1 **A story of nasal horns: A new species of *Iguana* Laurenti, 1768 (Squamata,**
2 **Iguanidae) in Saint Lucia, St Vincent & the Grenadines, and Grenada (Southern**
3 **Lesser Antilles) and its implications for the taxonomy of the genus *Iguana***

4

5 MICHEL BREUIL¹, BARBARA VUILLAUME², DAVID SCHIKORSKI², ULRIKE
6 KRAUSS³, MATTHEW N. MORTON⁴, PIUS HAYNES⁵, JENNIFER C. DALTRY⁶,
7 ELISABETH CORRY⁴, GLENROY GAYMES⁷, JOANNE GAYMES⁷, NICOLAS BECH⁸,
8 MISEL JELIC⁹ & FRÉDÉRIC GRANDJEAN⁸

9

10 ¹*Muséum national d'Histoire naturelle, Laboratoire des Reptiles et Amphibiens, Bâtiment 30,*
11 *57, rue Cuvier, CP n° 30, 75231 Paris cedex 05, France.*

12 ²*Laboratoire Labofarm-Genindexe, 4 rue Théodore Botrel, 22600 Loudéac, France.*

13 ³*Maison du Soleil, Dauphin Road, La Borne, P O Box GM 1109, Saint Lucia, West Indies.*

14 ⁴*Durrell Wildlife Conservation Trust, Les Augres Manor, Trinity, Jersey JE3 5BP, Great*
15 *Britain.*

16 ⁵*Department of Forestry, Ministry of Agriculture, Fisheries, Physical Planning, Natural*
17 *Resources and Co-operatives, Union, Saint Lucia, West Indies.*

18 ⁶*Fauna & Flora International, David Attenborough Building Pembroke Street, Cambridge*
19 *CB2 3QZ, UK.*

20 ⁷*Forestry Department, Ministry of Agriculture, Industry, Forestry, Fisheries and Rural*
21 *Transformation, Richmond Hill, Kingstown, St Vincent & the Grenadines.*

22 ⁸*Laboratoire Écologie et Biologie des Interactions, équipe EES, UMR CNRS 6556, Université*
23 *de Poitiers, 5 rue Albert Turpin, 86073 Poitiers Cedex 9, France.*

24 ⁹*Division of Zoology, Faculty of Sciences, University of Zagreb, Rooseveltov trg 6, 10 000*
25 *Zagreb, Croatia.*

26 **Corresponding author:** Email: breuil.michel@gmail.com

27

28 **Abstract**

29 The Lesser Antilles, in the Eastern Caribbean, were long considered to have only two species
 30 in the genus *Iguana* Laurenti 1768: the Lesser Antillean iguana *Iguana delicatissima*, which is
 31 endemic to parts of the Lesser Antilles, and the common green iguana *Iguana iguana*, which
 32 also occurs throughout Central and South America. However, herpetologists and reptile
 33 collectors have pointed out strong physical differences between some of the island populations
 34 of *Iguana iguana* and those from the continent. Drawing on both morphological and genetic
 35 data, this paper describes a third species *Iguana insularis* sp. nov. from the southern Lesser
 36 Antilles, specifically the countries of Saint Lucia, St Vincent & the Grenadines, and Grenada.
 37 The new species is described based on the following unique combination of characters:
 38 Presence of high median and medium to small lateral horns on the snout; Small subtympenic
 39 plate not exceeding 20% of the eardrum size; Two or three scales of decreasing size anterior to
 40 the subtympenic plate; Fewer than ten small to medium triangular gular spikes; Medium sized
 41 dewlap; Low number of small to medium dispersed nuchal tubercles; Dark brown iris, with the
 42 white of the eye visible; Oval, prominent nostril; Short and relatively flat head; High dorsal
 43 spines; No swelling of the jowls in reproductively active males; Colour of head, body and tail
 44 changing from green to pale grey or creamy white in old adults; Vertical black stripes on body
 45 and tail, fading with age in some populations. This paper furthermore distinguishes two
 46 subspecies: *Iguana insularis insularis* from the Grenada Bank (comprising Grenada and the
 47 Grenadine islands), and *Iguana insularis sanctaluciae* from Saint Lucia. The form on the
 48 island of Saint Vincent has not been identified. Both subspecies are globally threatened by
 49 unsustainable hunting (including the pet trade) and by invasive alien species, including
 50 hybridization from invasive iguanas from South and Central America (*I. iguana* and *I.*
 51 *rhinolopha*, considered here as full species) that have become established in all three countries.
 52 The authors call for stronger measures to conserve the remaining purebred *Iguana insularis* sp.

nov. throughout its range and for further research to identify other cryptic species and subspecies of *Iguana* in the Lesser Antilles.

