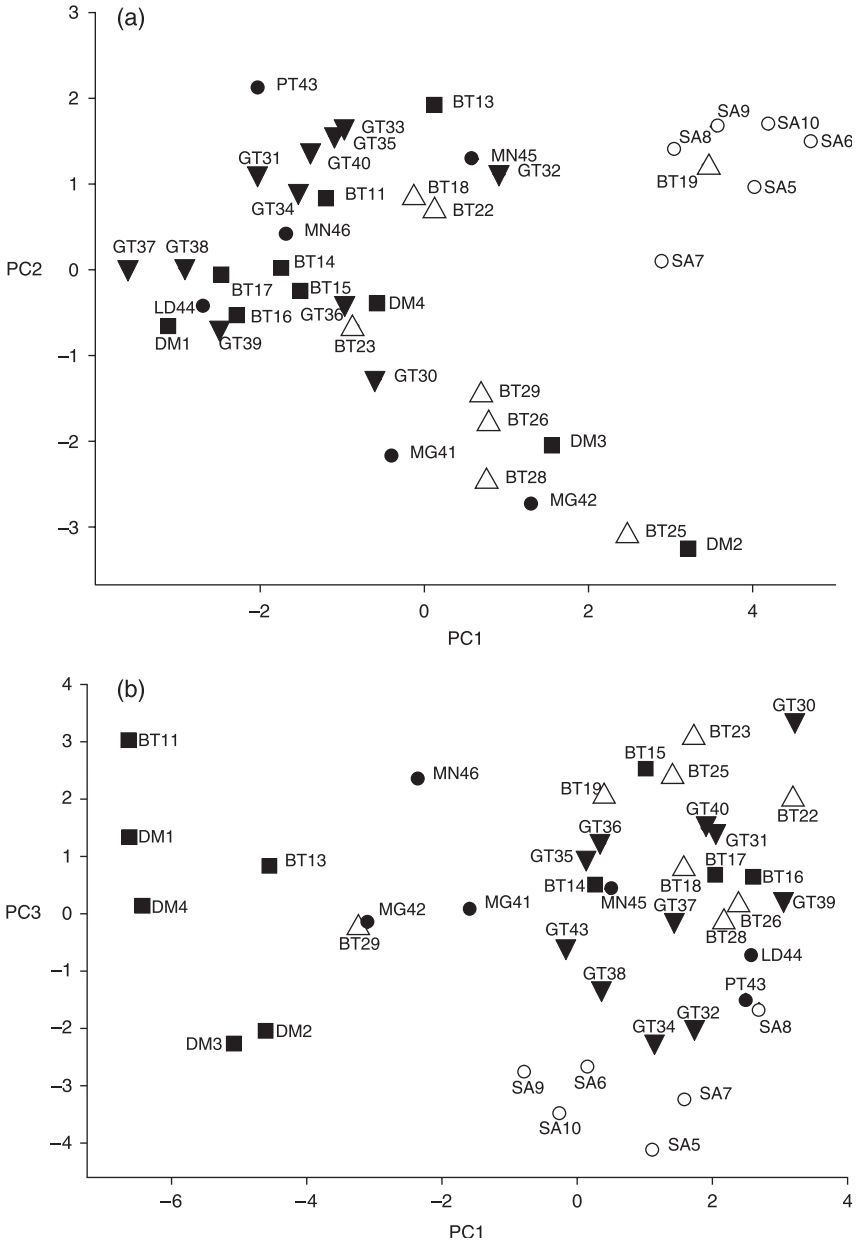
Appendix III

Uncorrected genetic distances between populations from the southern lineage of the *Anolis bimaculatus group* (Stenson *et al.* 2004). Nominal species names are followed by locality of origin. 1 *oculatus* S Caribbean. 2 *oculatus* north. 3 *oculatus* central east. 4 *oculatus* central Caribbean. 5 *marmoratus* SE Basse Terre. 6 *marmoratus* SW Basse Terre. 7 *marmoratus* Desirade. 8 *marmoratus* Petite Terre. 9 *marmoratus* S Grande Terre. 10 *marmoratus* NW Basse Terre. 11 *marmoratus* NE Basse Terre. 12 *marmoratus* SE Grande Terre. 13 *marmoratus* Les Saintes. 14 *schwartzi* outgroup. 15 *schwartzi* outgroup. 16 *leachi* Barbuda. 17 *leachi* Antigua. 18 *sabanus* Saba. 19 *nubilus* Redonda. 20 *bimaculatus* Nevis. 21 *gingivinus* Anguilla. 22 *marmoratus* N Grande Terre. 23 *bimaculatus* St Kitts. 24 *gingivinus* St Martin. 25 *lividus* Montserrat. 26 *ferreus* Marie Galante.

