

## Multilocus phylogeny, species age and biogeography of the Lesser Antillean anoles

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### Molecular Phylogenetics and Evolution

DOI:  
[10.1016/j.ympev.2018.06.014](https://doi.org/10.1016/j.ympev.2018.06.014)

Published: 01/10/2018

Peer reviewed version

[Cyswllt i'r cyhoeddiad / Link to publication](#)

*Dyfyniad o'r fersiwn a gyhoeddwyd / Citation for published version (APA):*  
Thorpe, R., Barlow, A., Surget-Groba, Y., & Malhotra, A. (2018). Multilocus phylogeny, species age and biogeography of the Lesser Antillean anoles. *Molecular Phylogenetics and Evolution*, 127, 682-695. <https://doi.org/10.1016/j.ympev.2018.06.014>

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<b>Manuscript number</b>	MPE_2017_634
<b>Title</b>	Multilocus phylogeny, species age and biogeography of the Lesser Antillean anoles
<b>Article type</b>	Research Paper

### Abstract

Lesser Antillean anoles provide classic examples of island radiations. A detailed knowledge of their phylogeny and biogeography, in particular how the age of species relate to the ages of their respective islands and the age of their radiation, is essential to elucidate the tempo and mechanisms of these radiations. We conduct a large scale phylogenetic and phylogeographic investigation of the Lesser Antillean anoles using multiple genetic markers and comprehensive geographic sampling of most species. The multilocus phylogeny gives the first well-supported reconstruction of the interspecific relationships, and the densely sampled phylogeography reveals a highly dynamic system, driven by overseas dispersal, with several alternative post-dispersal colonisation trajectories. The age of these anole radiations corresponds with the ancient Miocene Island arc, but the ages of extant species are relatively young (about the age of the younger arc, or less). The species age is compatible with other small terrestrial amniotes. The difference between the age of the radiation and the age of the extant species suggests substantial species turnover on older arc islands, most likely through competitive replacement. Although extant anoles are extremely speciose, this may represent only a fraction of their biodiversity over time. While several cases of paraphyly enable us to infer some recent colonization events, the relatively young age of extant species, the high levels of species turnover through time, and the absence of the younger arc in the early and middle stages of the radiation, does not allow the early inter-island colonization to be reliably inferred. Reproductive isolation in allopatry takes a very considerable time (in excess of 8my) and sympatry appears to occur only late in the radiation. The resolved multilocus phylogeny, and relative species age, raise difficulties for some earlier hypotheses regarding size evolution, and provide no evidence for within-island speciation.

<b>Keywords</b>	Anolis; multilocus phylogeny; Lesser Antilles; species age; species turnover; island colonization.
<b>Taxonomy</b>	Biological Sciences, Evolutionary Biology, Phylogeny, Island Biogeography, Speciation
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<b>Suggested reviewers</b>	Richard Glor, Richard Brown, Jonathan Losos

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Dear Editor

We are submitting the manuscript entitled “Multilocus phylogeny, species age and biogeography of the Lesser Antillean anoles” to be considered for publication in the journal *Molecular Phylogeny and Evolution*.

We provide the first resolved multilocus species tree for these radiations and combine this with a series of densely sampled phylogeographic analysis within-species to indicate species age. We relate this to geological data. This allows us to deduce considerable species turnover on older islands and show that attempts to define early-stage colonization sequence are spurious and that the classic evolution of size in these radiations needs to be reconsidered. We show recent colonization events (via paraphyly) and that reproductive isolation and subsequent sympatry require a very considerable amount of time in allopatry.

We trust this will be of interest to a wide audience.

Yours

Roger S Thorpe, Corresponding author.

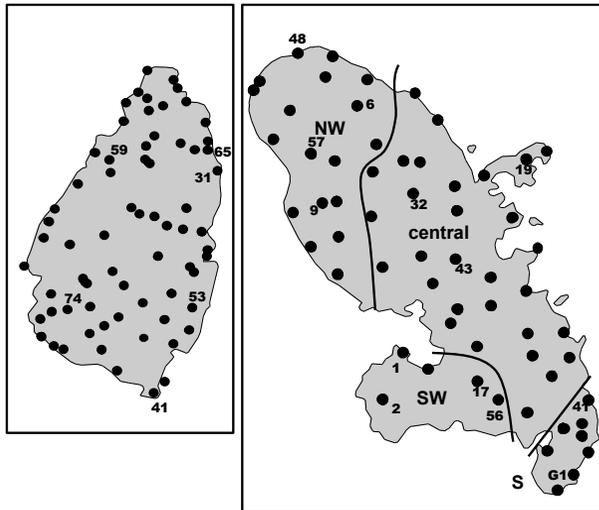
## **Highlights**

- A multilocus study provides a resolved phylogeny for Lesser Antillean anoles.
- Dense phylogeographic sampling within-species indicates the age of species.
- Old radiations are composed of young species, with species turnover on older islands.
- Reproductive isolation occurs only after a very prolonged time in allopatry.
- Only recent colonization events can be deduced from the phylogeny.

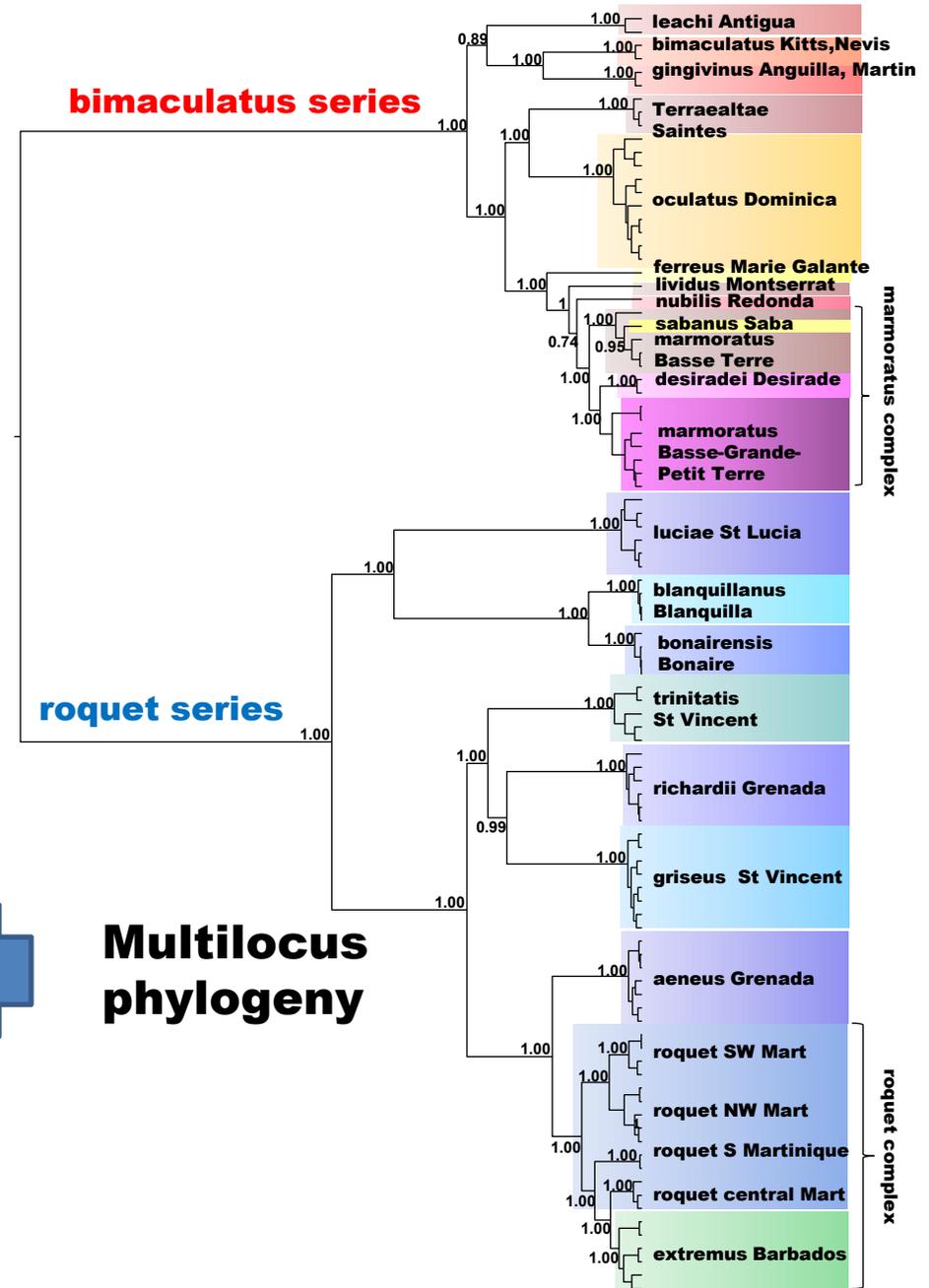
# Lesser Antillean anoles



## Dense phylogeographic sampling



## Multilocus phylogeny



## Graphical abstract legend

A combination of a resolved multilocus phylogeny and dense phylogeographic sampling indicates species age and recent colonization events

# 1 **Multilocus phylogeny, species age and biogeography of the Lesser Antillean anoles.**

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16

17 **Declaration of interest:** None

18

19

## 20 **ABSTRACT**

21

22 Lesser Antillean anoles provide classic examples of island radiations. A detailed knowledge  
23 of their phylogeny and biogeography, in particular how the age of species relate to the ages of  
24 their respective islands and the age of their radiation, is essential to elucidate the tempo and  
25 mechanisms of these radiations. We conduct a large scale phylogenetic and phylogeographic  
26 investigation of the Lesser Antillean anoles using multiple genetic markers and  
27 comprehensive geographic sampling of most species. The multilocus phylogeny gives the  
28 first well-supported reconstruction of the interspecific relationships, and the densely sampled  
29 phylogeography reveals a highly dynamic system, driven by overseas dispersal, with several  
30 alternative post-dispersal colonisation trajectories. The age of these anole radiations  
31 corresponds with the ancient Miocene Island arc, but the ages of extant species are relatively  
32 young (about the age of the younger arc, or less). The species age is compatible with other  
33 small terrestrial amniotes. The difference between the age of the radiation and the age of the  
34 extant species suggests substantial species turnover on older arc islands, most likely through  
35 competitive replacement. Although extant anoles are extremely speciose, this may represent  
36 only a fraction of their biodiversity over time. While several cases of paraphyly enable us to  
37 infer some recent colonization events, the relatively young age of extant species, the high  
38 levels of species turnover through time, and the absence of the younger arc in the early and  
39 middle stages of the radiation, does not allow the early inter-island colonization to be  
40 reliably inferred. Reproductive isolation in allopatry takes a very considerable time (in excess  
41 of 8my) and sympatry appears to occur only late in the radiation. The resolved multilocus  
42 phylogeny, and relative species age, raise difficulties for some earlier hypotheses regarding  
43 size evolution, and provide no evidence for within-island speciation.

44

## 45 **Keywords**

46 *Anolis*, multilocus phylogeny, Lesser Antilles, species age, species turnover, island  
47 colonization.

48

49

## 50 **1. Introduction**

51  
52 Island archipelagoes tend to be biodiversity hotspots (Myers et al., 2000), and have been the  
53 focus of many evolutionary studies. The production of that biodiversity (that is, the radiation  
54 of a group in an archipelago by classical geographic Darwinian evolution) can be thought of  
55 as loosely following a series of stages. First, the initial colonization of an island in the  
56 archipelago; second, the dispersal among islands, third the divergence of the various isolated  
57 (allopatric) island forms into separate species; and last the continued inter-island colonization  
58 resulting in independent species living in sympatry (Losos and Ricklefs, 2009). The highly  
59 speciose anoles in the Lesser Antillean archipelago provide examples of island radiations  
60 where the tempo and mode of this process can be studied. Here, we investigate these  
61 radiations using a well- resolved multilocus molecular phylogeny, and densely sampled  
62 phylogeography, to elucidate these processes and expose the utility and limitations of these  
63 methods.

64 Anoles are small, neotropical/subtropical, insectivorous tree lizards that are the  
65 subject of numerous evolutionary and ecological studies (Losos, 2009). The genus (*sensu*  
66 *lato*) is very speciose, and we follow Losos (2009), Poe (2013) in treating *Anolis* as a single  
67 genus with the main clades recognised as series (but see Nicholson et al., 2012, and Poe et al.,  
68 2017). The northern Lesser Antilles (Dominica northwards) are inhabited by the *bimaculatus*  
69 series, and the southern Lesser Antilles (Martinique southwards) and associated islands, are  
70 inhabited by the *roquet* series (Fig. 1). We use the term series, because of its convenience in  
71 distinguishing between various phylogenetic levels; for example the name *roquet* is used at  
72 three levels, 1) for the *roquet* series occupying the southern Lesser Antilles, 2) for the *roquet*  
73 complex that includes *A. extremus* from Barbados, and 3) for the nominal species *A. roquet*  
74 on Martinique.

75 Phylogenetic studies (e.g. Nicholson et al., 2005) show that the Lesser Antillean  
76 *bimaculatus* and *roquet* series are as distantly related as anoles can be, and must have  
77 colonised this island chain independently. Both *roquet* and *bimaculatus* series are  
78 monophyletic, and exclusively Lesser Antillean, in the sense that they do not naturally have  
79 extant members in South America, or Greater Antilles, respectively. They do however, have  
80 sister taxa in South/Central America and the Greater Antilles respectively, which suggests  
81 they may be the product of single colonizations of the Lesser Antilles (northern *bimaculatus*  
82 from the Greater Antilles, and southern *roquet* from South America), with subsequent  
83 divergence within their mutually exclusive northern and southern sections of the island chain.

84 The Lesser Antilles are composed of two volcanic arcs, which are superimposed from  
85 Martinique southwards. The older outer arc is Eocene to Miocene (Wadge, 1994) and is  
86 currently represented by relatively low elevation islands, while the younger, inner arc is  
87 composed of mountainous islands that arose between 8 my ago in the late Miocene and the  
88 present (Bouysse, 1984), with most islands being 5 my old or younger (Briden et al., 1979).  
89 Both arcs are a product of subduction of the Atlantic Ocean crust under the Caribbean plate  
90 (Maury et al., 1990), with a subsequent independent volcanic origin of each island. The  
91 exceptions to this are Barbados, which is an accretionary prism (Speed, 1994), and the very  
92 ancient La Desirade (Briden et al., 1979). Also, two species from the *roquet* series are found  
93 south of the Lesser Antilles on continental shelf islands off the South American coast  
94 (Blanquilla and Bonaire). In any event, although the situation may be complicated by  
95 instances of island coalescence, the islands and island banks (e.g. St Kitts/Nevis bank) have  
96 generally arisen independently from the sea over time (Surget-Groba and Thorpe, 2013), so  
97 that overseas inter-island colonization is a dominant feature of the biogeography of these  
98 anoles.

99 Each Lesser Antillean island, or island bank, has either one or two endemic anole  
100 species, with no significant island or islet uninhabited (Fig.1). Females may lay a series of

101 single eggs every six weeks or so, with adults living a few years. There can be high  
102 population densities (Malhotra and Thorpe, 1991) and population turnover, and aspects of  
103 their life history (e.g. sperm storage and multiple inseminations) are compatible with a  
104 facility to colonize among islands and rapidly expand population size (Eales et al., 2010).  
105 Even so, these are low-vagility animals, with the per-generation gene exchange among  
106 islands effectively close to zero compared to the massive population turnover within an  
107 island. Numerous studies (Thorpe et al., 2015 and references therein) have shown that while  
108 there may be distinct phylogeographic divisions, and (largely unrelated) geographic variation  
109 in quantitative traits within an island species, morphological continuity among geographic  
110 sites testifies to their conspecificity (see, however, Thorpe et al., 2010 for Martinique).

111 Thus, Lesser Antillean anoles generally represent a system in which allopatric species  
112 are isolated from one another on separate islands/island banks with deep sea between, with  
113 the potential for gene flow between species effectively zero throughout their entire  
114 evolutionary histories. Where two species occur in sympatry on a single island, they maintain  
115 morphological distinctiveness in widespread syntopy and without evidence of gene flow  
116 (Thorpe et al., 2015) and can therefore be considered to have independent evolutionary  
117 trajectories. In these cases, phylogenetic studies have shown that these island/island-bank  
118 species are mutually monophyletic. The exceptions to this general rule are multispecies  
119 complexes (*roquet* and *marmoratus* complexes), where precursor islands may coalesce  
120 resulting in secondary contact of previously allopatric “species”, and nominal species may be  
121 paraphyletic (Materials and Methods).

122 These Lesser Antillean anole radiations have been used to study character  
123 displacement and alternative theories of size evolution (Losos, 2009), as well as infer  
124 colonization sequence (Stenson et al., 2004; Losos, 2009). Among other factors these studies  
125 have been limited by poorly resolved phylogenies and poor sampling of many island species.  
126 Here we provide a well resolved, multilocus (mtDNA and five nDNA genes) phylogeny and,  
127 in a supporting analysis, dense sampling of numerous species to give a robust estimate of  
128 within-species divergence, and a perspective on the age of these species.

129

## 130 **2. Materials and methods**

131

### 132 *2.1 Molecular methods*

133

134 DNA sequences consisted of published sequences (Thorpe et al., 2015, and references  
135 therein) and novel sequences generated for this study. Total DNA was extracted from  
136 autotomised tail tip tissue using a high salt method (Aljanabi and Martinez, 1997). Fragments  
137 of the mitochondrial cytochrome b (cyt b) gene and nuclear genes genes 3' nucleotidase  
138 (NT3), prolactin receptor (PRLR), G protein-coupled receptor 149 (R35), recombination  
139 activating gene 1 (RAG1), and Rhodopsin, were then PCR amplified using the cyt b primers  
140 in Thorpe *et al.* (2015); the PRLR and NT3 primers in Townsend *et al.* (2008); the R35  
141 primers in Leaché (2009); the RAG1 primers Mart\_FL1 and Amp\_R1 described in Crottini et  
142 al. (2012) and Hoegg et al. (2004); and the Rhodopsin primers Rod3 and Rod4 in Glor et al.  
143 (2004). Reactions were performed in 11 µl volumes, comprising ABgene ReddyMix™ PCR  
144 Master Mix (cat. no. AB-0575/LD/A), 0.27µM of each primer and ~10-20 ng of template  
145 DNA. Products from PCR were cleaned using the enzymes exonuclease 1 and thermo-  
146 sensitive alkaline phosphatase, and direct sequencing carried out by Macrogen Inc.  
147 (dna.macrogen.com) using both forward and reverse primers. Sequence chromatograms were  
148 proof-read, aligned and checked for unexpected stop codons or frameshift mutations using  
149 the software CodonCode Aligner version 3.5.6.

150

## 151 2.2 Phylogenetic methods

152

153 There were two primary phylogenetic analyses. The first (Analysis 1) aims to produce a well  
 154 resolved interspecific phylogeny, the second (Analysis 2) aims to produce a robust estimate  
 155 of the age of individual species in relation to the age of the appropriate anole radiation (series  
 156 or clade).

157

### 158 2.2.1 Phylogenetic methods Analysis 1: Multilocus tree.

159

160 In order to maximize the possibility of producing a phylogenetic tree with resolved inter-  
 161 specific relationships, the mtDNA gene cytochrome b, and five single-copy nuclear genes  
 162 (NTF3, PRLR, R35, RAG1, Rhodopsin) were used. Previous studies (Thorpe et al., 2015 and  
 163 references therein) have revealed the phylogeographic structure within well sampled  
 164 individual species. For Analysis 1, where there are numerous collection sites within a species,  
 165 sites were selected to represent these major phylogeographic regions. Other species have  
 166 fewer collection sites per island. The geographic sampling of DNA sequences is shown in  
 167 Fig. 2. All species from the *roquet* series, together with *A. oculatus*, and *A. marmoratus* from  
 168 the *bimaculatus* series, have multiple sites per species. All other species from the *bimaculatus*  
 169 series are represented by at least one site per island/islet.