Key words: Caribbean, endemism, hybridization, *Iguana*, introgression, Lesser Antilles, microsatellites, mtDNA, speciation.

Introduction

The islands of the Lesser Antilles curve around the Eastern border of the Caribbean Sea between the Greater Antilles and South America and are noted for their rich diversity of endemic and globally threatened reptiles (Hedges 2018). Iguanas are among the most iconic animals of this archipelago, but opinions on their nomenclature and distribution have changed many times over the past few centuries.

Linnaeus (1758) described the common green iguana as *Lacerta iguana*, whereas Laurenti (1768) described the Lesser Antillean iguana as *Iguana delicatissima* and the common species as *I. tuberculata*. Both authors based their descriptions on drawings and specimens (Breuil 2002, 2013, 2016; Pasachnik *et al.* 2006). Later, Wiegmann (1834) described a third species with pronounced horns on its snout, *I. rhinolopha*, from Mexico. Duméril & Bibron (1837) subsequently recognised three *Iguana* species, using the names *I. tuberculata* for the common green iguana, *I. nudicollis* for the Lesser Antillean iguana and *I. rhinolopha* for the horned Mexican iguana, but found only two characters to separate *I. tuberculata* from *I. rhinolopha*.

The first mention of an iguana on the island of Saint Lucia was by Levacher (1834), but no information was given to determine the species. Breen (1844) commented that the iguanas were “an excellent sport for the native *chasseurs* (hunters)”. Bonnacour(t), a traveller in the mid-19th Century, caught two specimens in Saint Lucia, which are now housed in the

80 Muséum National d'Histoire Naturelle (MNHN) in Paris, France (Breuil 2013, 2016). Duméril
81 & Duméril (1851) recognised some morphological similarities between the horned specimens
82 from Saint Lucia and the horned iguanas Duméril & Bibron (1837) had described in Mexico.
83 This was corroborated by Boulenger (1885), who considered that a stuffed specimen from
84 Saint Lucia belonged to the “variety” *rhinolopha*, together with specimens from Central
85 America. Confusingly, however, Provancher (1890) reported the presence of *I. delicatissima*
86 on Saint Lucia on the basis of a stuffed specimen observed in a house (Fig. 1), but his
87 description and drawing of the specimen were too imprecise to confirm the species’ identity.
88 Dunn (1934) remarked that “The reports of *i. rhinolopha* from St Kitts and from Sta. Lucia is
89 very strange... Possibly the horned mutation has appeared independently in that island”.
90 Referring to *rhinolopha*, Barbour (1935) considered that: “The Antillean specimens are
91 probably based on specimens incorrectly labelled as to locality” and added “If there really ever
92 were iguanas on these islands, the mongoose has exterminated them”. (Small Asian
93 mongooses, *Urva javanica*, were widely introduced to many of the Caribbean islands towards
94 the end of the 19th Century in an attempt to control rats and, possibly in Saint Lucia’s case, the
95 venomous snake *Bothrops caribbaeus*: Des Vœux 1903, Nellis & Everard 1983).

96

97 Farther south, Garmann (1887) remarked “the Grenada specimens are intermediate
98 between *tuberculata* and *rhinolopha*. They have one prominent series of tubercles on the neck,
99 and several scattered ones above the hind extremities. The tubercles on the snout are not so
100 prominent as in *rhinolopha* from Central America, but the arrangement is the same. The
101 tubercles on the neck are comparatively few as compared with those on Nicaraguan types”.
102 Later, Barbour (1914) advised “a careful revision of these two species, made with the aid of
103 extensive collections from many localities, will be necessary before their exact status can be
104 settled”. He added: “That they are really distinct I have no doubt whatever, but as yet their
105 ranges cannot be accurately defined. Stejneger suspects that if intermediates really do exist,
106 they may be explained by the fact that the species have been carried by human agency ‘in
107 innumerable instances’, and that the intermediates may be ‘hybrids from introduced stock, or

108 because of their geographic distribution' (*ex litt.*). I favour the latter explanation, as apparently
 109 the accidental introduction of vertebrates by human agency is a far rarer phenomenon than is
 110 often realized". According to Dunn (1934) and Barbour (1935), Grenada was inhabited by
 111 *Iguana iguana iguana*.