2	0.02510																								
3	0.02909	0.02407																							
4	0.05422	0.04920	0.05515																						
5	0.13844	0.13342	0.13972	0.13141																					
6	0.12187	0.12186	0.12387	0.12587	0.08660																				
7	0.13045	0.12542	0.13074	0.13745	0.08383	0.08862																			
8	0.13246	0.12844	0.13174	0.12743	0.05090	0.07755	0.06786																		
9	0.12144	0.12042	0.12088	0.12544	0.05594	0.07555	0.06593	0.01998																	
10	0.13583	0.12980	0.13579	0.12775	0.08246	0.05042	0.08446	0.07946	0.07946																
11	0.13643	0.13141	0.13972	0.12438	0.02395	0.09164	0.08283	0.05988	0.06193	0.08749															
12	0.12644	0.12242	0.12375	0.12341	0.05689	0.07150	0.06986	0.02994	0.02597	0.07343	0.06188														
13	0.11468	0.10965	0.11632	0.11571	0.15144	0.13729	0.13640	0.14043	0.13746	0.13923	0.14040	0.13142													
14	0.17498	0.16894	0.16875	0.17284	0.16275	0.15303	0.17677	0.16674	0.16579	0.15397	0.17279	0.15166	0.15717												
15	0.17308	0.16605	0.16488	0.16896	0.16191	0.15415	0.17491	0.16489	0.16393	0.15309	0.16944	0.15180	0.15124	0.01711											
16	0.14791	0.14891	0.14485	0.15486	0.16497	0.13913	0.14886	0.15386	0.14988	0.14296	0.15994	0.15084	0.15213	0.16290	0.16099										
17	0.15381	0.15581	0.15074	0.16077	0.17182	0.14807	0.15774	0.16276	0.15678	0.15191	0.16578	0.15975	0.16108	0.16985	0.16796	0.01611									
18	0.13368	0.12965	0.13365	0.13567	0.09645	0.03627	0.09144	0.08843	0.08642	0.06138	0.09645	0.08039	0.14101	0.16181	0.16595	0.14587	0.15276								
19	0.13064	0.12562	0.12665	0.13266	0.09457	0.09077	0.09344	0.08743	0.08741	0.09070	0.08841	0.08846	0.13702	0.16603	0.16515	0.14599	0.14987	0.08854							
20	0.14577	0.14377	0.14550	0.14276	0.15354	0.14513	0.15954	0.14752	0.14956	0.14896	0.15654	0.14752	0.14295	0.14996	0.15009	0.13988	0.15097	0.14594	0.15408						
21	0.13565	0.12661	0.13287	0.13465	0.14484	0.14309	0.14989	0.13986	0.13594	0.13795	0.15283	0.13786	0.14663	0.15596	0.15008	0.14600	0.14990	0.15482	0.15192	0.12271					
22	0.12738	0.12329	0.12455	0.12325	0.06225	0.07305	0.07531	0.03416	0.02813	0.07797	0.06426	0.00801	0.13350	0.15568	0.15583	0.15306	0.16093	0.08094	0.09209	0.14870	0.14095				
23	0.14202	0.14107	0.14294	0.13996	0.14909	0.14032	0.15503	0.14301	0.14507	0.14503	0.15211	0.14301	0.13748	0.14702	0.14714	0.13692	0.14902	0.14812	0.15131	0.00603	0.11608	0.14415			
24	0.14074	0.13068	0.13466	0.13667	0.14771	0.15206	0.15071	0.14469	0.14170	0.14392	0.15374	0.14569	0.14807	0.15980	0.15391	0.14682	0.14975	0.16080	0.15093	0.12177	0.01709	0.14681	0.11484		
25	0.09884	0.09076	0.08668	0.10181	0.11388	0.09817	0.10078	0.09474	0.09173	0.10108	0.11488	0.09473	0.11019	0.15214	0.14922	0.14136	0.14718	0.10801	0.10500	0.13722	0.13507	0.09921	0.13243	0.14217	
26	0.13754	0.13347	0.13194	0.13444	0.12394	0.09841	0.11686	0.10273	0.10881	0.09425	0.11890	0.10371	0.13256	0.17182	0.16791	0.13983	0.14972	0.10625	0.10833	0.15059	0.14714	0.10510	0.14608	0.14871	0.11320
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**

Appendix IV

(a) Principal component analysis of the total data set for females. Legend as in Fig. 4. (b) Principal component analysis of the total data set for males. Legend as in Fig. 4



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