170

171 All well-recognized, nominal, species are included for both series, and putative  
 172 species from precursor islands, e.g., the four lineages on Martinique in secondary contact  
 173 after the coalescence of the precursor islands (Thorpe et al., 2010), are treated as separate  
 174 entities. For the *roquet* series these are *A. luciae* from St Lucia, *A. trinitatis* (smaller) and *A.*  
 175 *griseus* (larger) from St Vincent, *A. aeneus* (smaller) and *A. richardii* (larger) from Grenada,  
 176 *A. bonairensis* from Bonaire, *A. blanquillanus* from Blanquilla, *A. extremus* from Barbados,  
 177 and NW Martinique *A. roquet*, SW Martinique *A. roquet*, S Martinique *A. roquet* and central  
 178 Martinique *A. roquet* from Martinique. The Barbados species *A. extremus* (nested within  
 179 Martinique roquet) and the four Martinique lineages are hereafter referred to as the *roquet*  
 180 complex. The *bimaculatus* series excludes the small bodied *wattsi* clade, which is sister to the  
 181 remaining larger bodied *bimaculatus* series (Poe et al., 2017). The species included are, *A.*  
 182 *leachi* from Barbuda and Antigua, *A. bimaculatus* from the St Kitts and Nevis bank, *A.*  
 183 *gingivinus* from Anguilla and St Martin, *A. terraaltae* from Les Saintes group of small  
 184 islands, *A. oculatus* from Dominica, *A. ferreus* from Marie Galante, *A. lividus* from  
 185 Montserrat, *A. nubilis* from Redonda, *A. sabanus* from Saba, *A. desiradei* from La Desirade,  
 186 western *A. marmoratus* from west and central Basse Terre, eastern *A. marmoratus* from  
 187 Grande Terre, eastern Basse Terre, and Petite Terre. The population from the islets of Petite  
 188 Terre off Grande Terre are not recognized in this study as a nominal species, but are sampled.  
 189 The populations from the islets of Îlet-à-Kahouanne and Tête-à-Anglais off northern Basse  
 190 Terre are not recognized as nominal species and not included. The multispecies complex of  
 191 *A. sabanus*, eastern *A. marmoratus*, western *A. marmoratus*, and *A. desiradei* is hereafter  
 192 referred to as the *marmoratus* complex (Fig. 2).

192

193 Phylogenetic analysis of the concatenated cyt b and nuclear datasets were conducted  
 194 using a Bayesian method with a Yule tree prior in BEAST v. 1.8.2. (Drummond et al., 2012).  
 195 Heterozygous positions in nuclear sequences were treated as missing data. Datasets were  
 196 partitioned by gene and each assigned separate molecular clock and substitution models, with  
 197 the latter selected under the Bayesian Information Criterion in MEGA5 (Tamura et al., 2011).  
 198 Preliminary runs with relaxed clock models failed to reject non-zero evolutionary rates and so  
 199 strict clock models were utilised. MCMC chains ran for sufficient length to achieve  
 200 convergence and sufficient sampling of all parameters (ESS > 200), verified using the  
 program TRACER v. 1.6 (Rambaut et al., 2014). The maximum clade-credibility (MCC) tree

201 was obtained and annotated with relevant statistics from the posterior sample of trees using  
202 the program TREEANNOTATOR. Additional phylogenetic estimates were also conducted  
203 under maximum likelihood (ML) using RAxML-HPC2 8.2.3 (Stamatakis 2014) on the  
204 CIPRES Portal (Miller et al., 2010) using the iguanid *Polychrus marmoratus* as the outgroup.  
205 The dataset was partitioned as described above and the ML tree estimated using a GTR+G  
206 models and clade support assessed by 500 bootstrap replicates using a GTR+CAT model  
207 (which approximate the GTR+G model while offering greatly increased computational  
208 speed). We additionally analysed the aligned nuclear sequences using identical methods to  
209 check for consistency between relationships inferred using only nuclear sequences with those  
210 inferred using the complete dataset.

211

### 212 2.2.2 Phylogenetic methods Analysis 2: Molecular dating

213

214 The extent of molecular divergence between a pair of extant species may give an upper  
215 bound to the time of their divergence, but this will tend to be exaggerated by deep lineage  
216 coalescence, and especially by the extinction of any intermediate species. The latter may be a  
217 particular problem in radiations with considerable species turnover and lead to a gross  
218 overestimation of the age of a species. Assuming complete lineage sorting following  
219 colonization, and no subsequent bottlenecking, the extent of divergence within a species  
220 should give a more realistic estimate of time of colonization and origin, but will be  
221 underestimated by lineage extinction resulting from genetic drift, and or under-sampling  
222 within the species. The latter can be managed by comprehensively sampling the geographic  
223 range of a species, as this will minimize the possibility of not sampling a major divergent  
224 phylogeographic lineage. For this analysis, we employed just the cyt b gene, because mtDNA  
225 will more closely match population divergence and be less prone to incomplete lineage  
226 sorting due to lower effective size ( $N_e$ ) in comparison to nuclear markers. Moreover, it  
227 allowed us to efficiently maximize the number of sites with sequences, thereby minimizing  
228 the problem of under-sampling within-species divergence. Hence for Analysis 2, the number  
229 of sites per species was maximized (Fig 2). Sample site numbers for Analysis 2 that are not  
230 also used in Analysis 1 are given for each species in Thorpe et al. (2015), or Appendix A in  
231 supplementary materials. This gave us dense to very dense sampling for all the *roquet* series  
232 species (even the small island of Blanquilla has several sampled sites and St Lucia has over  
233 80), with *A. oculatus* (Dominica), and the western and eastern *A. marmoratus* from the  
234 *bimaculatus* series, being well sampled.

235

236 We calibrated our Analysis 2 phylogenetic tree by constraining the age of the tree  
237 root. This age was estimated by reanalysis of the dataset and calibrations used in a previous  
238 phylogenetic study of iguanian lizards (Townsend et al., 2011), in order to recover the mean  
239 age of the *Anolis* crown group. Based on reanalysis of the Townsend et al. (2011) dataset, we  
240 calibrated the *Anolis* tree root using a normal prior with a mean age of 44.9 mybp and a 95%  
241 confidence interval of 36.1–53.3my (T. Townsend, pers. comm.).

241

## 242 3. Results

243

### 244 3.1 Analysis 1: Multilocus tree

245

246 We generated a combined total of 2453bp DNA sequence from five single copy nuclear  
247 genes (621 bp of NTF3, 516 bp of PRLR, 344 bp of R35, 729 bp of RAG1, 330 bp of  
248 Rhodopsin), for the numbered sites in Fig 2, together with 1041 bp mitochondrial DNA (cyt  
249 b) sequences for these sites. Concatenated analysis of nuclear sequences without  
250 mitochondrial DNA gave a phylogeny with well supported interspecific relationships above

251 the level of species complexes (Appendix B in supplementary materials). While concatenated  
 252 analysis of all sequences provided complete resolution (posterior clade probabilities all  
 253 >0.95) of interspecific relationships within the *roquet* series and almost complete resolution  
 254 within the *bimaculatus* series (except at the *nubilis* and *marmoratus* node) (Fig. 3). The  
 255 topology was confirmed by the congruent maximum likelihood tree (Appendix C in  
 256 supplementary materials). The analysis 1 phylogeny supported the monophyly of almost all  
 257 nominal species with multi-individual sampling, except where there are multispecies  
 258 complexes. In the *bimaculatus* series, the *marmoratus* complex has *A. sabanus* (Saba) nested  
 259 within the western *marmoratus* (Basse Terre) lineage rendering it paraphyletic, and *A.*  
 260 *desiradei* as sister to the eastern *marmoratus* (Grande Terre plus) lineage. The *roquet*  
 261 complex contains *A. extremus* (Barbados) nested among the Martinique “species” from the  
 262 precursor islands, with the central Martinique *A. roquet* as the sister lineage.

263 Within the *roquet* series, a major division exists between the lineage (*A. luciae*,  
 264 *bonairensis*, *blanquillanus*) and the lineage (*A. roquet*, *extremus*, *trinitatis*, *aeneus*, *richardii*,  
 265 *griseus*). Notably these two primary lineages within the *roquet* series do not inhabit  
 266 geographically distinct regions. The lineage (*A. roquet*, *extremus*, *trinitatis*, *aeneus*, *richardii*,  
 267 *griseus*) then splits into a lineage (*A. trinitatis*, *richardii*, *griseus*) from the more southerly  
 268 LA islands of St Vincent and Grenada, and a more widely distributed lineage (*A. roquet*,  
 269 *extremus*, *aeneus*) from Martinique, Barbados and Grenada. The large species of *A. richardii*  
 270 and *A. griseus*, from Grenada and St Vincent respectively, are sister taxa, while the small  
 271 species (*A. aeneus*, *A. trinitatis*) are not. Neither of the large and small pairs on St Vincent  
 272 (small *A. trinitatis*, large *A. griseus*), and Grenada (small *A. aeneus*, large *A. richardii*) are  
 273 sister species. All these major divisions of the *roquet* series are well supported.

274 However, in the *bimaculatus* series there are some geographic trends. The northern  
 275 species *A. leachi*, *A. bimaculatus*, and *A. gingivinus* (from Barbuda/Antigua, St Kitts/Nevis,  
 276 Anguilla/St Martin respectively) group together, as do those from the more southerly regions  
 277 of the *bimaculatus* series range, that is, *A. terraaltae* (Les Saintes) and *A. oculatus*  
 278 (Dominica). The species from the more central part of the *bimaculatus* series range, *A.*  
 279 *ferreus*, *A. lividus*, *A. nubilis*, and the *marmoratus* complex, also group together.

280 One of the purposes of the multilocus Analysis 1 is to contribute to defining the  
 281 evolutionary units or “species” to be dated in Analysis 2. For the *roquet* series the nominal  
 282 species *A. luciae*, *A. trinitatis*, *A. griseus*, *A. aeneus*, *A. richardii*, *A. bonairensis*, and *A.*  
 283 *blanquillanus* are reciprocally monophyletic and on this criteria are not excluded from the  
 284 dating in Analysis 2. *Anolis extremus* (Barbados) is nested inside the four major lineages of  
 285 the *roquet* complex from Martinique in conformity with previous studies (Thorpe and  
 286 Stenson, 2003; Thorpe et al., 2010; Surget–Groba and Thorpe, 2013). Investigations of the  
 287 geology, phylogeography and population genetics of this complex elucidate how the four  
 288 *roquet* “species” occupied four of the precursor islands (NW Martinique, SW Martinique, S  
 289 Martinique and central Martinique) that have geologically recently joined to form current day  
 290 Martinique resulting in secondary contact with varying degrees on introgression. The nominal  
 291 species *A. extremus* evolved on Barbados after having probably been colonized from the  
 292 central Martinique precursor island. Consequently, these five reciprocally monophyletic  
 293 lineages are regarded as independent entities for the purposes this study, and join the seven  
 294 nominal species above in being eligible for dating in Analysis 2.

295 The species of the *bimaculatus* series are less well sampled and the situation is more  
 296 complex. The Dominican species (*A. oculatus*) is monophyletic and is eligible for inclusion  
 297 in the dating analysis. The situation with the *marmoratus* complex is less well studied than  
 298 the *roquet* complex. Once again there appears to be two broad reciprocally monophyletic  
 299 allospecies associated with precursor islands of Basse Terre and Grand Terre (although the  
 300 Grande Terre plus outlying islands lineage now also occupies eastern Basse Terre). However,

301 *A. sabanus*, while being distinctly different in appearance, is not reciprocally monophyletic  
 302 with the Basse Terre lineage, but is nested within it. Moreover, *A. desiradei* and Grande Terre  
 303 *A. marmoratus* are sister lineages nested within the *marmoratus* complex. The recognition of  
 304 these allopatric species inevitably has arbitrary aspects, and this allows various interpretations  
 305 of the evolutionary units to be dated.

306

### 307 3.2 Analysis 2: Molecular dating

308

309 We assembled a dataset of 459 mitochondrial DNA sequences from the *roquet* and  
 310 *bimaculatus* series, comprising 1041bp of aligned cyt b sequence (all sites in Fig. 2). We  
 311 found high levels of haplotype diversity. Sequences from 339 individuals of nine species in  
 312 the *roquet* series yielded 319 unique cyt b haplotypes. Reduced sampling for the *bimaculatus*  
 313 series prevents a robust comparison, but the rates of haplotype discovery in the two well-  
 314 sampled species suggests similar levels of diversity. The large-sample, single-gene Yule tree  
 315 (Appendix D in supplementary materials) is generally congruent with the reduced-sample,  
 316 multilocus tree from Analysis 1. However, details of the *marmoratus* complex from the  
 317 *bimaculatus* series differ. Here, the western *A. marmoratus* lineage (Basse Terre) is no longer  
 318 monophyletic, since two individuals from western Basse Terre join *A. nubilis* (Redonda) as  
 319 an out-group to the otherwise congruent *marmoratus* complex. Hence, the inclusion of  
 320 western *A. marmoratus* as an evolutionary unit to be dated is compromised, as is the dating of  
 321 the whole *marmoratus* complex, as these units include the nominal species *A. nubilis* in  
 322 contradiction to the multilocus tree.

323 For the *roquet* series, the *roquet* complex is eligible to be dated, as potentially are the  
 324 “species” NW *A. roquet*, SW *A. roquet*, S *A. roquet*, central *A. roquet*, *A. extremus*, *A.*  
 325 *trinitatis*, *A. aeneus*, *A. richardii*, *A. griseus*, *A. luciae*, *A. bonairensis*, and *A. blanquillanus*.  
 326 However, the latter has to be excluded because there are too few samples within the species  
 327 to adequately sample the diversity, and S Martinique and central Martinique *roquet* have to  
 328 be excluded because of the potential for bottlenecks reducing the within species diversity.  
 329 Although the central Martinique lineage now occupies quite a large area, the lack of  
 330 phylogeographic structure (Thorpe and Stenson, 2003; Thorpe et al., 2010), and relative low  
 331 diversity, is suggestive of bottlenecking. However, this still allows a strong sample of  
 332 species to be dated within the *roquet* series. The situation with the *bimaculatus* series is less  
 333 useful. The species *A. leachii*, *A. bimaculatus*, *A. ferreus*, *A. nubilis*, *A. sabanus*, and *A.*  
 334 *terraltae*, are not sufficiently well sampled to allow robust dating based on within-species  
 335 diversity. Moreover, the diversity of those on the smaller islands and islets (e.g. Redonda, Les  
 336 Saintes) may be impacted by bottlenecking. Dating of some of the components of the  
 337 *marmoratus* complex is also difficult given the complications explored above (incongruence,  
 338 outliers and species limits).

339 The median and 95% HPD of the appropriate time to most recent common ancestor  
 340 (TMRCA) dates are given in Table 1, and illustrated in Fig 4. The age of the *roquet* series,  
 341 based on within-series divergence is about 32 mybp, while the *bimaculatus* series, using the  
 342 same criteria is younger at about 22 mybp. The age of the eligible species in the *roquet* series  
 343 (NW *A. roquet*, SW *A. roquet*, *A. extremus*, *A. trinitatis*, *A. aeneus*, *A. richardii*, *A. griseus*,  
 344 *A. luciae*, and *A. bonairensis*) are all under 5 my with an mean age of 2.5 my. Hence, the well  
 345 sampled individual species in the *roquet* series are very much younger than the series itself:  
 346 on average only a thirteenth of the age of their series. Even the multispecies *roquet* complex  
 347 is only 7.6 my old, approximately a quarter of the age of its series.

348 The Dominican anole (*A. oculatus*) from the *bimaculatus* series is relatively young at  
 349 just under 4 my and the eastern *A. marmoratus* lineage (Grande Terre plus offshore islets)  
 350 dates at a very similar 4.4my. If the incongruent *A. nubilis*+outliers are excluded, the western

351 *A. marmoratus* lineage (western Basse Terre plus *A. sabanus*) is also a comparable 3.6 my  
 352 old. The *marmoratus* complex is 6.9 my old if the *A. nubilis*+outliers are excluded, and 7.6  
 353 my if not. In any event there a few species to be robustly dated, but, one again, they are much  
 354 younger than the age of the series (about a fifth depending on the definition of a “species”).

355

#### 356 4. Discussion

357

##### 358 4.1 Species relationships

359

360 Earlier molecular phylogenies of Lesser Antillean anoles relied heavily on mtDNA analyses  
 361 (Creer et al., 2001; Stenson et al., 2004), although other data (allozymes for the former,  
 362 microsatellites for the latter) were included. These studies of the *bimaculatus* (Stenson et al.,  
 363 2004) and *roquet* (Creer et al., 2001) series were far less well resolved and supported than the  
 364 current multilocus study, which has only one key node with relatively poor support (in the  
 365 *bimaculatus* series) (Fig. 3). Even so there is broad congruence between the trees from these  
 366 earlier studies and the multilocus tree. They do, however, differ in node support and in the  
 367 important detail of the topology. A recent phylogeny of all extant *Anolis* species (Poe et al.,  
 368 2017), based on mtDNA and a nuclear exon, failed to resolve the relationships within either  
 369 the *roquet* or *bimaculatus* series as the nodes were generally very poorly supported at this  
 370 level. The *bimaculatus* and *roquet* phylogenies of Poe et al. (2017) are notably incongruent  
 371 with the well-supported phylogeny in this study.

372 One novel aspect of the resolved *roquet* series phylogeny is that the two larger species  
 373 (*A. griseus*, St Vincent: *A. richardii*, Grenada) are sister taxa, and that neither of the two  
 374 species pairs on St Vincent (*A. griseus* and *A. trinitatis*), or Grenada (*A. aeneus*, *A. richardii*),  
 375 are sister taxa. There is evidence from Thorpe et al. (2010) and Surget-Groba et al. (2012),  
 376 that there can be notable reduction in gene flow between populations from different habitat  
 377 types within an island. However, this study does not provide phylogenetic/biogeographic  
 378 evidence of within-island speciation.

379 One of the better known aspects of Lesser Antillean anole biogeography is the  
 380 tendency for solitary anoles to be of intermediate size while with sympatric pairs one tends to  
 381 be large and the other small. However, this is not absolute and there are several problems  
 382 with this characterization, not the least when alternative hypotheses (e.g. character  
 383 displacement versus size assortment) are to be rigorously tested. Roughgarden and Pacala  
 384 (1989) suggest that the size differential in sympatric pairs is due to secondary colonization by  
 385 larger anoles driving the original anole to become smaller to avoid competition, and  
 386 subsequently being driven extinct. This study does not support of this hypothesis, as although  
 387 on St Vincent the smaller congener is older, on Grenada, it is the larger of the pairs which is  
 388 older. Analysis of size evolution across these radiations requires fully-resolved species trees,  
 389 and the absence of these inevitably imposed limits on earlier attempts at to test causal  
 390 hypotheses (Butler and Losos, 1997; Creer et al., 2001). Further phylogenetic challenges to  
 391 the analysis of this relative size evolution come from the limited number of independent  
 392 evolutionary events (degrees of freedom) available. The resolved phylogeny of the *roquet*  
 393 series in this study indicates that the current larger species are sister taxa and evolved only  
 394 once, and while an analysis of the *bimaculatus* and *wattsi* series requires a similarly resolved  
 395 species tree, it is apparent that the small-bodied *wattsi* group is monophyletic (Nicholson et  
 396 al, 2012) and small body size likely evolved only once. This natural limit to the number of  
 397 independent evolutionary events may restrict the power of a statistical test. Another challenge  
 398 is the difference between absolute size and relative size. While it is clear that in both series,  
 399 one of the sympatric pairs is relatively larger and the other relatively smaller, this does not  
 400 hold well for inter-island comparisons when sizes are treated as categorical (small,

401 intermediate, large). For example, *A. aeneus* may be categorized as small (Losos, 2009), and  
 402 is smaller than its sympatric congener on Grenada, but it is still a robust and fairly large anole  
 403 of comparable size to those classified as intermediate, such as the *roquet* species from  
 404 Martinique (Appendix E in supplementary materials). Field experiments have shown size to  
 405 be a target of selection (Thorpe et al., 2005a), and size may vary substantially within a  
 406 species, showing considerable sexual, spatial and temporal variation. Males are generally  
 407 substantially larger than females across all species for both radiations, and certain ecotypes  
 408 within a species (e.g. montane ecotypes in Dominica and Basse Terre) may be notably larger  
 409 than others (Thorpe et al., 2015). Studies have also shown considerable temporal variation in  
 410 some, but not all, Lesser Antillean species, with subfossils of some Late Pleistocene species  
 411 from the *bimaculatus* series were larger than current forms, for example *A. ferreus* (Marie  
 412 Galante) were 25% larger (Bochaton et al., 2017) and *A. leachii* 60% larger (Losos, 2009) in  
 413 their relatively recent past. These factors are all further complicated by the practical issues of  
 414 quantifying size parameters in an organism with indeterminate growth, and the prospect of  
 415 evolutionary steps being overwritten by species turnover. Consequently, there is much more  
 416 to be done in critically analyzing this phenomena using well resolved species trees, adequate  
 417 sampling at various levels, and taking into account the above issues.