112

113 Following Boulenger's lead, Dunn (1934) recognised two species in the genus *Iguana*:
 114 *I. iguana* (with subspecies *iguana* and *rhinolopha*) and *I. delicatissima*. Lazell (1973)
 115 compared 139 "*I. iguana*" from Central and South America and the West Indies with 29 *I.*
 116 *delicatissima* collected between Martinique and Anguilla, and detected only one consistent
 117 difference between *I. iguana* and *I. delicatissima*: the existence in the former of a subtympenic
 118 plate at least 80% as large as the tympanum. Lazell (1973) rejected *rhinolopha* as a subspecies
 119 because he thought that the nasal horns were polytopic and polyphyletic characters, having
 120 observed them in iguanas from the Grenadines, Saint Lucia and parts of Central America.
 121 Based on their morphology, Lazell (1973) recognized three groups of *I. iguana* in the Lesser
 122 Antilles (Fig. 2): (1) The Northern group (Montserrat, Saba and, in the Greater Antilles, Saint
 123 Croix), distinguished by a higher proportion of melanistic individuals, large tubercular nape
 124 scales and dorsal crest spikes; (2) The Guadeloupe group (present only in Les Saintes and
 125 Basse Terre) which were "quite ordinary, and resemble those from northeastern South
 126 America. They may be patternless and/or grey: characteristics that are rare or absent in other
 127 parts of the range of *I. iguana*"; and (3) The Southern group between Saint Lucia and Grenada,
 128 characterised by vertical banding on the body and by nasal horns. Lazell considered the
 129 variation between the three groups to be clinal. For example, iguanas on the islands between
 130 Saint Lucia and Grenada have few tubercular nape scales; iguanas from Guadeloupe have
 131 more and larger ones; and those from the Northern group have very large and numerous
 132 tubercles.

133

134 Owing to their large size, striking colouration and horns, the Southern group is in
 135 demand for the international pet trade, and individuals are being smuggled out of these

136 counties and marketed variously under the trade names “Saint Lucia iguana” and, from the
137 Grenadines, “pink rhino iguana” and “white zebra rhino iguana” (Daltry pers. obs.;
138 Noseworthy 2017).

139

140 In recent decades, this picture has been complicated by the discoveries both of
141 hybridization between different species of *Iguana* and evidence of multiple invasions by
142 iguanas from Latin America. When Lazell conducted his studies in the 1960s, both *I.*
143 *delicatissima* and *I. iguana* were abundant and sympatric in Les Saintes (Guadeloupe), but not
144 syntopic, and at that stage there was no evidence of one species displacing the other. It has
145 since become clear that *I. iguana* is an invasive alien species in the Guadeloupean Archipelago
146 (Breuil 2002, 2003), and that frequent interbreeding has taken place between *I. delicatissima*
147 and *I. iguana* in Les Saintes, Grande-Terre and Basse-Terre, resulting in fertile and
148 morphologically intermediate hybrids (Breuil 2002, 2003). Breuil (2013, 2016) reported that *I.*
149 *iguana* was first introduced from French Guiana to Les Saintes in the mid-19th Century, and
150 Breuil (2009) and Breuil *et al.* (2010) explained how this species arrived on Basse-Terre. The
151 unfortunate result of this introduction of *I. iguana* has been the elimination of the native *I.*
152 *delicatissima* through hybridization and competition from Terre-de-Bas and Terre-de-Haut
153 (Les Saintes) and Grande-Terre, a process that is continuing at present on Basse-Terre (Breuil
154 *et al.* 2010; Vuillaume *et al.* 2015; Breuil 2013, 2016). More recently, *Iguana x Cyclura*
155 hybrids have been recorded from Little Cayman Island (Moss *et al.* 2017), showing the lack of
156 isolating mechanisms between these Caribbean genera.

157

158 From Guadeloupe, the alien iguanas have spread North and South. Father Pinchon
159 brought *I. iguana* from Les Saintes to Martinique, and this invasive species now ranges over
160 southern Martinique (Breuil 2011). Following Hurricane Luis in September 1995, dozens of
161 iguanas were carried on rafts composed of logs, vegetation, house debris and garbage from
162 Guadeloupe to Antigua, Barbuda and Anguilla (Daltry pers. obs.; Censky *et al.* 1998; Hodge *et*
163 *al.* 2011): the Guadeloupe origin of these iguanas was inferred from their morphology (Breuil

1999). Both Anguilla and Barbuda now have growing populations of non-native *I. iguana* (Henderson & Breuil 2012). Additional iguanas have arrived in the West Indies as pets, putatively originating from breeding centres in Central America (Kraus 2009). These iguanas tend to be bigger than the Guadeloupean form, often with a yellow-orange iris, flat median horns on their snouts, big tubercular nape scales and a very big subtympenic plate. During the breeding season the males are often bright orange. These invasive alien iguanas have recently become established in the wild in Saint Martin, Saint Barthélemy, Martinique and Saint Lucia in the Lesser Antilles (Breuil 2013, 2016). Besides being transported as pets and by storms, invasive iguanas have also spread as stowaways. In 2018, for example, hybrid *iguana x delicatissima* were detected for the first time near the main port in Dominica, leading local conservationists to infer that *I. iguana* had recently arrived with shipping containers from other Caribbean islands (Jeanelle Brisbane, WildDominique, pers. comm.). In addition to having become the greatest threat to the Critically Endangered *I. delicatissima* in the Lesser Antilles (van den Burg *et al.* 2018), the invasive *I. iguana* have severe negative impacts for other wildlife and humans on other islands, *e.g.* Puerto Rico, the Caymans and Dominican Republic (Pasachnik *et al.* 2012; Falcón *et al.* 2012, 2013; M. Goetz, pers. comm.).

Invasive alien *I. iguana* were reportedly smuggled as juveniles into Saint Lucia in the late 1980s. Credible reports of free-living hatchlings in the vicinity of Soufriere (Southwest Saint Lucia) date back to 2007, putatively having escaped from a cage in the grounds of a hotel in Soufriere despite warnings from the Forestry Department to keep the animals and their offspring well secured. As the invasive iguanas began to multiply in spite of efforts by the Forestry Department and Durrell Wildlife Conservation Trust to catch and cull them, the native iguana population has become threatened by possible hybridization and competition (Morton & Krauss 2011; Krauss *et al.* 2014). At the time of writing, the invasive iguana population is growing in Southwest Saint Lucia, while the indigenous iguana population is less than 15 km away, in the Northeast. The Government of Saint Lucia recognises the indigenous Saint Lucia iguana as a distinct and fully protected species, despite it having long been regarded by the

192 scientific community as merely a variant of *Iguana iguana*.

193

194 The status of the iguanas in Grenada and St Vincent & the Grenadines is less well
195 understood because iguanas in both countries have long been regarded as a single, relatively
196 abundant game species that can be hunted during the open season and freely transported by
197 hunters and buyers within their respective borders. Specimens examined by the authors
198 indicate that invasive *I. iguana* from Central and South America have invaded and multiplied
199 on the larger islands at least, including the main islands of Grenada and St Vincent. Unaware
200 of the possible diversity in iguana taxa, in 2005 the St Vincent & the Grenadines Forestry
201 Department relocated 260 indigenous iguanas from Palm Island to the nearby Tobago Cays
202 (also in the Grenadines) and the Kingstown botanical gardens on Saint Vincent in response to
203 complaints from the owners of a resort on Palm Island that the iguanas were becoming a
204 nuisance. During the hunting season (October to January inclusive), hunters commonly collect
205 and transport live iguanas from the Grenadine islands to sell as bushmeat on Saint Vincent (G.
206 Gaymes, pers. obs.).

207

208 As this narrative shows, understanding the distribution and taxonomy of iguanas in the
209 Lesser Antilles has been repeatedly frustrated by differences of opinion among scientists on
210 nomenclature and diagnostic characters, the accidental and deliberate movement of both native
211 and invasive alien iguanas between islands, and hybridisation between members of the genus
212 *Iguana*. There have, however, been some recent breakthroughs. Breuil (2002, 2013, 2016)
213 identified more than 15 morphological characters to reliably differentiate *I. delicatissima* from
214 *I. iguana* (see also Vuillaume *et al.* 2015). Breuil (2013, 2016) also proposed diagnostic
215 characters to distinguish iguanas from Central America, South America, Montserrat, Saba and
216 Saint Lucia. Malone & Davis (2004) and Stephen *et al.* (2013) provided preliminary genetic
217 data that suggested that the Saint Lucia iguana forms an independent radiation in the Lesser
218 Antilles, but they did not consider the horned iguanas on islands South of Saint Lucia, such as
219 the Grenadines (which Lazell, 1973, had placed in the same phenotypic group as the Saint