418 The recognition of allopatric species has an arbitrary element to it, which is exposed  
 419 in both the *roquet* and *marmoratus* complexes. In the *roquet* complex, *extremus* from  
 420 Barbados is nested among the previously allopatric lineages of the Martinique *roquet*  
 421 nominal species. However, detailed population genetic study (Thorpe et al., 2010) shows that,  
 422 generally, the different lineages within this nominal species exchange nuclear genes where  
 423 they meet, as if they were conspecific. *Anolis roquet* on Martinique are regarded as nominally  
 424 conspecific, while *A. extremus*, at least as phylogenetically divergent as most Lesser  
 425 Antillean anoles, is found on distant Barbados (with no real prospect of genetic exchange  
 426 with the Martinique populations) and is regarded as a sound nominal species. The situation in  
 427 the less well-studied *marmoratus* complex from the *bimaculatus* series is even more  
 428 complex. In a parallel situation to that in the *roquet* complex, there are two prospective  
 429 precursor islands, Basse Terre and Grande Terre, which have recently approached, but are  
 430 currently separated by a narrow, shallow, channel. As in the *roquet* complex these precursors  
 431 have matching lineages (albeit with less lineage – precursor congruence) without evidence of  
 432 complete genetic isolation where they meet on eastern Basse Terre (Malhotra, 1992). Hence  
 433 they are nominally conspecific as *A. marmoratus*. Also *A. desiradei* (La Desirade) is sister to  
 434 the Grande Terre *A. marmoratus* lineage and is therefore nested inside the *marmoratus*  
 435 complex. The La Desirade population is quite phylogenetically divergent to its sister lineage  
 436 and here is regarded as a separate species. Although the Saban population is phylogenetically  
 437 nested within Basse Terre *A. marmoratus*, it is morphologically distinct, and at a considerable  
 438 geographic distance, and is regarded as the species *A. sabanus*. The population from the islets  
 439 of Petite Terre (off shore to Grande Terre) are not phylogenetically divergent and we do not  
 440 recognize these as separate species based on current available information. We did not  
 441 include the populations from the islets of Îlet-à-Kahouanne and Tête-à-Anglais offshore to  
 442 north Basse Terre, but see no published evidence to warrant their recognition as separate  
 443 species (Meiri, 2016), and its phylogenetic relationships in Poe et al. (2017) are very poorly  
 444 supported, make little geographic sense, and have little phylogenetic congruence with this, or  
 445 previous, studies.

#### 446 447 4.2 The evolutionary and geological timescale

448  
449 The *roquet* and *bimaculatus* (excluding the *wattsi* group) series arose around 32 and 22 mybp  
 450 respectively (Fig. 4, Table 1) after the origin of the older outer arc of Lesser Antillean islands

451 in the Eocene to Miocene (Wadge, 1994), but before the origin of the younger inner arc  
 452 (Bouysse, 1984). These geological dates are compatible with the invasion of the older arc  
 453 from the south (S America) by the *roquet* series, and from the north (Greater Antilles) by the  
 454 *bimaculatus* series, that is, step one in the above model. The subsequent invasion of the  
 455 younger arc, once again by the *roquet* series in the south, and *bimaculatus* series in the north  
 456 (step 2), could be achieved once the individual younger islands arose (circa <8 mybp). The  
 457 difference in age of the two series is misleading, and it does not mean that the *roquet* series  
 458 invaded the Lesser Antilles before the *bimaculatus* series. The *wattsi* complex of small  
 459 northern anoles, which are phylogenetically (Poe et al., 2017) and morphologically distinct  
 460 from the more morphologically robust *bimaculatus* series, are not included in this analysis.  
 461 Their inclusion as part of the *bimaculatus* series would increase the diversity, and hence  
 462 estimated age, of this series. The current north-south distribution of anoles in the Lesser  
 463 Antilles is not shown in other animal groups and, given the dynamics of species turnover, we  
 464 cannot necessarily assume that the relative distribution of these two series has been stable  
 465 over time.

466 Based on within-species divergence, the extant species are estimated to have arisen  
 467 after the geological origin of their respective islands (Fig 4, Table 1, Appendix F in  
 468 supplementary materials), as one would expect if the dating of the origin of both island and  
 469 species is correct. One notable exception to this is *A. extremus* on Barbados. Barbados,  
 470 unlike most other Lesser Antillean islands is not volcanic in origin, but is an accretionary  
 471 prism covered by sedimentary rock. Although the underlying rock is ancient it is thought that  
 472 it uplifted only recently (Bender et al., 1979) and the sedimentary capping suggests an age of  
 473 emergence about a 0.5 to 1.0 million years (Speed, 1994). There is substantial, hierarchal  
 474 phylogeographic structure in *A. extremus* within Barbados (which is compatible with the  
 475 slightly greater, between-species divergence, within the *roquet* complex) (Table 1). There are  
 476 no suitable series of adjacent islets to act as alternative refugia with divergent populations  
 477 from which mainland Barbados could be recolonized. Hence, the situation cannot readily be  
 478 explained by anything other than at least some of the Barbados accretional prism being above  
 479 water and inhabitable for much longer than 1 mybp. This is discussed in detail in Thorpe et al.  
 480 (2005b) and the dates for the *roquet* complex and its constituent lineages, including *extremus*  
 481 from Barbados, are compatible with the previous focused studies (i.e. 95% limits generally  
 482 overlap).

483 Both the geological and molecular dating in the *marmoratus* complex and associated  
 484 islands are complicated. La Desirade (Maury et al., 1990) is very ancient (predating the origin  
 485 of all the lineages discussed here), while the dating of Grande Terre is complicated in a  
 486 similar way to that of Barbados:- that, is the underlying rocks may be older, but it has a more  
 487 recent sedimentary limestone cap and one cannot be sure that none of Grande Terre (or in this  
 488 case, any other associated island or islet within easy colonization distance) was not above  
 489 water and available for the *marmoratus* complex to inhabit. Consequently, the best date  
 490 available is that of high elevation Basse Terre dated at 4-6 mybp (Maury, 1990). These  
 491 geological dates overlap the 95% HPD values for the complex (all lineages), although they  
 492 are below the mean value. However, here the phylogenetic information may be less reliable  
 493 (in contradiction to the multilocus study) as another species (*A. nubilis*) and two Basse Terre  
 494 specimens are included as outliers in this complex. This will exaggerate the within-complex  
 495 divergence, and once these are excluded the geological dates are more compatible with the  
 496 within-complex, and within-“species” ages of 6.9 mybp for the *marmoratus* complex, and 3.6  
 497 mybp for the western *A. marmoratus* (Basse Terre, Saba).

498 One of the notable facets of Table 1 is the discrepancy between the age of a species  
 499 estimated from within species divergence, compared to the age estimated from between-  
 500 species divergence. While in some situations (such as the *roquet* complex) between-species

501 divergence is no greater than within-species divergence than one would expect, in others the  
 502 discrepancy is very notable. For example, the within-species divergence of *A. luciae* is likely  
 503 to be reliable as it is based on exhaustive phylogeographic sampling, with little likelihood of  
 504 bottlenecking having occurred on this large, high-elevation island. The within-species  
 505 estimate for the age of *A. luciae* is only 3.3my (2.3 - 4.3 95% HPD), while the between-  
 506 species estimate is 23.4 (17.2- 29.6 95% HPD). While this is an extreme case, it nevertheless  
 507 holds true as a generalization for situations where the phylogeny, phylogeographic sampling,  
 508 and insensitivity to bottlenecking, allow meaningful estimates of within-and among species  
 509 divergence (e.g., *A. luciae*, *A. trinitatis*, *A. griseus*, *A. aeneus*, *A. richardii*, and *A. oculus*).  
 510 It is clear that using between-species divergence to estimate species age could lead to a very  
 511 misleading, gross over-estimation. On small, or low-elevation, islands bottlenecking can  
 512 potentially greatly reduce within-species divergence so that species age cannot be reliably  
 513 estimated from within-species divergence. In these situations, and where phylogeographic  
 514 sampling does not allow an estimate of within-species divergence, then at least between  
 515 species divergence may give an upper bound to the species age, however unrealistic it is as an  
 516 estimate of the real age. However, considerable caution is required when using these inter-  
 517 species estimates, because they can give ages greater than the age of the island, emphasizing  
 518 their unreliability.

519

#### 520 *4.3 Species age and inter-island colonization*

521

522 The other, and perhaps most important revelation from Table 1, is the age of the species  
 523 compared to the age of the entire series. While the series are Oligocene in origin, the species  
 524 are Pleistocene to Pliocene, with even the large species complexes no older than very late  
 525 Miocene. The average age of a species in the *roquet* series (excluding underestimations due  
 526 to potential bottlenecking or inadequate sampling) is only about 8% of the age of the series.  
 527 Although it is an extreme case, we use *A. luciae* from St Lucia as an example, because it is  
 528 exhaustively sampled and therefore unlikely to give an underestimate of species age due to  
 529 inadequate sampling. St Lucia combines both young and old arc elements, and is dated at  
 530 about 18 mybp (Briden et al., 1979), while the current extant species age is estimated at only  
 531 3.3 my old. Could St Lucia have been unoccupied by anoles prior to the establishment of *A.*  
 532 *luciae*? This is most unlikely, given the complete occupation of every island and islet in the  
 533 Lesser Antilles. Given the size and elevation of the island, and the phylogeographic structure  
 534 of the species, it is also unlikely that bottlenecking has substantially underestimated species  
 535 age. This study provides no evidence of within-island speciation, so serially repeated *in situ*  
 536 within-island speciation, with the new species repetitively replacing the old, is also an  
 537 unlikely explanation. It is also unlikely that the species age (estimated by mtDNA) has been  
 538 grossly under-estimated by serially repeated, or at least recent, selective sweeps eradicating  
 539 all earlier haplotypes. The most likely explanation is that there is species turnover with the  
 540 island being occupied by a series of different anoles through time with colonizers replacing  
 541 residents by competitive exclusion, perhaps (but not necessarily) with additional factors, such  
 542 as disease and extreme physical events (volcanism, hurricanes), impacting the process. We  
 543 are not aware of any anole extirpations due to recent hurricanes, volcanism or disease, and  
 544 even the massive volcanic event in Dominica 28 ky ago did not expurgate *A. oculus*  
 545 (Malhotra and Thorpe, 2000). These additional proximal reasons may be irrelevant to the  
 546 broad picture of competitive replacement by new colonizers. In any event, the age of the  
 547 Lesser Antillean anole species is not exceptional, and is what one would expect for a small  
 548 terrestrial amniote. The species ages in this study are compatible with estimates of mean  
 549 species age in other northern hemisphere squamates of 3.3 my (Dubey and Shine, 2010), the  
 550 average persistence time of an island population of birds in the Lesser Antilles of about 2 my,

551 (Ricklefs and Bermingham, 2007), and a modal age of 1-2 my for small North American  
 552 mammals (Prothero 2014). What emerges is that the current biogeographic pattern, in  
 553 geological terms, is likely to be just a temporary time-slice of a very dynamic situation, with  
 554 substantial species turnover throughout the long life of the radiations.

555 Species turnover has important implications, not least for attempts to understand the  
 556 colonization sequence within the Lesser Antilles (i.e. step 2 inter-island colonization). As the  
 557 *bimaculatus* series phylogenetically splits into northern, middle and southern islands, it is  
 558 tempting to interpret this as an earlier-to-later colonization sequence from north to south  
 559 down the Lesser Antillean chain (Stenson et al., 2004). However, given that 1) the younger  
 560 arc did not exist at the origin of either of the series, and 2) that the species involved in the  
 561 early inter-island colonization sequence no longer exist, attempts to reconstruct these early  
 562 stages (Stenson et al., 2004; Losos, 2009) are inevitably spurious.

563 Although reconstructing the early stages of inter-island colonization may be  
 564 problematic, recent events, such as parapyly (where one island species is nested inside  
 565 another island species) may enable some recent inter-island colonizations to be reconstructed  
 566 (Fig. 5). Indeed, if no species or haplotypes were lost, one would expect the phylogeny for a  
 567 radiation to be a complete, sequential, pectinate comb with each species nested inside the  
 568 next. In fact, parapyly appears to be relatively rare, the early events being eradicated by  
 569 lineage loss and species turnover. There are a few examples of species parapyly established  
 570 here (the number depending on the arbitrary recognition of allopatric species). The Barbados  
 571 anole is nested within the nominal (paraphyletic) *A. roquet* species, and *A. sabanus* (Saba)  
 572 and *A. desiradei* (La Desriade) are nested within the nominal (paraphyletic) *A. marmoratus*  
 573 species.

574 The origin and colonization sequence of the four *A. rouquet* lineages on the respective  
 575 precursor islands of Martinique, and *A. extremus* from Barbados, are discussed in detail in  
 576 Thorpe et al. (2010) and Surget-Groba and Thorpe (2013). Barbados appears to have been  
 577 colonized from the relatively distant Martinique complex (Fig 5), being a sister lineage to the  
 578 central Martinique lineage within the *roquet* Martinique complex (Thorpe and Stenson, 2003;  
 579 Thorpe et al., 2010; Surget-Groba and Thorpe, 2013). The colonization sequence within this  
 580 complex suggested by Thorpe et al. (2010) and Surget-Groba and Thorpe (2013) is the  
 581 divergence of the south and southwest *A. roquet* on their respective precursor islands, the  
 582 colonization of the central Martinique precursor from the south Martinique precursor, the  
 583 subsequent colonization of Barbados from this central Martinique, and the colonization of the  
 584 northwest Martinique precursor from the southwest Martinique precursor.

585 In the *marmoratus* complex, from the northern *bimaculatus* series, nominal species on  
 586 small islands are nested inside a nominal species from a main island complex, with primary  
 587 lineages that may correspond to precursor islands. Unlike the situation in Martinique where  
 588 the four lineages correspond very closely with the four precursor islands, here there are two  
 589 primary parapatric lineages (western and eastern *marmoratus*) that correspond less closely  
 590 with the two presumed precursor islands of Basse Terre and Grande Terre. In this case  
 591 eastern *A. marmoratus* (primarily Grande Terre) extends substantially into eastern Basse  
 592 Terre (Fig. 2B, 5). The two main islands, Basse Terre and Grande Terre, currently approach  
 593 at a narrow, low elevation isthmus, but presumably these were separate islands in the past.  
 594 While alternative scenarios are possible, the simplest explanation is that the western and  
 595 eastern lineages diverged on Basse Terre and Grande respectively after about four to six  
 596 million years ago when they were both emerged separate islands (Fig. 5), and the eastern  
 597 lineage, based originally in Grande Terre, has subsequently spread into eastern Basse Terre.  
 598 Subsequently to this east–west split, La Desriade was colonized from eastern *A. marmoratus*  
 599 on Grande Terre, and geographically distant Saba was relatively recently colonized from  
 600 western *A. marmoratus* on Basse Terre (Fig 5). It is also reasonable to assume that Petite

601 Terre has recently been colonized by eastern *A. marmoratus* on adjacent Grande Terre, as it is  
 602 nested within this lineage (Fig. 5). Although the critical populations of *A. marmoratus* (i.e.,  
 603 those involved in the eastern and western *marmoratus* contact) have not been the subject of  
 604 similar population genetic research as *A. roquet* (Thorpe et al., 2010), morphological  
 605 continuity among eastern and western lineage populations (Malhotra, 1992) suggests the  
 606 situation is the same as in Martinique. Hence, we have nominal species that are nested inside,  
 607 and are phylogenetically shallower than, the main island primary lineages which are formally  
 608 treated as conspecific.

609 Examples of similar cases of parapatry exist in other Lesser Antillean lizards. For  
 610 example, west Basse Terre also appears to be the source of the Dominican gecko  
 611 (*Sphaerodactylus fantasticus*) as the Dominican population is nested within the western  
 612 Basse Terre lineage for these geckos (Thorpe et al., 2008), while the Dominican lineage of *S.*  
 613 *festus* is nested within the northern Martinique lineage (Surget-Groba and Thorpe, 2013). In  
 614 all these cases, a prerequisite for parapatry to be exposed is multiple sampling of each island  
 615 species. In the *bimaculatus* series several species are represented by only single samples, so  
 616 even if parapatry existed with extant species it would not be exposed by this study.

617 Without parapatry it can be difficult to infer the colonization process even with sister  
 618 species. The large-bodied *A. richardii* (Grenada and Grenadines) and *A. griseus* (St Vincent)  
 619 are sister species, but their age is similar (2.4 and 2.1 my respectively) so it is not possible to  
 620 know whether the colonization direction was from Grenada/Grenadines to St Vincent, or *vice*  
 621 *versa*, or even from a third, now extinct species on another island. Similarly, the islands of  
 622 the South American coast (Bonaire and Blanquilla), and St Lucia form a distinct lineage in  
 623 the *roquet* series (dated by internal divergence at around 23 mybp). While it is reasonable to  
 624 expect that these offshore S American island were colonized from the Lesser Antilles species,  
 625 the divergence of this *luciae/bonairensis/blanquillanus* clade, and the  
 626 *bonairensis/blanquillanus* clade (similarly dated at around 7 mybp) substantially predates the  
 627 age of *A. luciae* precluding it as the colonizer. Given the suspected species turnover, the  
 628 colonizer of these S. American islands could have come from any of the (presumably) Lesser  
 629 Antilles occupied at the time by members of this clade of the *roquet* series.

#### 630 631 4.4 Potential dispersal outcomes

632  
633 It is clear that in Lesser Antillean anoles, and we expect in other radiation, Step 2 is not  
 634 simply a question of the original colonizer dispersing to a series of empty islands in sequence.  
 635 In the potential colonization of an unoccupied island, the two possible outcomes would be  
 636 success or failure. We have no evidence on how frequently natural extinction of these species  
 637 occurs, without congeneric competition, leaving islands unoccupied. However, given the high  
 638 population densities and the current occupation of every island, perhaps most colonization  
 639 attempt will be from one occupied island to another. And here we postulate five potential  
 640 outcomes from such a process.

641 A) The colonizing species is reproductively isolated from the resident species and  
 642 becomes extinct due to stochastic early extinction, or being out-competed by the resident. It is  
 643 axiomatic that this can leave no obvious biogeographic signature, even if it is a frequent  
 644 outcome.

645 B) The colonizing species (small founder population) interbreeds freely with the  
 646 resident species, resulting in introgression. The colonizer may leave no obvious genetic  
 647 signature if the colonizer's genes are too rare to be detected, or are lost due to drift or  
 648 negative selection. The evidence that allopatry over substantial time does not necessarily  
 649 result in reproductive isolation (Thorpe et al., 2010) suggests this may be a very frequent  
 650 outcome. An example of this may be the Caravelle Peninsular population of *A. roquet*, as it is

651 the only Martinique precursor island population without its own distinct genetic lineage. It  
 652 appears that when this precursor island joined the central Martinique region its anole  
 653 population was replaced by the central Martinique population. Given the general lack of  
 654 reproductive isolation among these precursors (Thorpe et al., 2010) it is likely to be  
 655 introgression rather than an example of process A above, except if the Caravelle Peninsula  
 656 was occupied by a different species, very divergent from the *roquet* complex.