220 Lucia iguana). Vuillaume *et al.* (2015) studied the genetic variation of iguanas in the Lesser
221 Antilles from Saint Lucia to Saint Martin (French West Indies). Following this work, Breuil *et*
222 *al.* (in preparation) work on the genetic and morphological originality of the insular population
223 of Saba and Montserrat.

224

225 The objectives of this paper are:

226 [1] To clarify the taxonomic status of the iguanas of the Southern Lesser Antilles using
227 new morphological and genetic data from Saint Lucia, St Vincent & the Grenadines,
228 and Grenada.

229 [2] To present new information on the distribution, threats and ecology of this group, and
230 recommendations for their conservation.

231

232 **Materials and methods**

233 Morphological, molecular (*i.e.* mitochondrial DNA and microsatellites markers), and
234 biological data were used to characterise the iguanas of Saint Lucia, Grenada and St Vincent &
235 the Grenadines, and compare them to other populations of *Iguana iguana sensu lato*.

236

237 **Morphological analysis**

238 The morphological characters used to examine the iguanas followed Breuil (2013, 2016), most
239 of which are meristic characters that were easy to record from digital pictures taken by the
240 authors of wild individuals and from specimens at the Museum of Comparative Zoology
241 (MCZ) in Harvard, USA, and the Museum National d'Histoire Naturelle (MNHN) in Paris,
242 France.

243

244 We also examined photographs of *Iguana* found on the Internet using the Google
245 Images search engine for the islands of Saint Vincent, the Grenadines and Grenada. The use of

Internet images for taxonomic research was advocated by Leighton *et al.* (2016) for studying spatial patterns in phenotypic traits that are objective, binary and easy to see, irrespective of the angle, to supplement fieldwork. To identify diagnostic characters, we retained only pictures that reported precise localities, and eliminated areas known to have iguanas introduced from Central and South America.

Molecular analysis

Collection and preparation of genetic material

Genomic DNA was isolated from 39 specimens from tissue, shed skin and/or blood samples, using the QIAamp DNA Mini Kit (QIAGEN, Deutschland) and following the manufacturer's recommendations (Table 1). Not all specimens were used for both mtDNA and microsatellites analysis. Samples from the Lesser Antilles were collected by the authors and from French Guiana by François Catzefis (CNRS, France) and Benoît de Thoisy (Institut Pasteur, Cayenne, French Guiana).

Mitochondrial DNA (ND4)

903 base pairs (bp) of the ND4 mitochondrial DNA gene were amplified using primer pair 5'-CAC CTA TGA CTA CCA AAA GCT CAT GTA GAA GC-3' and 5'-GCT TCT ACA TGA GCT TTT GGT AGT CAT AG-3'. A Qiagen multiplex PCR kit was used to conduct each PCR, with a total reaction volume of 25 µL containing 20ng DNA template, 12.5 µL Qiagen PCR Master Mix, 2.5 µL Qiagen Q-solution, and 2.5 µL primer mix at 10µM each. PCR reactions were carried out in a SimpliAmp thermal cycler under the following conditions: initial denaturation at 95°C for 15 min, followed by 35 cycles of denaturation at 95°C for 30 s, annealing at 52°C for 30 s, and extension at 72°C for 90 s, with a final extension step at 60°C for 30 min. The amplification was verified by electrophoresis using LabChip GX Analyser (Caliper Life Sciences, USA) and successful PCR products were then vacuum-purified using MANU 30 PCR plates (Millipore) before being sequenced using the ABI Big-Dye Terminator

v3.1 Cycle Sequencing Kit (Thermo). Cycle sequencing reactions were finally purified with Sephadex G-50 Fine (GE Healthcare) and sequenced on an ABI 3130xl DNA sequencer (Applied Biosystems). Sequence chromatograms were analyzed in SEQUENCHER (v5.3; Gene Codes Corp., Ann Arbor). Sequence alignment was prepared with MAFFT (v7.187; Katoh *et al.* 2005). For comparisons we chose a 340-bp fragment of the ND4 locus common to all our specimens.