657 C) The colonizing species (very large founder population or island coalescence)  
 658 interbreeds to varying extents with the other or resident species, resulting in varying degrees  
 659 of introgression, but recognition as a single nominal species. This leaves a genetic and  
 660 biogeographic signature and each anole series in the Lesser Antilles appears to provide an  
 661 example of this. The extent of introgression between the four precursor Martinique island  
 662 population of the nominal species *A.roquet*, is an example (Thorpe et al., 2010; Surget Groba  
 663 et al., 2012). The colonization of eastern Basse Terre from adjacent Grande Terre by the  
 664 eastern *A. marmoratus* may be an example of a large founder population, or past island  
 665 coalescence.

666 D) The colonizing species is reproductively isolated from the resident and  
 667 outcompetes and replaces the resident. The ongoing invasion of *A. cristatellus* in Dominica  
 668 and its replacement of the similar (intermediate) sized, syntopic, resident *A. oculatus* in the  
 669 south west of the island is direct evidence of at least the first stage of this process (Eales et  
 670 al., 2010; Malhotra et al., 2007). This is also what is inferred for the St Lucian populations  
 671 (see above), and may have occurred frequently on the older arc islands. Theories, such as size  
 672 assortment (Losos, 2009), suggest that an intermediate (solitary) anole could not successfully  
 673 invade when an island is already occupied by an anole of the same size, but the evidence here  
 674 does not support this.

675 E) The colonizing species is reproductively isolated from the resident species and  
 676 survives and coexists in sympatry with it (Step 4). In the north of the northern Lesser Antilles  
 677 the sympatry of the smaller-bodied *wattsi* group with the relatively larger *bimaculatus* series  
 678 provides an example. In the south of the southern Lesser Antilles the species pairs on  
 679 Grenada (*A. aeneus* –smaller, *A. richardii* -larger) and St Vincent (*A. trinitatis* –smaller, *A.*  
 680 *griseus*-larger) provide additional examples. The estimated age of the species suggests that  
 681 the smaller *A.trinitatis* was the resident in St Vincent before the colonization by *A.griseus*. In  
 682 Grenada the estimated age of the species are closer and overlap, but the larger *A. richardii* is  
 683 slightly older and may perhaps have been the resident while *A. aeneus* was the colonizer. It is  
 684 not possible to know the extent of sympatry in the past, or if these islands are currently  
 685 saturated with sympatric pairs. One likely case is Marie Galante which has a large anole (*A.*  
 686 *ferreus*), but no smaller partner. It is not apparent why some islands have two species and  
 687 some just one. There is a geographic trend, with the southern islands of the south series, and  
 688 some northern islands of the north series having two species, while the central islands in the  
 689 chain (both series) have just a single species. However, this does not appear to have anything  
 690 to do with the age of the current extant species, island age, or island size.

691 We can gain an insight into the relative frequency of types C (introgression) and D/E  
 692 (replacement/sympatry) by dating the outcomes from island coalescence, natural sympatry  
 693 and artificial (invasive species) sympatry. The secondary contact after the coalescence of  
 694 precursor island populations from Martinique, even after about 8 my of divergence (Table 1),  
 695 show widespread introgression of varying degrees, and always more than across ecotones  
 696 within a single lineage (Thorpe et al., 2010). Even at about 10 my divergence the invasive  
 697 species of *A.aeneus* and *A. trinitatis* in Trinidad show some hybridization (Hailey et al.,  
 698 2009). However, the naturally occurring sympatry on St Vincent (*A. trinitatis*, *A. griseus*) and  
 699 Grenada (*A.richardii*, *A. aeneus*) occurs after about 15 and 20 my divergence respectively.  
 700 Similarly, there is no introgression between the invasive *A. extremus* and resident *A. luciae*

701 on St Lucia after about 32 my divergence (Giannassi et al., 1997). In the northern Lesser  
702 Antilles the small-bodied *wattsii* group is naturally sympatric with the larger bodied  
703 *bimaculatus* series. Since the *wattsii* group and *bimaculatus* series are reciprocally  
704 monophyletic (Poe et al., 2017) their divergence must be greater (perhaps much greater) than  
705 the within-*bimaculatus* series divergence of 22 my. Hence, it appears that allopatric isolation  
706 does not rapidly result in reproductive isolation and that more than 8, but less than 15 my of  
707 divergence, is required to achieve this. Consequently, for these anole radiations, introgression  
708 is a far more likely outcome in the first half of the radiation process, than replacement or  
709 sympatry if the colonized island is already occupied.

710

#### 711 *4.5 Conclusions from the island radiation model and Lesser Antillean anoles*

712

713 One can infer several stages of the radiation model in the Lesser Antillean anole radiations.  
714 Step 1, the initial colonization (the southern *roquet* series radiation from S. America, the  
715 northern *bimaculatus* series from the Greater Antilles) is uncontroversial. Step 2, inter-island  
716 dispersal can be inferred for relatively recent events e.g., Barbados from Martinique at circa 3  
717 mybp, (or even later in precursor island coalescence), but is opaque, or overwritten by species  
718 turnover, in the early stages of the radiation (i.e., 8-32 mybp). The phylogeographic and  
719 quantitative trait divergence within an island species (Step 3) is well documented (Thorpe et  
720 al., 2015 and references therein), but a very long time (in excess of 8 my) is required for  
721 reproductive isolation. Step 4, (sympatry) is evidenced in a few instances, but these are all  
722 quite old (the youngest at 15 my divergence), never involve more than two species, and are  
723 inferred to occur only in the second half of the radiation process.

724 The genus *Anolis sensu* Losos (2009) is regarded as the most speciose amniote genus  
725 with around 400 extant species. This study suggests that, at least in the case of the Lesser  
726 Antilles and associated islands, estimates based on extant species may greatly under-estimate  
727 the number of species and diversity through geological time. However, this may not reflect  
728 the situation in the larger islands of the Greater Antilles, where extinction rates at equilibrium  
729 in these multispecies anole communities may be low (Rabosky and Glor, 2010).

730

#### 731 **Acknowledgements**

732

733 We wish to thank the numerous authorities of in the Lesser Antilles and associated islands for  
734 their support, Jonathan Losos for his comments on an earlier version of this work and Ted  
735 Townsend for his help in molecular dating.

736

#### 737 **Funding**

738

739 Data for this work was accumulated over a prolonged period, the very latter stages being  
740 supported by an award from The Leverhulme Trust (RF/2/RFG/2010/0008) to R.S.T.

741

#### 742 **Appendices A, B, C, D, E, & F. Supplementary material**

743

744 Supplementary data associated with this article can be found, in the online version, at

745

746 **References**

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- 892

893 **Table 1 Estimate of ages of Lesser Antillean islands and the *Anolis* species occupying**  
894 **them.** Estimate of island and species age from densely sampled island species. Species =  
895 nominal species or previously allopatric “species” from precursor islands. Island age =  
896 geological island age in million years from literature. Within = within series/species  
897 divergence with 95% HPD in brackets, \* = sampling inadequate for meaningful estimate.  
898 Among = among Series/species with 95% HPD in brackets. <sup>1</sup> These are allopatric “species”  
899 (from precursor island) in the *roquet* complex *sensu* Thorpe et al. (2015). <sup>2</sup> The range of the  
900 Central Martinique form also includes the Caravelle peninsula which is Oligocene (ca  
901 <34mybp). <sup>3</sup> Central and South Martinique include some low elevation areas which may have  
902 been under water until recently, and there is no strong phylogeographic structure. Hence  
903 these “Within” dates may be underestimates due to bottlenecking. <sup>4</sup> Martinique includes  
904 precursor islands from both the younger and older arcs. <sup>5</sup> Barbados is ancient rocks with  
905 some more recent limestone capping suggesting recent emergence, but the deep well-  
906 structured phylogeography suggests this species has been diverging in-situ for longer (Thorpe  
907 et al., 2005b). <sup>6</sup> In the south the younger arc is superimposed on the older arc so cited  
908 geological dates may reflect either young arc (St Vincent, Grenada) or older arc (St Lucia)  
909 volcanicity. <sup>7</sup> Bonaire and Blanquilla are old islands with younger limestone without  
910 sufficient data to confidently indicate a date of origin or emergence, although on the latter,  
911 low-elevation island populations may have been bottlenecked. <sup>8</sup> Marie Galante is mid  
912 Miocene overlain by more recent deposits (Martin-Kaye, 1969). <sup>9</sup> The range of the  
913 *marmoratus* complex includes both Basse Terre (younger arc), and Grande Terre, together  
914 with some allopatric populations on islands that can be very ancient (e.g., La Desirade). La  
915 Desirade may be Mesozoic, i.e., earlier than the radiation so this date is not used. Moreover,  
916 Grande Terre may be Lower to Mid Miocene (Martin-Kaye, 1969), but it thought to have  
917 emerged more recently (Maury et al., 1990). Dating the range of the nominal species is  
918 therefore complicated, and here we just consider the younger arc island, Basse Terre, with its  
919 main lineage distributed over the centre and west of the island at 4-6mybp (Maury et al.,  
920 1990) for the complex and its components. <sup>10</sup> One specimen among several, for both localities  
921 2 and 7 in western Basse Terre (maBT02\_08 and maBT07\_39 respectively), join  
922 incongruently (with Analysis 1) with *A. nubilis* (Appendix D in supplementary materials),  
923 rather than others from the same site or the western *marmoratus* lineage. This would  
924 artificially increase both the age of the complex and the eastern *marmoratus* lineage and they  
925 are excluded. Their inclusion would increase the age of the complex slightly to 7.6 mybp.  
926

Island/series	Species	Island age	Reference	Yule Within	Yule Among
<i>roquet</i> series				31.60 (23.8-39.1)	43.6 (34.8-52.6)
NW Martinique	NW Mart <sup>1</sup>	7.1	Briden et al 1979	2.38 (1.57-3.29)	4.19 (2.93-5.56)
SW Martinique	SW Mart <sup>1</sup>	8.3	Briden et al 1979	1.73 (1.07-2.45)	4.19 (2.93-5.56)
Central Martinique	Central Mart <sup>1</sup>	12.8-15.9 <sup>2</sup>	Briden et al 1979, Wadge 1994	1.46 (0.97-2.00) <sup>3</sup>	4.08 (2.96-5.29)
S Martinique	S Mart <sup>1</sup>	<34	Wadge 1994	1.40 (0.86-1.97) <sup>3</sup>	5.94 (4.35-7.65)

All Martinique	<i>roquet</i>	<34 <sup>4</sup>	Wadge 1994	7.56 (5.65-9.65)	10.1 (7.40-12.81)
Barbados	<i>extremus</i>	<sup>5</sup>	Speed 1994, Thorpe et al 2005	3.35 (2.37-4.33)	4.08 (2.96-5.29)
St Lucia	<i>luciae</i>	18.3 <sup>6</sup>	Briden et al 1979	3.30 (2.27-4.33)	23.4 (17.2-29.6)
St Vincent	<i>trinitatis</i>	3.5 <sup>6</sup>	Maury et al 1990	4.23 (2.99-5.64)	15.4 (1.5-19.6)
St Vincent	<i>griseus</i>	3.5 <sup>6</sup>	Maury et al 1990	2.12 (1.40-2.90)	15.4 (1.5-19.6)
Grenada	<i>aeneus</i>	>5 <sup>6</sup>	Maury et al 1990, Martin- Kaye 1969	1.82 (1.20-2.47)	10.1 (7.4-12.81)
Grenada	<i>richardii</i>	>5 <sup>6</sup>	Maury et al 1990, Martin- Kaye 1969	2.44 (1.66-3.26)	19.9 (15.0-25.1)
Bonaire	<i>bonairensis</i>	- <sup>7</sup>		1.21 (0.74-1.78)	7.22 (5.10-9.59)
Blanquilla	<i>blanquillanus</i>	- <sup>7</sup>		0.60 (0.33-0.91)	7.22 (5.10-9.59)
<i>bimaculatus</i> series				22.1 (16.8-27.8)	43.6 (34.8-52.6)
St Martin Bank	<i>gingivinus</i>	37	Briden et al 1979, Maury et al 1990	*	14.5 (9.91-20.0)
Saba	<i>sabanus</i>	0.4	Roobol and Smith 2004	*	2.12 (1.42-2.92)
Kitts Nevis bank	<i>bimaculatus</i>	3.4	Maury et al 1990	*	14.5 (9.91-20.0)
Antigua Barbuda Bank	<i>leachi</i>	40	Briden et al 1979	*	19.6 (14.9-24.6)
Redonda	<i>nubilis</i>	<1.5	Maury et al 1990	*	5.96 (4.21-7.97)
Montserrat	<i>lividus</i>	4.4	Briden et al 1979, Maury et al 1990	*	9.37 (6.95-12.0)
Illes des Saintes	<i>terraealtae</i>	4.7	Maury et al 1990	*	13.6 (10.1-17.3)
Marie Galante	<i>ferreus</i>	<sup>8</sup>		*	12.0 (8.87-15.2)
Guadeloupe (excl I d Saintes, Marie	<i>marmoratus</i> <i>complex</i> <sup>9,10</sup>	(4-6)	Maury et al 1990	*6.91 (5.12- 8.74)	7.61 (5.55-9.81)

Galante)					
Grande Terre + East BT + Petite Terre+Desirade	Eastern <i>marmoratus</i> + <i>desiradei</i> <sup>9</sup>	(4-6)	Maury et al 1990	5.74 (4.12- 7.37)	6.91 (5.12-8.74)
Desirade	<i>desiradei</i> <sup>9</sup>	mesozoic	Maury et al 1990	*	5.74 (4.12-7.37)
Grande Terre +eastern BT+ Petite Terre)	Eastern <i>marmoratus</i> <sup>9</sup>	(4-6)	Maury et al 1990	4.40 (3.10- 5.77)	5.74 (4.12-7.37)
Basse Terre (+Saba)	Western <i>marmoratus</i> <sup>10</sup>	4-6	Maury et al 1990	3.62 (2.48- 4.82)	6.91 (5.12-8.74)
Dominica	<i>oculatus</i>	<5	Maury et al 1990, Martin- Kaye 1969	3.98 (2.85- 5.18)	13.6 (10.1-17.3)

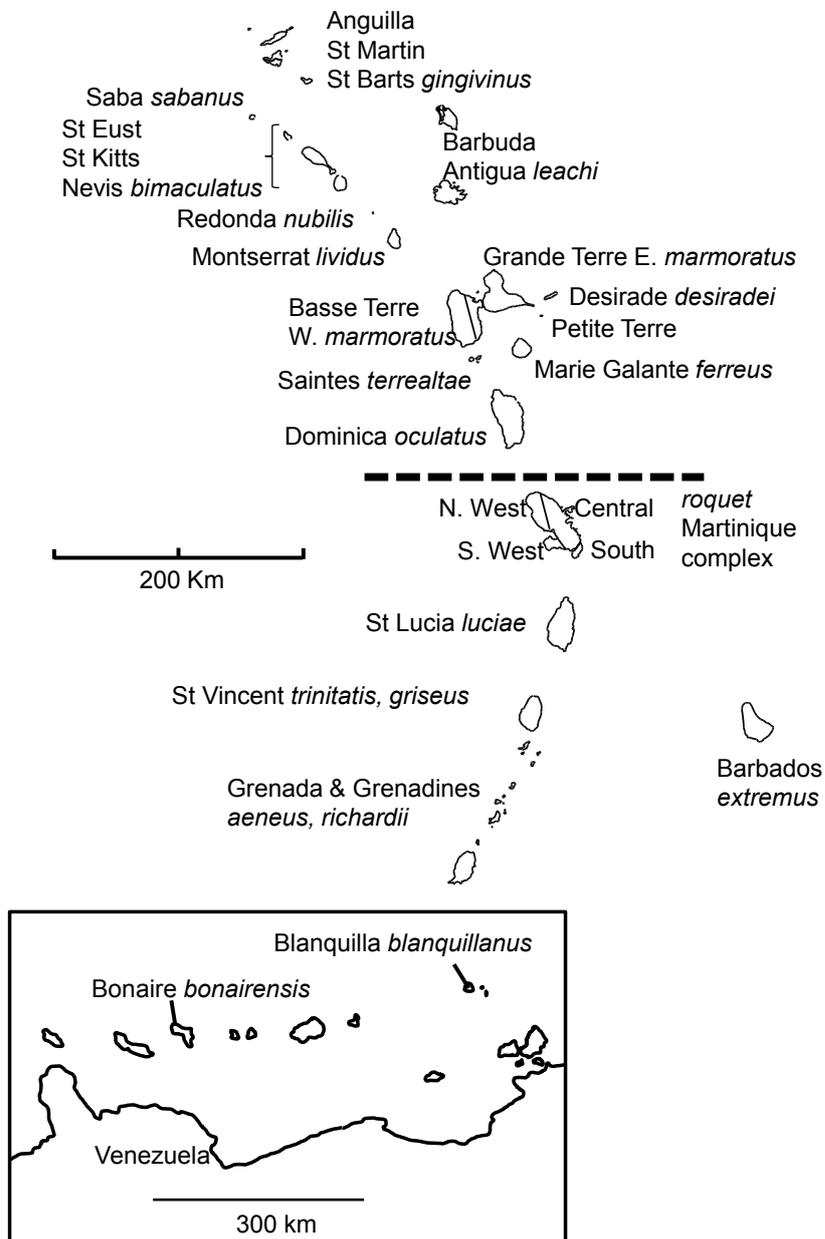
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931 Figure 1. Islands and *Anolis* species (in italics) in the Lesser Antilles and associated islands.  
 932 The *bimaculatus* series is north, and the *roquet* series, south of the dashed line. The insert  
 933 shows Bonaire and Blanquilla off the South American coast. The *wattsii* complex is not  
 934 included.

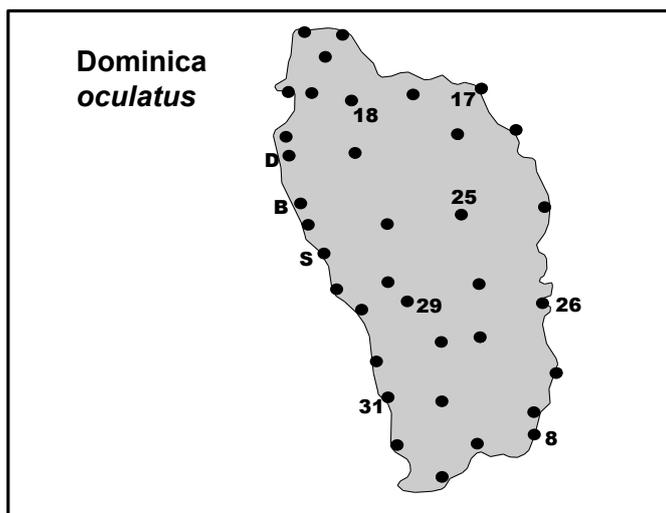
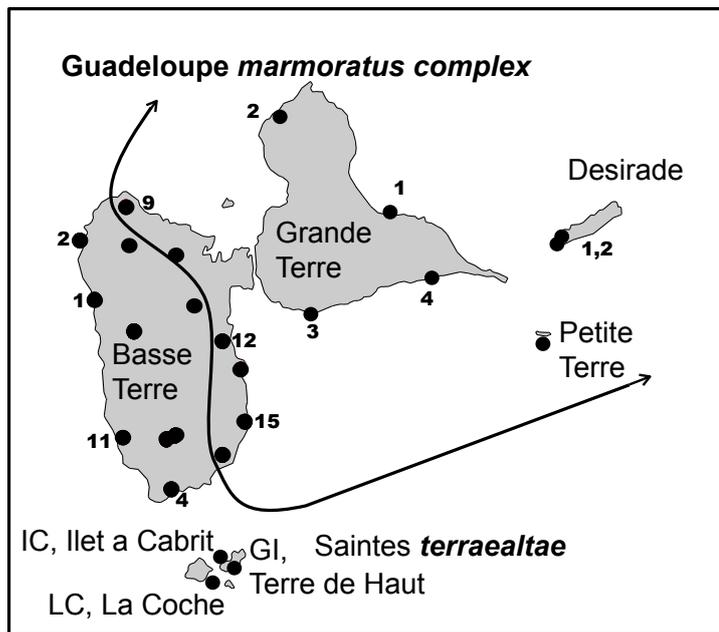


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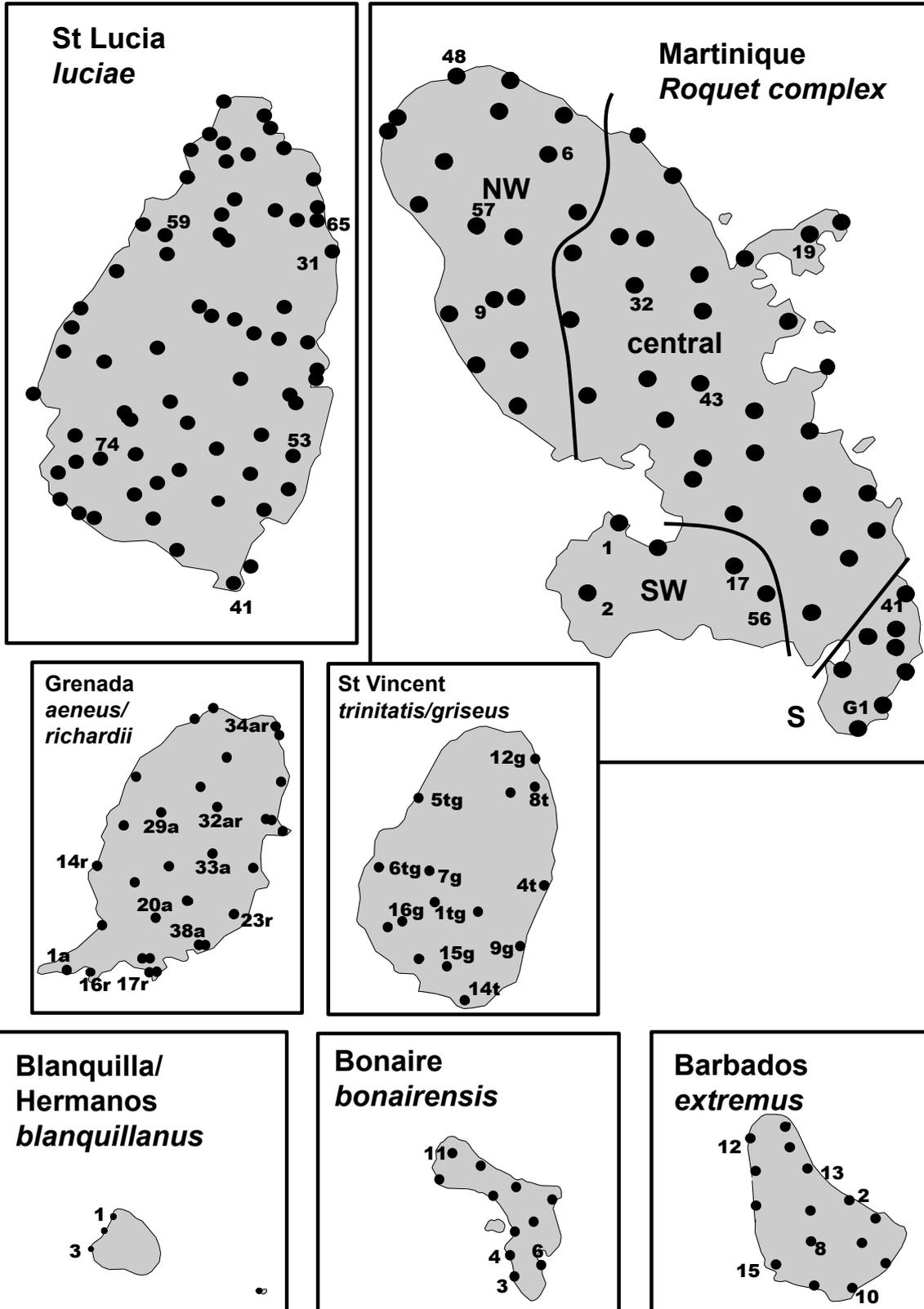
937 Figure 2. Islands with multiple sampling localities. 2A. *bimaculatus* series. 2B *roquet* series.  
 938 Not to scale. Localities employed in analysis 1 are numbered; additional localities (Analysis  
 939 2) are un-numbered. The lines in Guadeloupe and Martinique indicate the components of the  
 940 *marmoratus* and *roquet* complexes respectively. On the multiple species islands of St Vincent  
 941 and Grenada *A. trinitatis*, *A. griseus*, *A. aeneus* and *A. richardii* localities are indicated by t,  
 942 g, a and r respectively. The identity of all localities and the primary lineages of species are  
 943 found in Thorpe et al. (2015) for *A. marmoratus* on Basse Terre, *A. oculatus*, *A. trinitatis*, *A.*  
 944 *richardii*, *A. aeneus* and *A. luciae*; in Thorpe et al. (2005) for *A. extremus*; in Thorpe and  
 945 Stenson (2003) for the *roquet* complex on Martinique; in Thorpe (2017) for *A. bonairensis*;  
 946 and in Appendix A in supplementary materials for *A. blanquillanus* and eastern *A.*  
 947 *marmoratus*.

2A

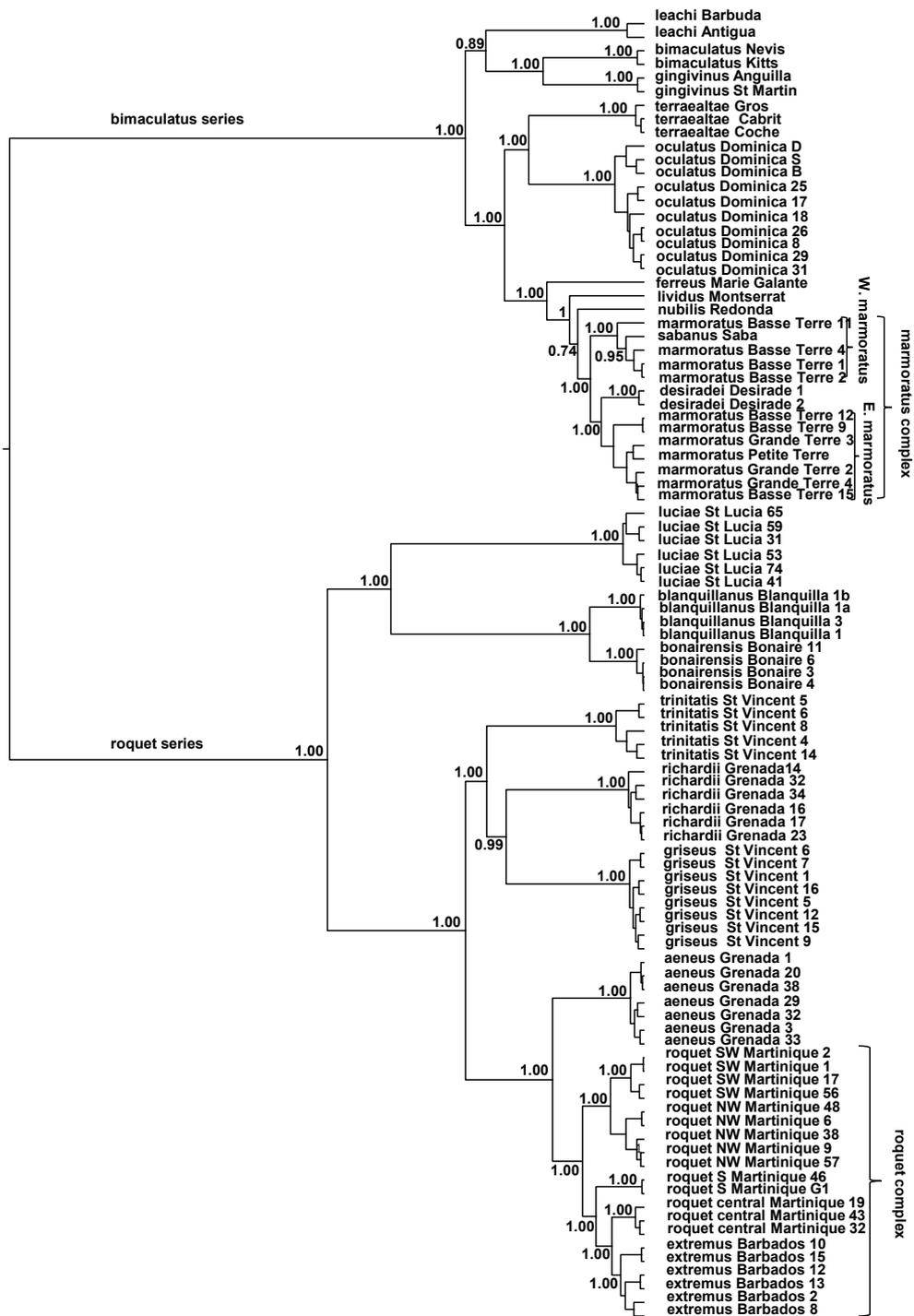


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2B

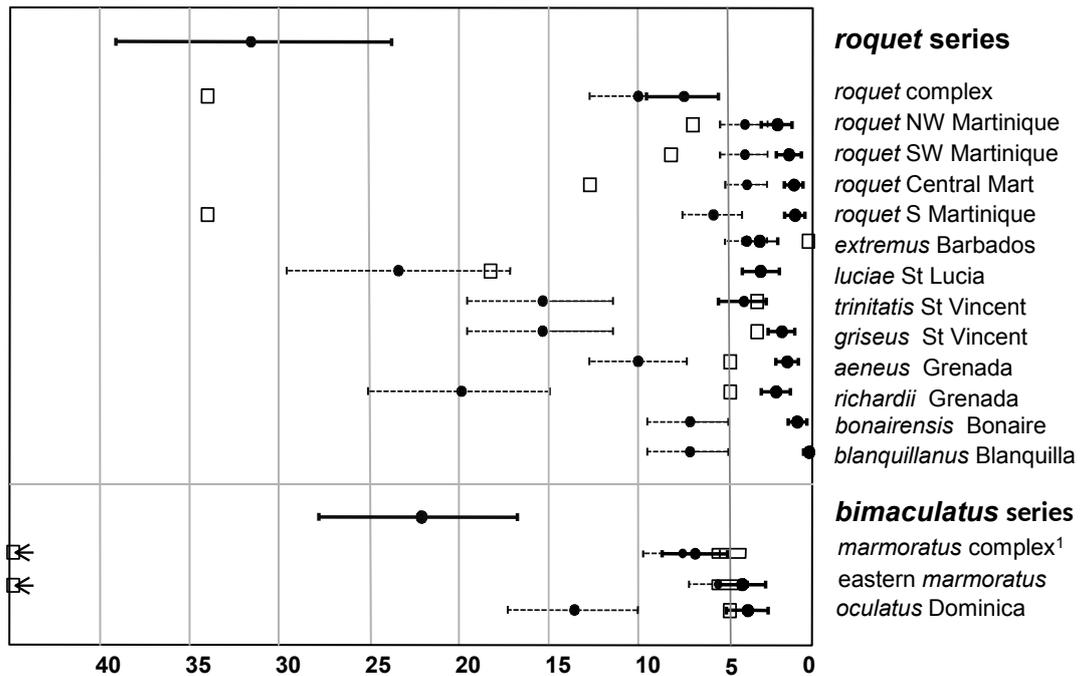


952 Figure 3. Analysis 1 Total evidence phylogeny of Lesser Antillean anoles based on  
 953 concatenated mitochondrial and nuclear genes. Number at nodes indicate posterior clade  
 954 probabilities at the level of nominal species, putative precursor “species”, and complexes, or  
 955 above. The species name, island and (where appropriate) locality number are indicated at  
 956 terminal nodes.



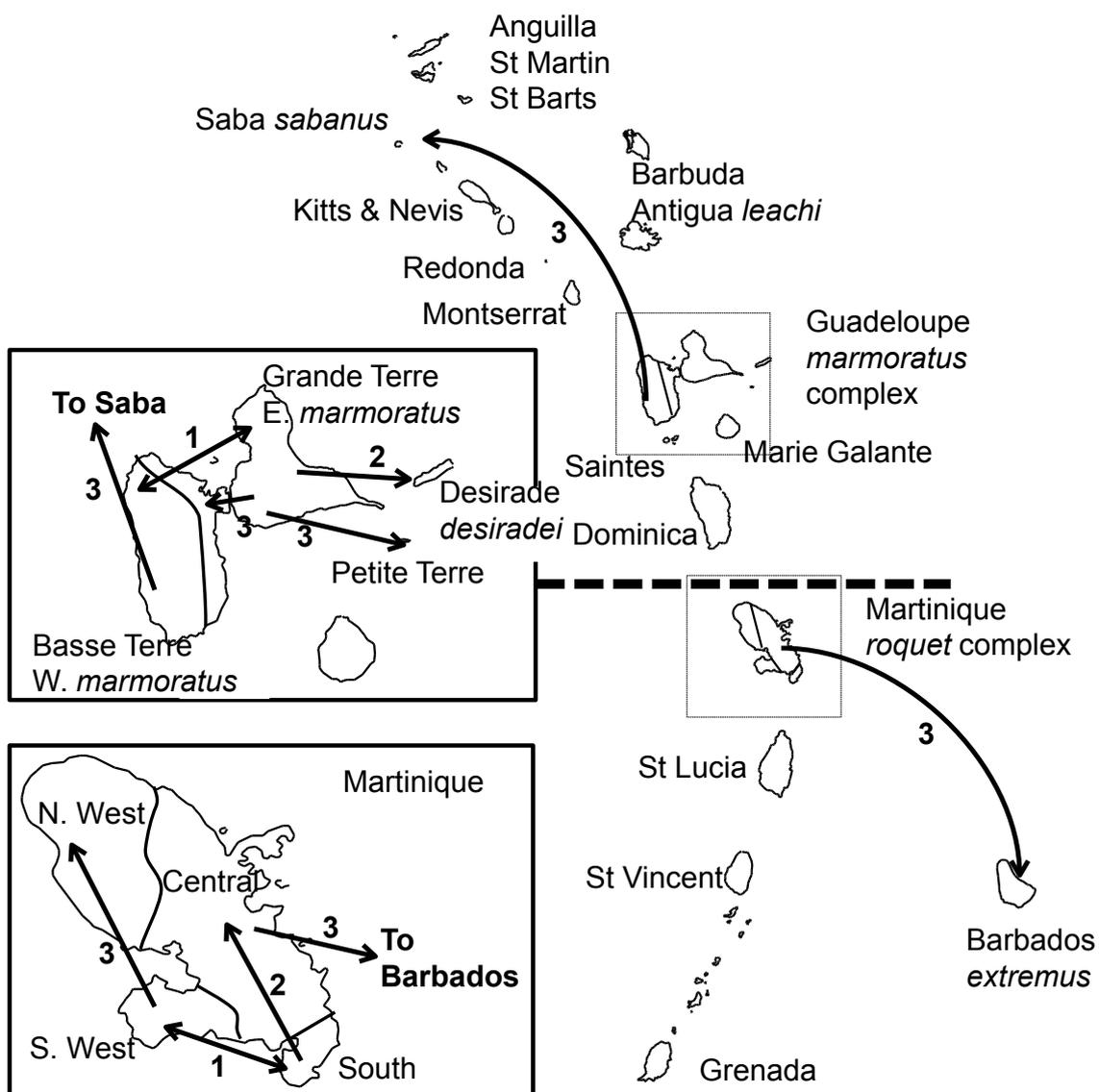
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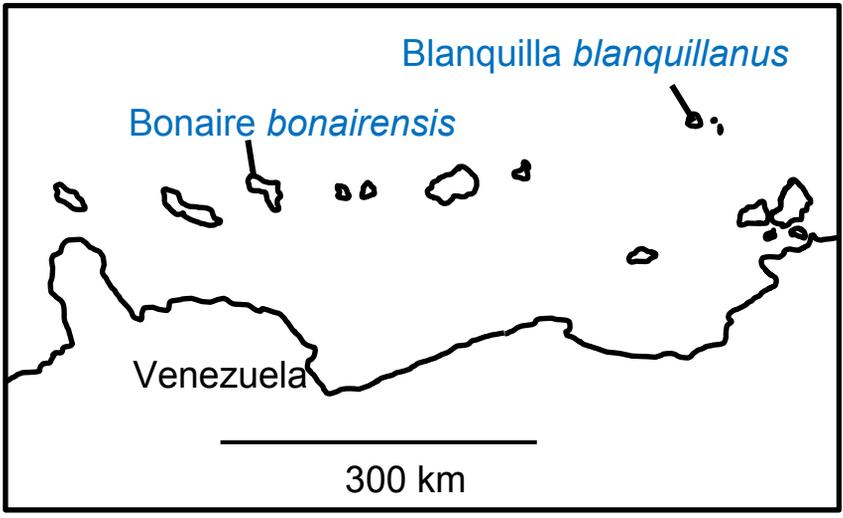
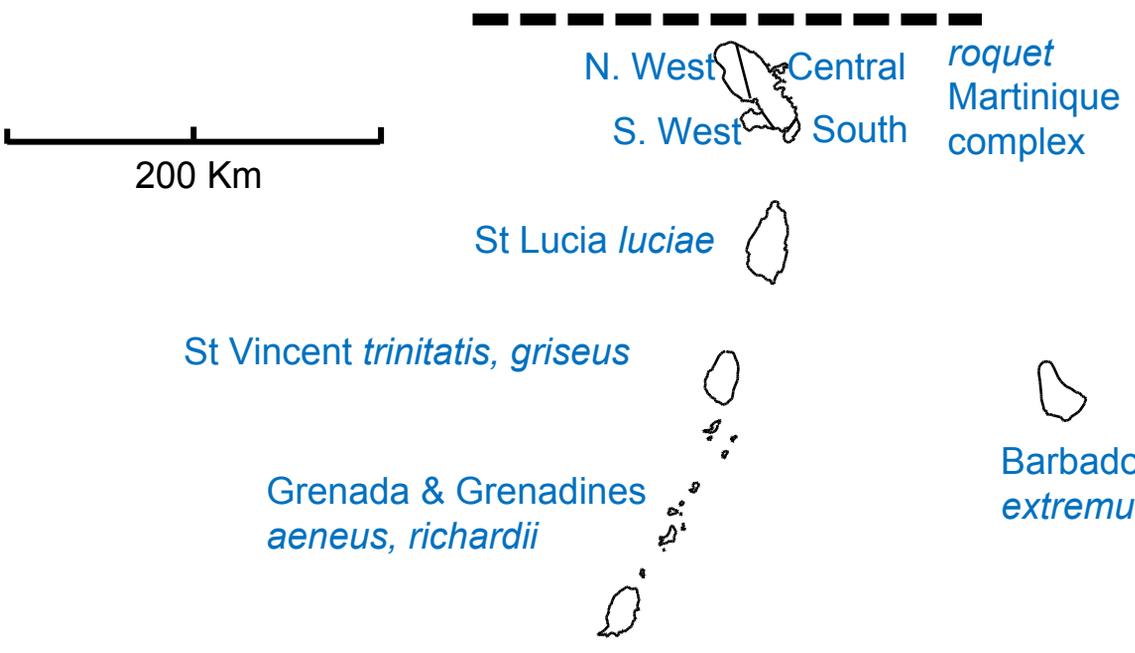
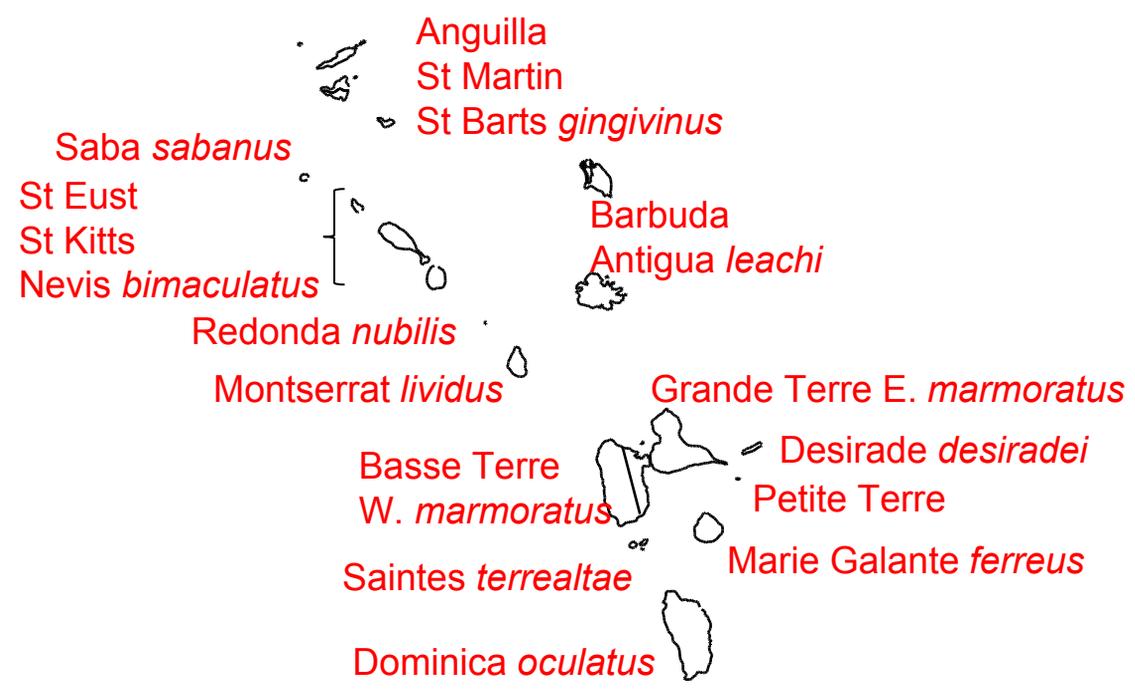
961 Figure 4. Age of series, species complexes and of substantially sampled species in relation to  
 962 island ages. The x axis represents time in millions of years before present. Series, species and  
 963 their islands are listed on the right. For each species and series, points and thick solid bars  
 964 show the median and 95% HPD of the within species or series TMRCA, respectively. Points  
 965 with thin dashed lines show the median and 95% HPD of the divergence time between  
 966 species and their nearest extant relative. Black squares show the ages of islands (with arrow  
 967 indicating the off-scale, possible, Mesozoic origin of La Desirade). <sup>1</sup> See Table 1 for  
 968 comments on the age of the *marmoratus* complex.  
 969