Microsatellites

This data set comprised 36 individuals representing seven insular and continental populations (Table 1). A panel of 17 microsatellite markers were amplified as described by Valette *et al.* (2012) and Vuillaume *et al.* (2015).

Phylogenetic analysis

For ND4 analysis, we aligned our ND4 sequences from the 21 specimens sampled by the authors (Table 1) with Genbank sequences obtained from previous studies (Malone *et al.* 2000; Malone & Davis 2004; Stephen *et al.* 2013; Martin *et al.* 2015). Phylogenetic trees were constructed using the Maximum Likelihood (ML) and Bayesian Inference (BI): The best-fit evolutionary model was calculated using the Bayesian Information Criterion in jModelTest2 (version 2.1.6; Darriba *et al.* 2012) while the ML analysis was conducted in MEGA6 (Tamura *et al.* 2013) based on the best-model obtained in jModeltest. Initial tree(s) for the heuristic search were obtained by applying the Neighbour-Joining method to a matrix of pairwise distances estimated using the Maximum Composite Likelihood (MCL) approach. A discrete Gamma distribution was used to model evolutionary rate differences among sites (5 categories). The BI was performed using MrBayes 3.2 (Ronquist *et al.* 2012) on the Cipres Science Gateway. Two independent runs with four MCMC chains were carried out for 50 million generations. The temperature parameter was set to 0.2 and chains were sampled every 5,000 generations. The first 12.5 million generations were discarded as burn-in. The effective

sample sizes of parameters were checked using TRACER 1.5 (Drummond & Rambaut 2007) and the convergence of runs was checked using AWTY (Nylander *et al.* 2008). Supported nodes in phylogram were indicated with bootstrap values $P \geq 70$ in ML and posterior probabilities (pp) values ≥ 0.95 in BI.

The Median-Joining (MJ) haplotype network (Bandelt *et al.* 1999) was constructed to analyze inter- and intraspecific relations among *Iguana* lineages. The MJ network was calculated and drawn using PopART (Population Analysis with Reticulate Trees) v1.7 (Leigh & Bryant 2015).

Genetic diversity

We tested departures from Hardy-Weinberg expectations and linkage disequilibria using exact tests based on the Markov chain (1,000 permutations) with the software FSTAT v. 2.9.3.2 (Goudet 2001). We adjusted the levels of significances for multiple tests using the standard Bonferroni correction (Rice 1989). We assessed the polymorphism over all loci for each population, computing allelic richness (AR), expected heterozygosity (H_e), allelic frequencies and inbreeding coefficient (F_{is}) (Weir & Cockerham 1984) using FSTAT v. 2.9.3.2 (Goudet 2001) with 1,200 permutations. The allelic frequencies allowed us to deduce private alleles for each population.

Genetic structure

We estimated pairwise fixation index (F_{ST}) values between populations (Weir & Cockerham 1984) using FSTAT v. 2.9.3.2 (Goudet 2001). Their associated significance was computed and tested using global tests implemented in FSTAT v. 2.9.3.2 (Goudet 2001) with a level of significance adjusted for multiple tests using the standard Bonferroni correction. In addition, relationships among populations were evaluated with a Factorial Correspondence Analysis (FCA) based on individual genotypes and using the FCA procedure implemented in GENETIX

v. 4.05.2 (Belkhir *et al.* 2004). We also accessed the genetic structure using the individual-based approach implemented by the software STRUCTURE (Pritchard *et al.* 2000). This Bayesian clustering approach estimated both the number (K) of genetic cluster(s) and the admixture coefficient of individuals to be assigned to the inferred clusters. We choose the admixture model and the option of correlated allele frequencies among populations. As recommended by Evanno *et al.* (2005), we replicated 20 independent runs for each value of K (with K varying from 1 to 10) with a total of 1 million iterations and a burn-in of 10,000. To determine the number of genetic clusters from STRUCTURE analyses, we used the STRUCTURE HARVESTER program (Earl & VonHoldt 2011) to compare the mean likelihood and variance per K values computed from the 20 independent runs.

Systematic analysis

Based on morphological and genetic analysis, the Southern group of iguanas first identified by Lazell (1973) is herein recognized as a new species endemic to Saint Lucia, St Vincent & the Grenadines, and Grenada, with at least two subspecies.

Iguana insularis new species

Southern Antillean horned iguana

Figs 3-6.

This new species is characterized by the following combination of features found in both subspecies:

- Presence of median and lateral horns on the snout that are generally enlarged at the base;
- Small subtympenic plate, not exceeding 20 % of the high of the tympanum;
- Two or three scales of decreasing size anterior of the subtympenic plate;

- 353 – Not more than 8 small to medium triangular gular spikes, exceptionally 10;
- 354 – Dewlap of medium size;
- 355 – Low number of small to medium dispersed nuchal tubercles;
- 356 – Dark brown iris (never yellow to orange), with the white of the eye visible except in
- 357 the juveniles;
- 358 – Oval prominent nostril, sometimes triangular;
- 359 – Short and relatively flat head;
- 360 – High dorsal spines;
- 361 – No swelling of the jowls in reproductively active males.
- 362 – Body of juveniles and young adults is predominantly bright green with 6-8 black
- 363 vertical bands; The body becomes very pale (almost white or cream white) in old
- 364 individuals and the vertical bands either fade (subspecies *insularis*) or remain black
- 365 (subspecies *sanctaluciaae*).
- 366 – Black bands on the tail, which typically remain conspicuous throughout life.

367

368 The new species has at least two subspecies, both described below: (1) The nominate
 369 subspecies on the Grenada Bank (comprising the main island of Grenada and the islands of the
 370 Grenadines), and (2) A subspecies restricted to the island of Saint Lucia. The most
 371 conspicuous difference between the two subspecies is the colouration of older adults. In both
 372 species the body colouration becomes pale, almost white, with age. However, in the nominate
 373 subspecies, the dark banding on the body is thinner and fades with age, whereas in Saint Lucia
 374 population, the bands are thicker and remain black. In both subspecies, the dewlap in the
 375 juveniles is green but in the Saint Lucia population the dewlap becomes entirely black with age
 376 whereas in the Grenada Bank iguanas the dewlap becomes cream white. These morphological
 377 differences prompted us to describe two subspecies on the Grenada Bank and Saint Lucia
 378 respectively, as presented below. Note that the form of *I. insularis* on St Vincent remains
 379 unverified due to lack of known pure-bred specimens from here.

380

381 ***Iguana insularis insularis* new subspecies**

382 Grenadines horned iguana, pink rhino iguana

383

384 **Holotype**

385 The holotype of *Iguana insularis insularis* housed in MCZ under the numbers X-17620/R-

386 79057 (Fig. 3). This specimen was caught by James Lazell on Bequia, St Vincent & the

387 Grenadines (10 April 1964).

388

389 **Sex:** Undetermined.

390 **Age:** Young, possibly 2 years old, based on its size.

391 **Morphological measurements:** Total length: 51.5 cm, SVL: 13.5 cm, tail length: 38 cm.

392 Height and width of the left subtympenic plate: 3.2 mm, 4.3 mm.

393 **Meristics:** Number of gular spikes, 5 medium + 2 small. Number of dorsal spikes to cloaca: 54

394 ± 1 .

395

396 **Paratypes**

397 Two other young specimens MCZ X-17619/R-79056 and X-17621/R-79058) from the same

398 location and the same collector.

399

400 **Diagnosis of *Iguana insularis insularis* (Figs 4, 5)**

401 We define the typical morphology of this new taxon based on our own observations on both

402 adults and juvenile specimens on Palm and Union Islands (St Vincent & the Grenadines),

403 complemented by the specimens from MCZ R-79056-57-58 collected on Bequia (also in St

404 Vincent & the Grenadines) and R-79747 from Sandy Bay, Grenada. The latter four are young

405 individuals with SVL from 128 mm to 135 mm, and thus lack some details specific to adults.

406

407 The iguanas from the Grenada Bank, including the Grenadines, are characterised by
408 the following association of characters in adults compared with iguanas from Saint Lucia (*I.*
409 *insularis sanctaluciae* ssp. nov.).

410

- 411 - In most old adults (both males and females), the green colouration and black bands
412 fade to an almost uniform light cream to nearly white, except on the posterior end of
413 the tail where the black banding persists;
- 414 - In old adults, the head is nearly light cream to white;
- 415 - The dewlap is predominantly white but may have some black scales;
- 416 - There are no black margins on the subtympenic plate and on the sublabial scales;
- 417 - The snout has 2 to 5 median horns (usually 3 or 4) and 2 to 6 less developed lateral
418 horns on each side;
- 419 - The horns may or may not remain black throughout the animal's life;
- 420 - There are light yellow scales on the head and on the dewlap in old adults;
- 421 - The tips of the dorsal spikes of mature adults during the breeding season are light
422 yellow to light orange;
- 423 - The anterior part of the dewlap is rounded.