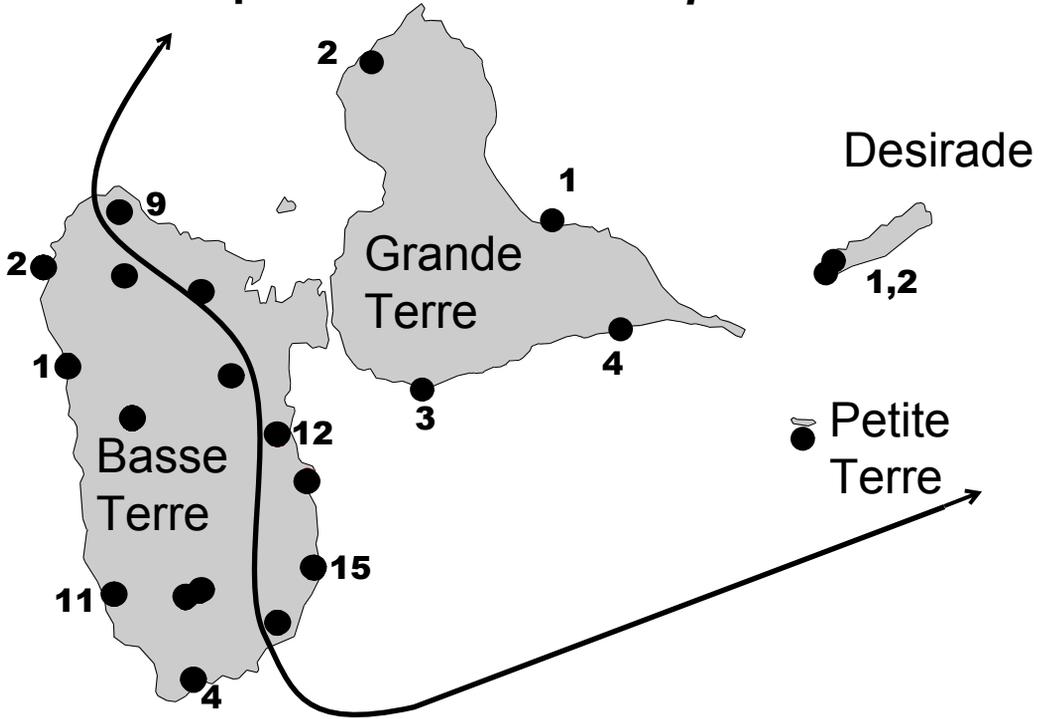
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972 Figure 5. Relatively recent colonization events suggested by paraphyly. There are two long-  
 973 distance events (colonization of Saba and Barbados) and a series of short distance  
 974 colonizations from large islands to adjacent smaller islands/islets. In the *marmoratus*  
 975 complex, 1), the divergence between the Basse Terre and Grande Terre allopatric lineages, is  
 976 2), followed by the colonization of La Desirade from Grande Terre, and more recently 3) the  
 977 colonization of Saba from the Basse Terre (western *marmoratus*) lineage, the colonization of  
 978 Petite Terre from the Grande Terre (eastern *marmoratus*) lineage, and the spread of the  
 979 eastern *marmoratus* lineage into eastern Basse Terre. In the *roquet* complex, 1) the  
 980 divergence of the South Martinique and SW Martinique lineages is followed by 2) the  
 981 colonization of central Martinique from south Martinique, and then 3) the colonization of  
 982 NW Martinique from SW Martinique, and colonization of Barbados from central Martinique.



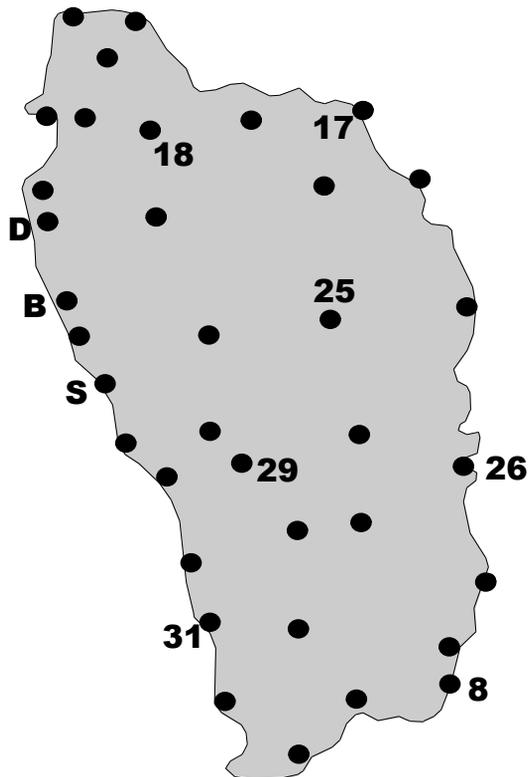


**Guadeloupe *marmoratus* complex**

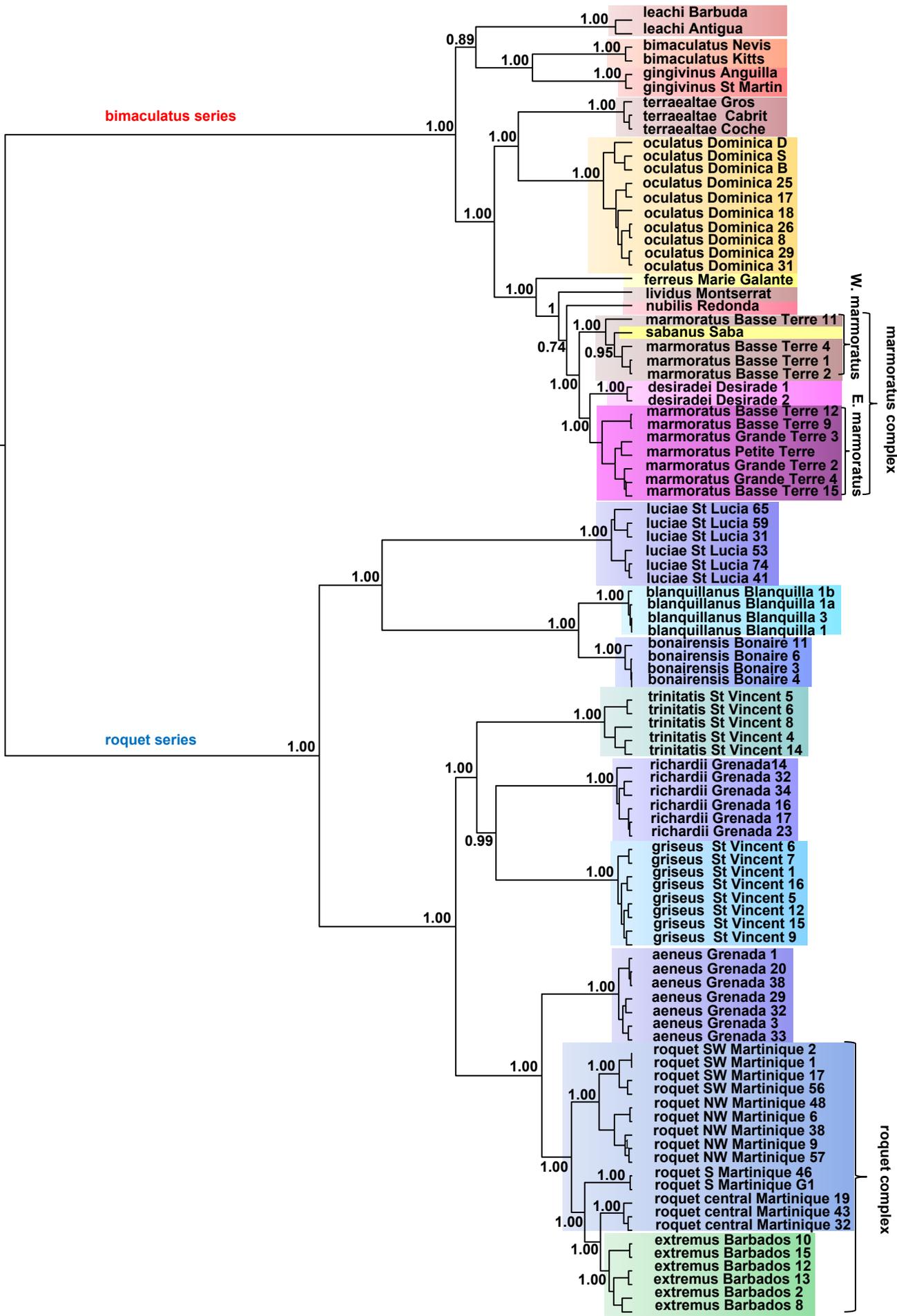


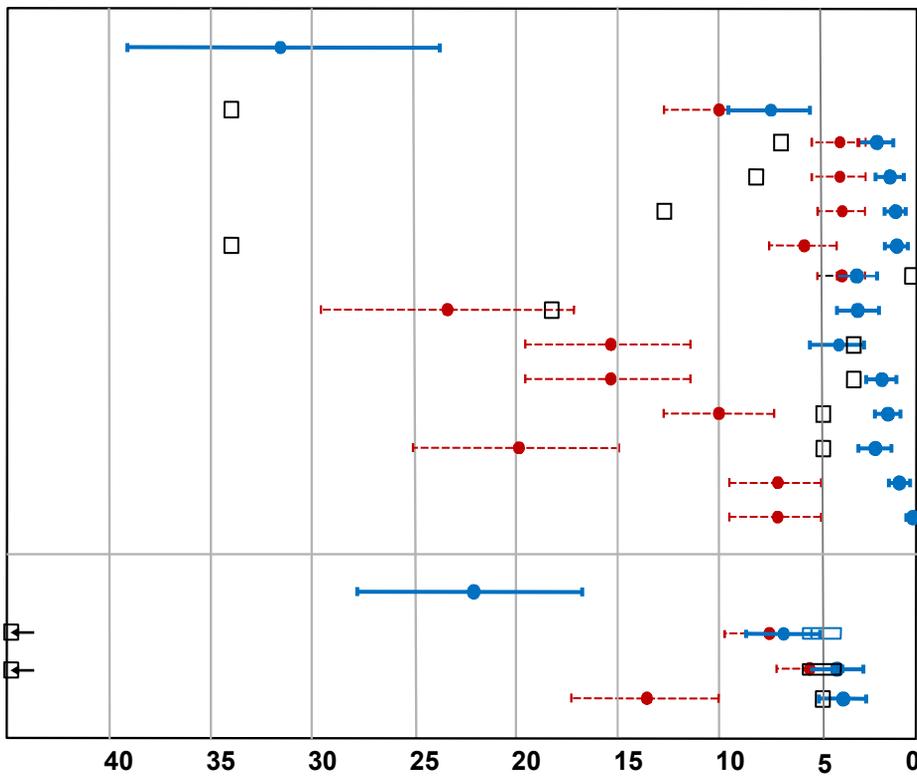
IC, Ilet a Cabrit  
 LC, La Coche  
 GI, Saintes *terraealtae*  
 Terre de Haut

**Dominica *oculatus***







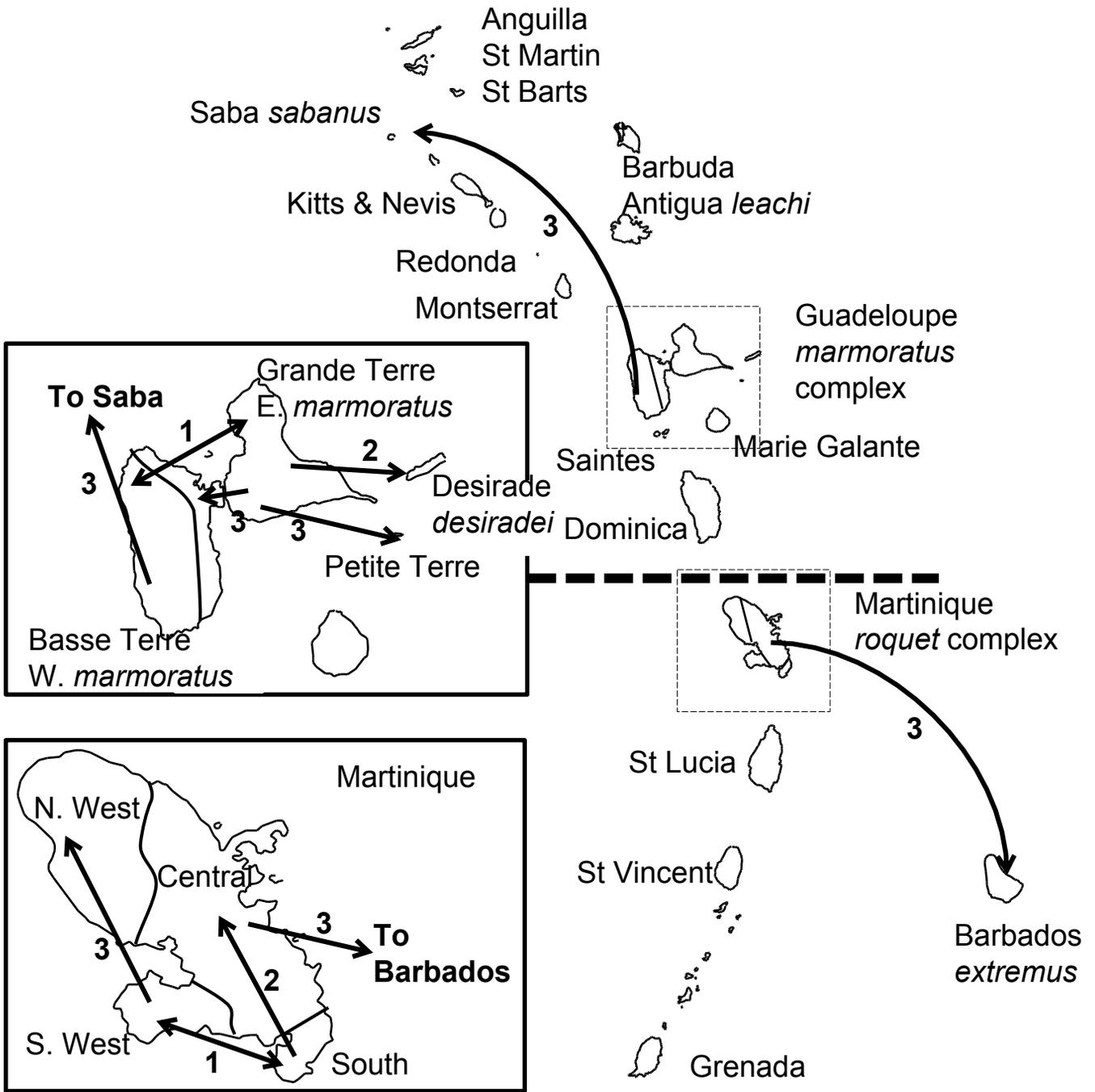


**roquet series**

- roquet* complex
- roquet* NW Martinique
- roquet* SW Martinique
- roquet* Central Mart
- roquet* S Martinique
- extremus* Barbados
- luciae* St Lucia
- trinitatis* St Vincent
- griseus* St Vincent
- aeneus* Grenada
- richardii* Grenada
- bonairensis* Bonaire
- blanquillanus* Blanquilla

**bimaculatus series**

- marmoratus* complex<sup>1</sup>
- eastern *marmoratus*
- oculatus* Dominica



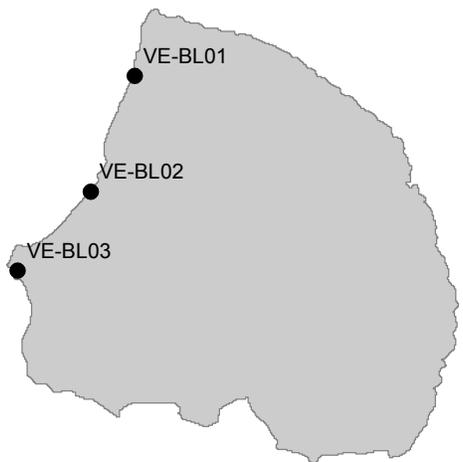
**Table 1 Estimate of ages of Lesser Antillean islands and the *Anolis* species occupying them.**

Estimate of island and species age from densely sampled island species. Species = nominal species or previously allopatric “species” from precursor islands. Island age = geological island age in million years from literature. Within = within series/species divergence with 95% HPD in brackets, \* = sampling inadequate for meaningful estimate. Among = among Series/species with 95% HPD in brackets. <sup>1</sup> These are allopatric “species” (from precursor island) in the *roquet* complex *sensu* Thorpe et al. (2015). <sup>2</sup> The range of the Central Martinique form also includes the Caravelle peninsula which is Oligocene (ca <34mybp). <sup>3</sup> Central and South Martinique include some low elevation areas which may have been under water until recently, and there is no strong phylogeographic structure. Hence these “Within” dates may be underestimates due to bottlenecks. <sup>4</sup> Martinique includes precursor islands from both the younger and older arcs. <sup>5</sup> Barbados is ancient rocks with some more recent limestone capping suggesting recent emergence, but the deep well-structured phylogeography suggests this species has been diverging in-situ for longer (Thorpe et al., 2005b). <sup>6</sup> In the south the younger arc is superimposed on the older arc so cited geological dates may reflect either young arc (St Vincent, Grenada) or older arc (St Lucia) volcanicity. <sup>7</sup> Bonaire and Blanquilla are old islands with younger limestone without sufficient data to confidently indicate a date of origin or emergence, although on the latter, low-elevation island populations may have been bottlenecked. <sup>8</sup> Marie Galante is mid Miocene overlain by more recent deposits (Martin-Kaye, 1969). <sup>9</sup> The range of the *marmoratus* complex includes both Basse Terre (younger arc), and Grande Terre, together with some allopatric populations on islands that can be very ancient (e.g., La Desirade). La Desirade may be Mesozoic, i.e., earlier than the radiation so this date is not used. Moreover, Grande Terre may be Lower to Mid Miocene (Martin-Kaye, 1969), but it thought to have emerged more recently (Maury et al., 1990). Dating the range of the nominal species is therefore complicated, and here we just consider the younger arc island, Basse Terre, with its main lineage distributed over the centre and west of the island at 4-6mybp (Maury et al., 1990) for the complex and its components. <sup>10</sup> One specimen among several, for both localities 2 and 7 in western Basse Terre (maBT02\_08 and maBT07\_39 respectively), join incongruently (with Analysis 1) with *A. nubilis* (Appendix D in supplementary materials), rather than others from the same site or the western *marmoratus* lineage. This would artificially increase both the age of the complex and the eastern *marmoratus* lineage and they are excluded. Their inclusion would increase the age of the complex slightly to 7.6 mybp.

Island/series	Species	Island age	Reference	Yule Within	Yule Among
<i>roquet</i> series				31.60 (23.8-39.1)	43.6 (34.8-52.6)
NW Martinique	NW Mart <sup>1</sup>	7.1	Briden et al 1979	2.38 (1.57-3.29)	4.19 (2.93-5.56)
SW Martinique	SW Mart <sup>1</sup>	8.3	Briden et al 1979	1.73 (1.07-2.45)	4.19 (2.93-5.56)
Central Martinique	Central Mart <sup>1</sup>	12.8-15.9 <sup>2</sup>	Briden et al 1979, Wadge 1994	1.46 (0.97-2.00) <sup>3</sup>	4.08 (2.96-5.29)
S Martinique	S Mart <sup>1</sup>	<34	Wadge 1994	1.40 (0.86-1.97) <sup>3</sup>	5.94 (4.35-7.65)

All Martinique	<i>roquet</i>	<34 <sup>4</sup>	Wadge 1994	7.56 (5.65-9.65)	10.1 (7.40- 12.81)
Barbados	<i>extremus</i>	<sup>5</sup>	Speed 1994, Thorpe et al 2005	3.35 (2.37-4.33)	4.08 (2.96-5.29)
St Lucia	<i>luciae</i>	18.3 <sup>6</sup>	Briden et al 1979	3.30 (2.27-4.33)	23.4 (17.2-29.6)
St Vincent	<i>trinitatis</i>	3.5 <sup>6</sup>	Maury et al 1990	4.23 (2.99-5.64)	15.4 (1.5-19.6)
St Vincent	<i>griseus</i>	3.5 <sup>6</sup>	Maury et al 1990	2.12 (1.40-2.90)	15.4 (1.5-19.6)
Grenada	<i>aeneus</i>	>5 <sup>6</sup>	Maury et al 1990, Martin- Kaye 1969	1.82 (1.20-2.47)	10.1 (7.4-12.81)
Grenada	<i>richardii</i>	>5 <sup>6</sup>	Maury et al 1990, Martin- Kaye 1969	2.44 (1.66-3.26)	19.9 (15.0-25.1)
Bonaire	<i>bonairensis</i>	- <sup>7</sup>		1.21 (0.74-1.78)	7.22 (5.10-9.59)
Blanquilla	<i>blanquillanus</i>	- <sup>7</sup>		0.60 (0.33-0.91)	7.22 (5.10-9.59)
<i>bimaculatus</i> series				22.1 (16.8-27.8)	43.6 (34.8-52.6)
St Martin Bank	<i>gingivinus</i>	37	Briden et al 1979, Maury et al 1990	*	14.5 (9.91-20.0)
Saba	<i>sabanus</i>	0.4	Roobol and Smith 2004	*	2.12 (1.42-2.92)
Kitts Nevis bank	<i>bimaculatus</i>	3.4	Maury et al 1990	*	14.5 (9.91-20.0)
Antigua Barbuda Bank	<i>leachi</i>	40	Briden et al 1979	*	19.6 (14.9-24.6)
Redonda	<i>nubilis</i>	<1.5	Maury et al 1990	*	5.96 (4.21-7.97)
Montserrat	<i>lividus</i>	4.4	Briden et al 1979, Maury et al 1990	*	9.37 (6.95-12.0)
Illes des Saintes	<i>terraealtae</i>	4.7	Maury et al 1990	*	13.6 (10.1- 17.3)
Marie Galante	<i>ferreus</i>	<sup>8</sup>		*	12.0 (8.87-15.2)
Guadeloupe (excl I d Saintes, Marie	<i>marmoratus</i> <i>complex</i> <sup>9,10</sup>	(4-6)	Maury et al 1990	*6.91 (5.12- 8.74)	7.61 (5.55-9.81)

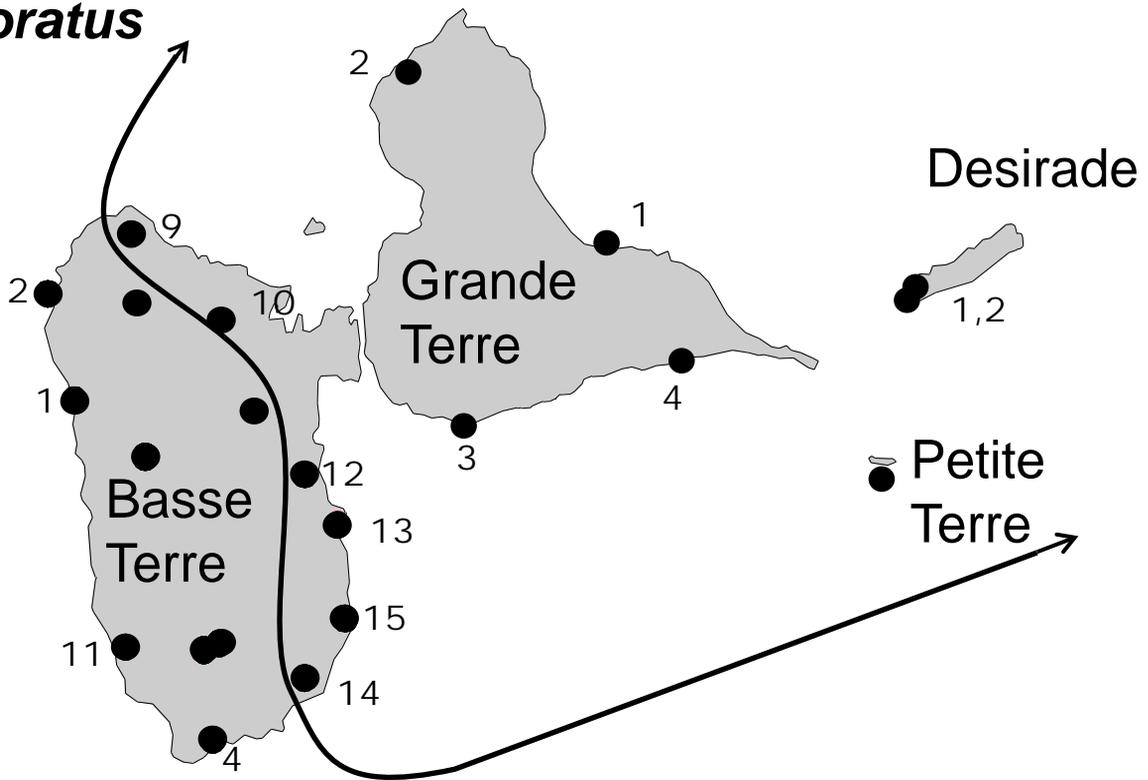
Galante)					
Grande Terre + East BT + Petite Terre+Desirade	Eastern <i>marmoratus</i> + <i>desiradei</i> <sup>9</sup>	(4-6)	Maury et al 1990	5.74 (4.12- 7.37)	6.91 (5.12-8.74)
Desirade	<i>desiradei</i> <sup>9</sup>	mesozoic	Maury et al 1990	*	5.74 (4.12-7.37)
Grande Terre +eastern BT+ Petite Terre)	Eastern <i>marmoratus</i> <sup>9</sup>	(4-6)	Maury et al 1990	4.40 (3.10- 5.77)	5.74 (4.12-7.37)
Basse Terre (+Saba)	Western <i>marmoratus</i> <sup>10</sup>	4-6	Maury et al 1990	3.62 (2.48- 4.82)	6.91 (5.12-8.74)
Dominica	<i>oculatus</i>	<5	Maury et al 1990, Martin- Kaye 1969	3.98 (2.85- 5.18)	13.6 (10.1-17.3)



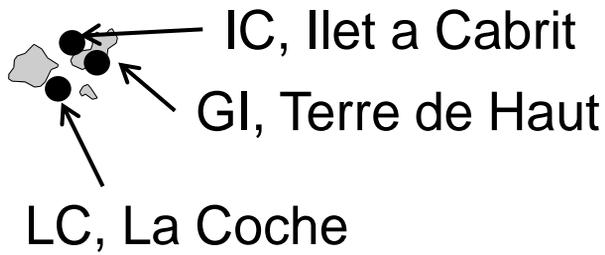
western  
*marmoratus*

eastern *marmoratus*

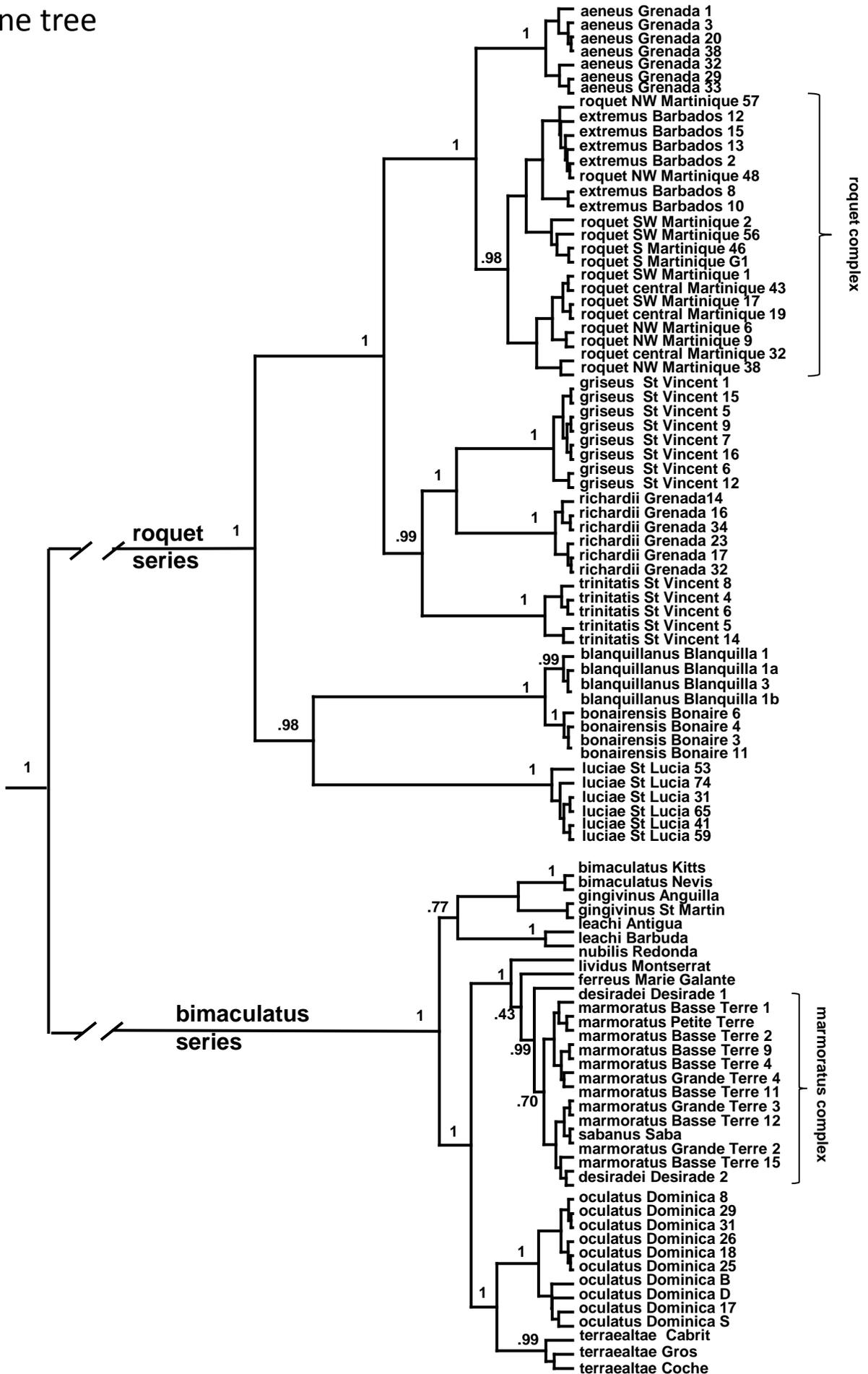
Guadeloupe  
*marmoratus* complex



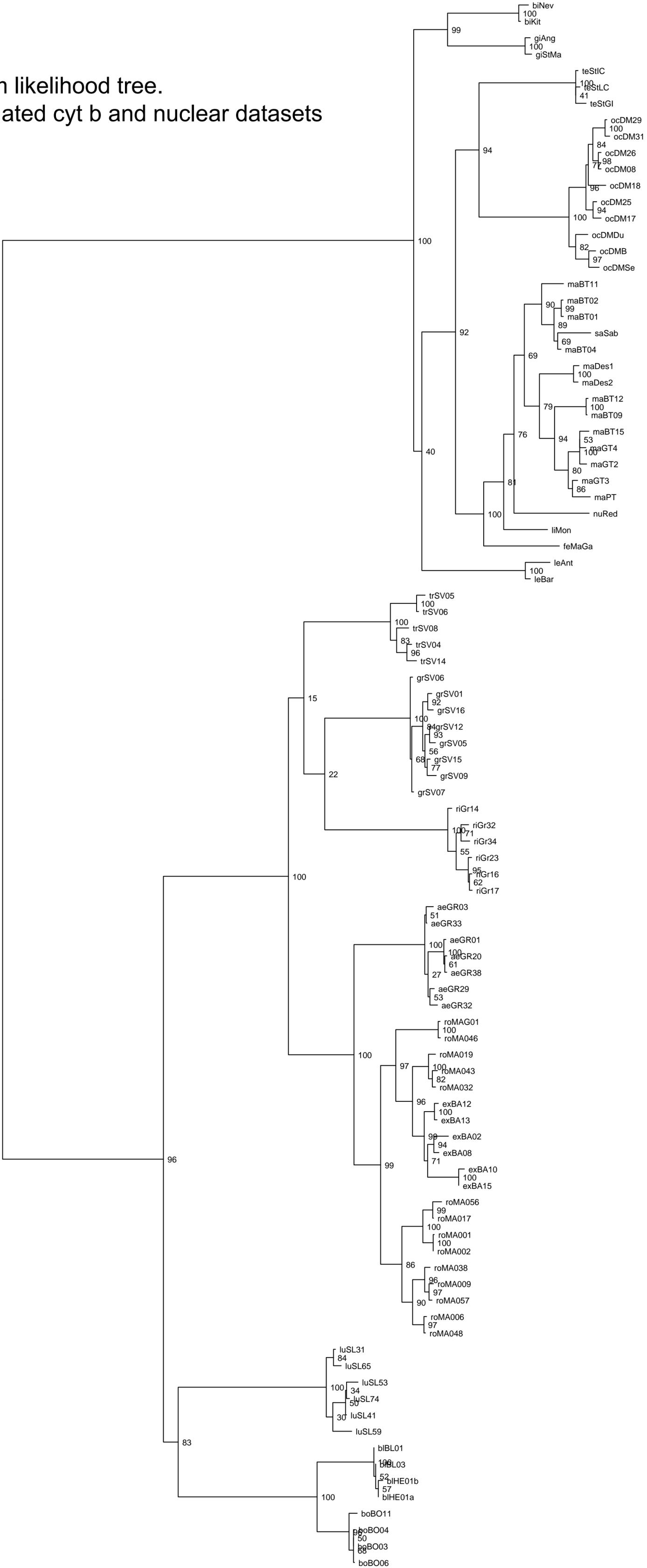
Les Saintes  
*terraealtae*



# Concatenated nuclear gene tree



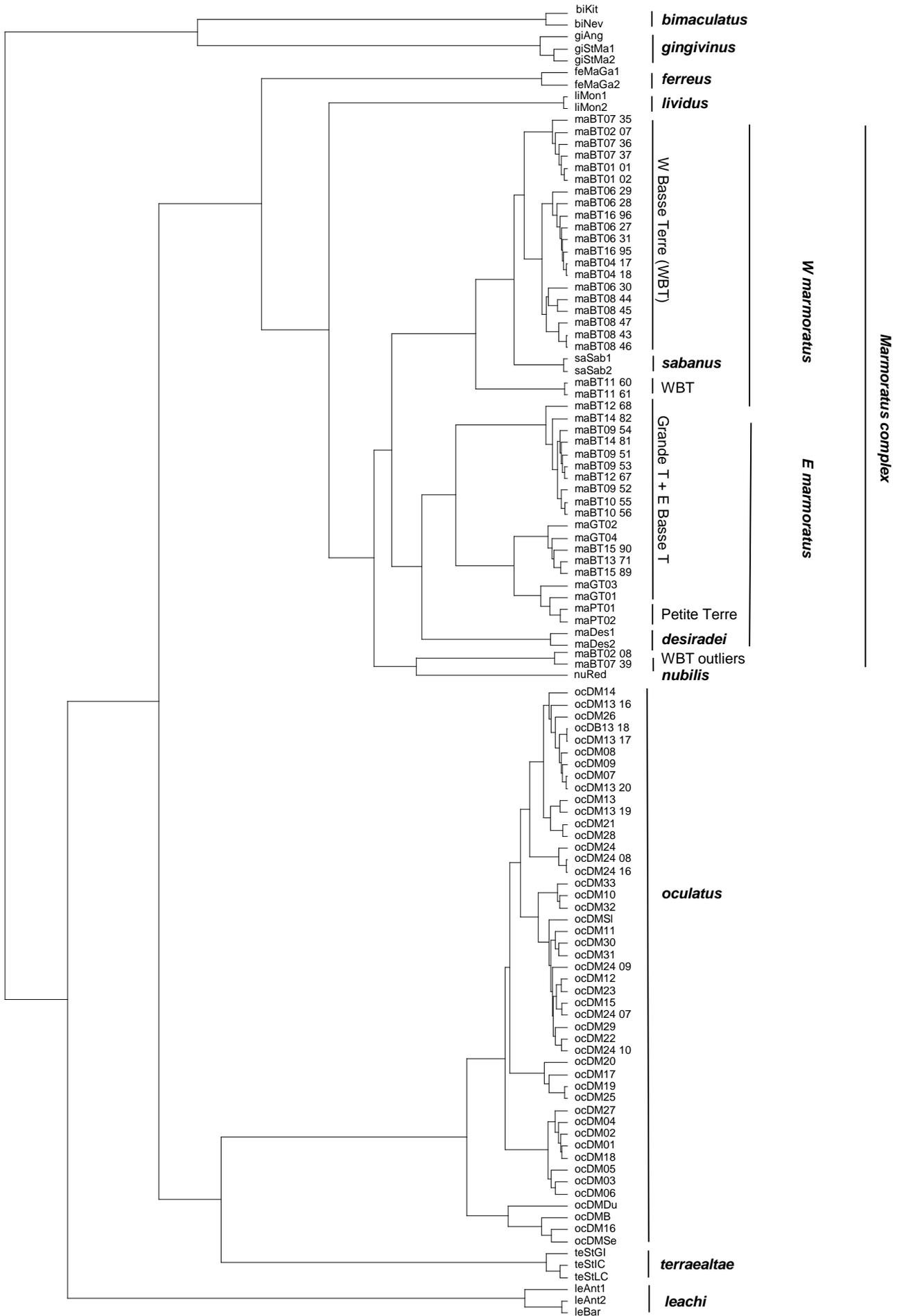
Maximum likelihood tree.  
concatenated cyt b and nuclear datasets



Poly

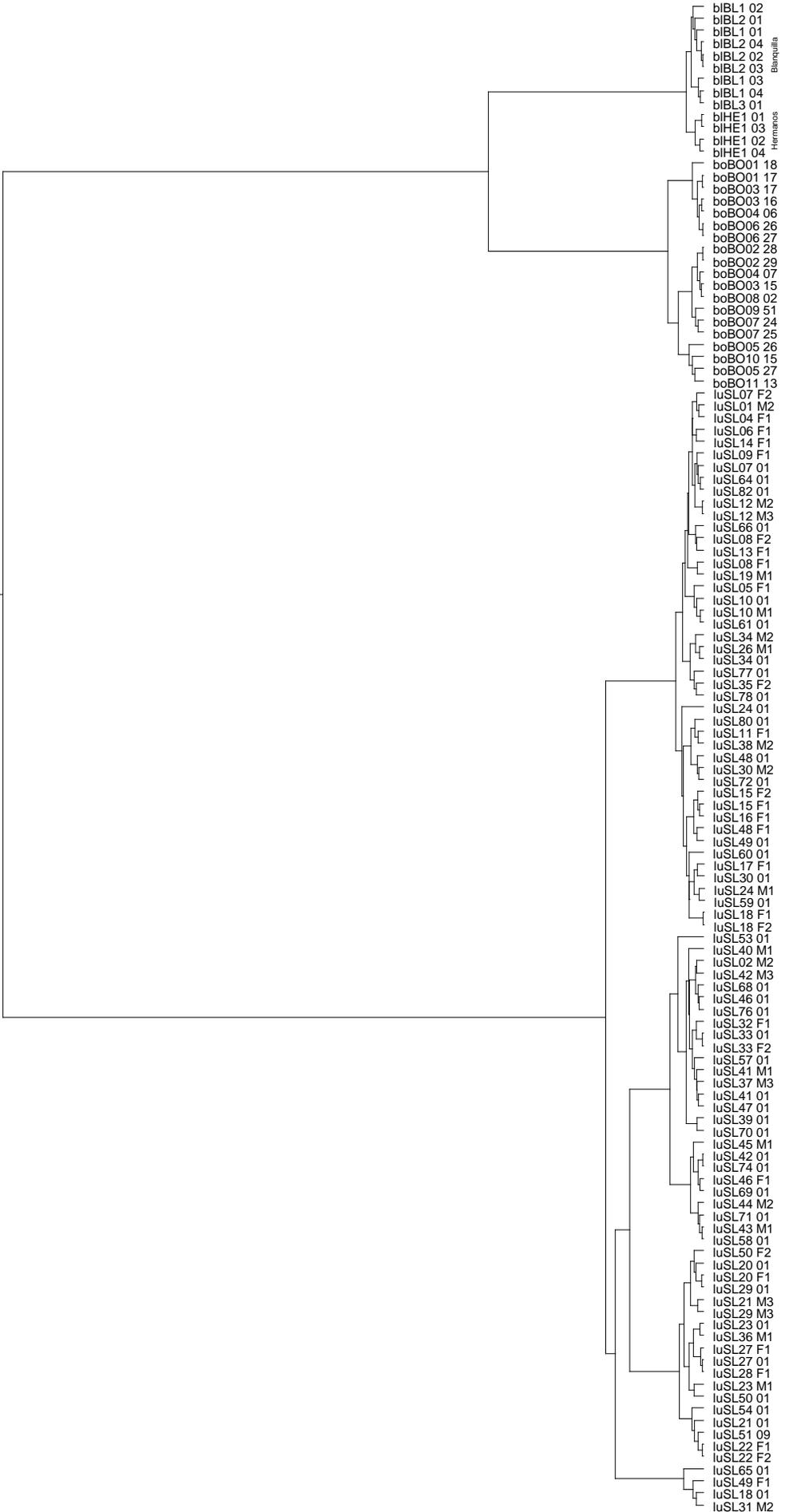


# Section B1



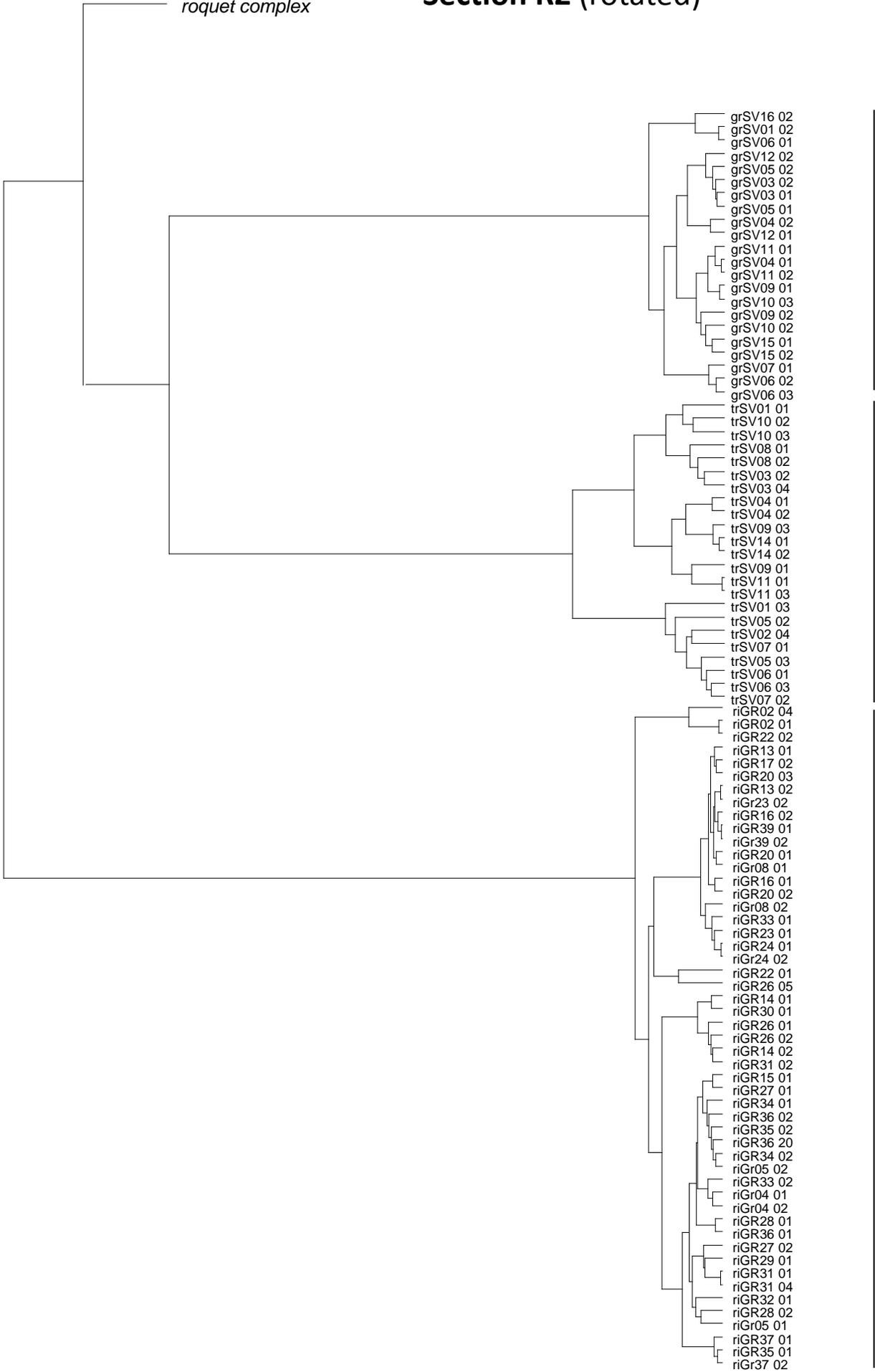


# Section R1



# Section R2 (rotated)

*roquet complex*

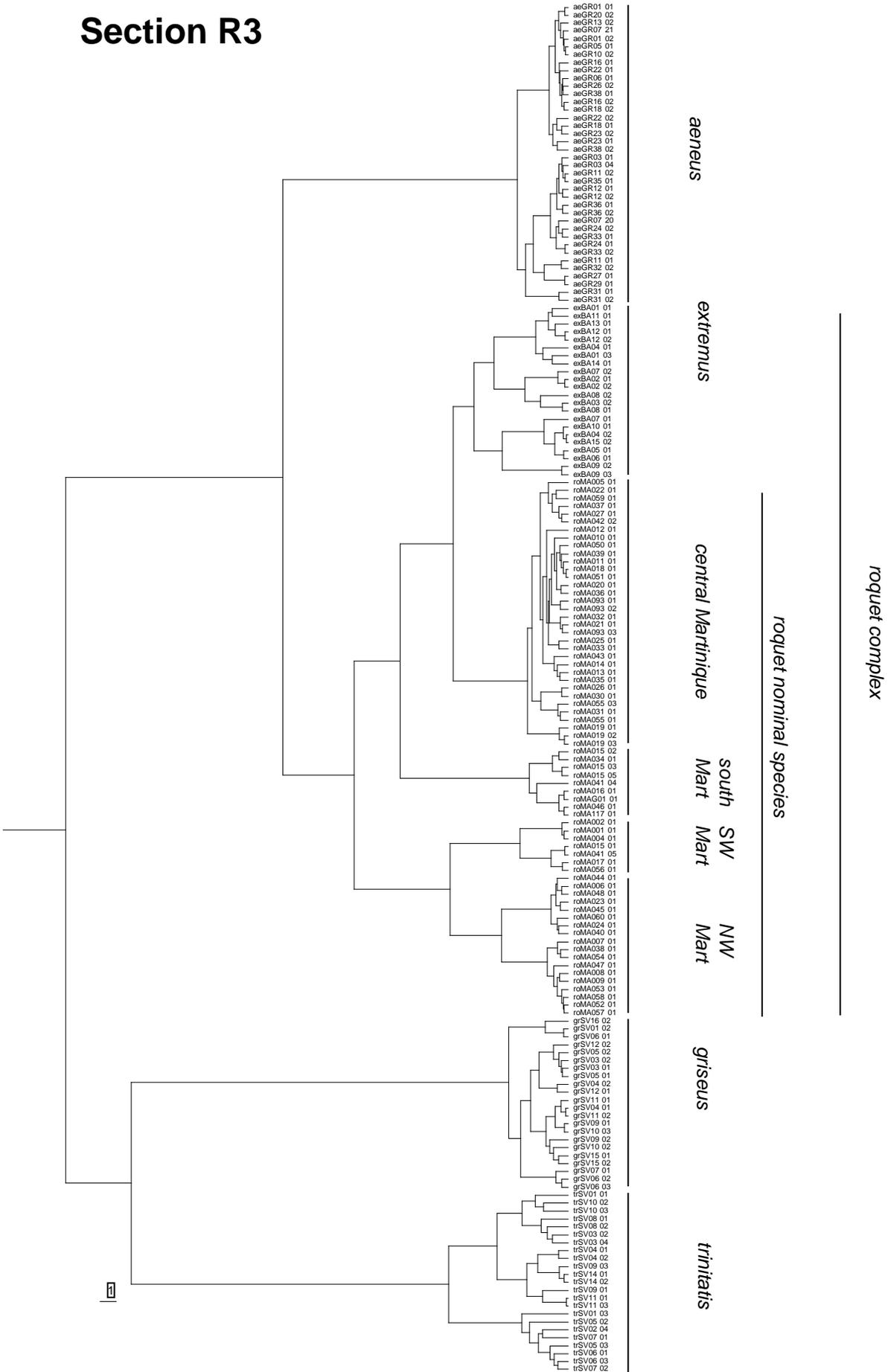


*griseus*

*trinitatis*

*richardii*

# Section R3



## Online size analysis

As anoles have asymptotic growth the five largest specimens (SVL) were selected from the sample of ten per site and site means, and 95% confidence limits (CIs) given. All localities are low elevation. The *aeneus* samples are from Morne Rouge and Fort Jeudy, Grenada (Thorpe et al 2015), the *roquet* complex samples are from south Martinique (site 4 transect VIII), and central Martinique (site 8 transect I) from Thorpe et al (2010), and from northwest Martinique NW Martinique (site 1 combined transect) from Surget-Groba et al (2012). Although *A. aeneus* and *A. roquet* may be put in different size categories (small and intermediate, respectively), they are approximately the same size with overlapping 95% CIs.

species	<i>aeneus</i>	<i>aeneus</i>	south Mart <i>roquet</i>	central Mart <i>roquet</i>	NW Mart <i>roquet</i>
site	Morne Rouge	Fort Jeudy	site 4 Trans VIII	site 8 Trans I	site 1 Comb Trans
mean SVL	68.4	71.5	69.8	71.6	70.7
95%CI	(66.5-70.3)	(70.1-72.8)	(68.7-70.9)	(69.5-73.7)	(70.0-71.4)

## ONLINE FILES

**Table 1 Estimate of island and species age.**

Island/series	Species	Island age	Reference	Yule Within	Yule Among
<i>roquet</i> series				31.60 (23.8-39.1)	43.6 (34.8-52.6)
NW Martinique	NW Mart <sup>1</sup>	7.1	Briden et al 1979	2.38 (1.57-3.29)	4.19 (2.93-5.56)
SW Martinique	SW Mart <sup>1</sup>	8.3	Briden et al 1979	1.73 (1.07-2.45)	4.19 (2.93-5.56)
Central Martinique	Central Mart <sup>1</sup>	12.8-15.9 <sup>2</sup>	Briden et al 1979, Wadge 1994	1.46 (0.97-2.00) <sup>3</sup>	4.08 (2.96-5.29)
S Martinique	S Mart <sup>1</sup>	<34	Wadge 1994	1.40 (0.86-1.97) <sup>3</sup>	5.94 (4.35-7.65)
All Martinique	<i>roquet</i>	<34 <sup>4</sup>	Wadge 1994	7.56 (5.65-9.65)	10.1 (7.40-12.81)
Barbados	<i>extremus</i>	- <sup>5</sup>	Speed 1994, Thorpe et al 2005	3.35 (2.37-4.33)	4.08 (2.96-5.29)
St Lucia	<i>luciae</i>	18.3 <sup>6</sup>	Briden et al 1979	3.30 (2.27-4.33)	23.4 (17.2-29.6)
St Vincent	<i>trinitatis</i>	3.5 <sup>6</sup>	Maury et al 1990	4.23 (2.99-5.64)	15.4 (1.5-19.6)
St Vincent	<i>griseus</i>	3.5 <sup>6</sup>	Maury et al 1990	2.12 (1.40-2.90)	15.4 (1.5-19.6)
Grenada	<i>aeneus</i>	>5 <sup>6</sup>	Maury et al 1990, Martin-Kaye 1969	1.82 (1.20-2.47)	10.1 (7.4-12.81)
Grenada	<i>richardii</i>	>5 <sup>6</sup>	Maury et al 1990, Martin-Kaye 1969	2.44 (1.66-3.26)	19.9 (15.0-25.1)
Bonaire	<i>bonairensis</i>	- <sup>7</sup>		1.21 (0.74-1.78)	7.22 (5.10-9.59)
Blanquilla	<i>blanquillanus</i>	- <sup>7</sup>		0.60 (0.33-0.91)	7.22 (5.10-9.59)
<i>bimaculatus</i> series				22.1 (16.8-27.8)	43.6 (34.8-52.6)
St Martin Bank	<i>gingivinus</i>	37	Briden et al 1979, Maury et al 1990	*	14.5 (9.91-20.0)
Saba	<i>sabanus</i>	0.4	Roobol & Smith 2004	*	2.12 (1.42-2.92)
Kitts Plus Nevis bank	<i>bimaculatus</i>	3.4	Maury et al 1990	*	14.5 (9.91-20.0)
Antigua Barbuda Bank	<i>Leachi</i>	40	Briden et al 1979	*	19.6 (14.9-24.6)
Redonda	<i>nubilis</i>	<1.5	Maury et al 1990	*	5.96 (4.21-7.97)
Montserrat	<i>lividus</i>	4.4	Briden et al 1979, Maury et al 1990	*	9.37 (6.95-12.0)
I D Saintes	<i>terraealtae</i>	4.7	Maury et al 1990	*	13.6 ( 10.1-17.3)
Marie Galante	<i>ferreus</i>	<sup>8</sup>		*	12.0 (8.87-15.2)
Guadeloupe (minus Saintes & Marie Galante)	<i>marmoratus</i> <sup>9</sup>			6.91 (5.12-8.74)	7.61 (5.55-9.81)
Grande Terre + East BT + Desirade	<i>marmoratus</i> <sup>9</sup>			5.74 (4.12-7.37)	6.91 (5.12-8.74)
Desirade	<i>marmoratus</i> <sup>9</sup>	mesozoic	Maury et al 1990	*	5.74 (4.12-7.37)
Grande Terre +eastern BT)	<i>marmoratus</i> <sup>9</sup>			4.40 (3.10-5.77)	5.74 (4.12-7.37)
Basse Terre	W Basse Terre <sup>9</sup>	4-6	Maury et al 1990	3.62 (2.48-4.82)	6.91 (5.12-8.74)

Dominica	<i>oculatus</i>	<5	Maury et al 1990, Martin-Kaye 1969	3.98 (2.85-5.18)	13.6 (10.1-17.3)
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## Legend

Estimate of island and species age from densely sampled island species (see online Table 1 for all island species and details). Species = nominal species or allospecies. Island age = geological island age in million years from literature (see online table 1). Within = within Series/species divergence with 95% HPD in brackets, \* = sampling inadequate for meaningful estimate. Among = among Series/species with 95% HPD in brackets. <sup>1</sup> These are allospecies of the nominal *roquet* complex *sensu* Thorpe et al (2015). <sup>2</sup> The range of the Central Martinique form also includes the Caravelle peninsula which is Oligocene (ca <34mybp). <sup>3</sup> Central and South Martinique include some low elevation areas which may have been under water until recently, and there is no strong phylogeographic structure. Hence these “Within” dates may be underestimates due to bottlenecks. <sup>4</sup> Martinique includes precursor islands from both the younger and older arcs. <sup>5</sup> Barbados is ancient rocks with some more recent limestone capping suggesting recent emergence, but the deep well-structured phylogeography suggests this species has been diverging in-situ for longer (Thorpe et al 2005). <sup>6</sup> In the south the younger arc is superimposed on the older arc so cited geological dates may reflect either young arc (St Vincent, Grenada) or older arc (St Lucia) volcanicity. <sup>7</sup> Bonaire and Blanquilla are old islands with younger limestone without sufficient data to confidently indicate a date of origin or emergence, although on the latter, low-elevation island populations may have been bottlenecked. <sup>8</sup> Marie Galante is mid Miocene overlain by more recent deposits (Martin-Kaye 1969). <sup>9</sup> The range of the nominal species *marmoratus* includes both Basse Terre (younger arc), and Grande Terre, together with some allopatric populations on islands that can be very ancient (e.g., La Desirade). Moreover, Grande Terre may be Lower to Mid Miocene (Martin-Kaye 1969), but it thought to have emerged more recently (Maury et al 1990). Dating the range of the nominal species is therefore meaningless, and here we just consider the younger arc island, Basse Terre, with its main lineage distributed over the centre and west of the island. One specimen among several, for both localities 2 and 7 in western Basse Terre (maBT02\_08 and maBT07\_39 respectively), are outliers (**Tree Fig N**), outside of the western Basse Terre clade. In other comparable phylogeographic analyses (Thorpe et al 2015) they group, compatible with their geographic position, with the other individuals from those localities in the western Basse Terre clade. Consequently, they are excluded from the dating process.

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