424

425 **Size**

426 The largest purebred *I. insularis insularis* measured by the authors had an SVL of 45 cm
427 (IGU77, an adult male on Palm Island, Fig. 4). Its tail was incomplete.

428

429 Another large individual fitting the morphology of this subspecies (but not yet
430 genetically tested) on Petit Bateau had a total length of 136 cm.

431

432 **Geographical distribution (Fig. 6)**

433 Of the c. 30 islands of Grenada Bank, including the Grenadine islands and the main island of
434 Grenada, 26 have been reported to have iguanas (Henderson & Powell 2018). The entire bank
435 is inferred to have been originally inhabited by *I. insularis insularis* but morphological and
436 genetic data indicate that several islands, including the main island of Grenada, have had
437 incursions of *I. iguana* from South American and/or Central American lineages.

438

439 From our collection of photographs of specimens captured by the authors and obtained
440 from internet searches, it is clear that most Grenadine islands still have the indigenous white,
441 horned and more or less black-banded phenotype, but there is the Central America phenotype
442 with various hybrids among them that make it difficult to confirm which islands still have
443 purebred populations of this subspecies. Further genetic testing is required to accurately map
444 the present distribution of *I. insularis insularis*.

445

446 **Etymology**

447 The specific name and thus the subspecific name refer to the numerous islands in the Southern
448 Antilles where the new species lives.

449

450 ***Iguana insularis sanctaluciae* new subspecies**

451 Saint Lucia horned iguana

452 Figs 7-11.

453

454 **Holotype**

455 The holotype of *Iguana insularis sanctaluciae* housed in MNHN Paris under the number
456 MNHN2362 and collected by Bonnacour(t) between 1850-1851. (Fig. 7)

457

458 This specimen is rigid, curved in its jar and it is nearly impossible to take accurate
459 measurements.

460

461 **Sex:** Male

462 **Age:** Adult

463 **Morphological measurements:** total length: 132 cm; SVL: 38.5 cm; tail length 93.5 cm; height
464 and width of left subtympanic plate: 16.7/14.6; height and width of right subtympanic plate:
465 16.4/15.5, height of 4th dorsal spike: 47.5 mm.

466

467 **Meristic characteristics:** Number of gular spikes 7; Number of horns 2 median with very
468 enlarged base + 3 small lateral on each side; Number of dorsal spikes to cloacae: 54

469

470 **Colouration:** type in alcohol with discolouration, the ground colouration is green light grey
471 with dark banding, 6 on the body and 10 on the tail, the scale of the dewlap are dark or half
472 dark, the dorsal spikes are ochre but seem to have lost their original colour.

473

474 **Type locality:** Saint Lucia, West Indies. No more information is known for this individual.

475

476 **Paratype**

477 The stuffed specimen MNHN 1996.8276 (Fig. 7) from the same island (Saint Lucia) and the
478 same collector.

479

480 **Diagnosis of *Iguana insularis sanctaluciae* (Figs 7-9)**

481 *Iguana insularis sanctaluciae* resembles *I. insularis insularis*, but differs by the following
482 association of characters:

- 483 – the scales of the jowls sometimes overlap;
- 484 – there are 7 or fewer triangular gular spikes of moderate size (cf. 8 or 9 exceptionally
485 10 gular spikes in *I. insularis insularis*);

- 486 – the vertical bands on the body are thicker, black and remain well developed in old
- 487 individuals (cf. narrow bands on the body that fade with age in *I. insularis insularis*);
- 488 – the dewlap is black in old individuals (cf. creamy white in *I. insularis insularis*);
- 489 – the subtympenic plate and the associated 2-3 anterior scales have black pigmentation
- 490 on their margins;
- 491 – Only the anterior dorsal spikes are orange in males (cf. most dorsal spikes have an
- 492 orange hue in *I. insularis insularis*).

493

494 **Size**

495 The largest adult male to be measured on Saint Lucia was 160 cm in length (50 cm SVL) and

496 weighed over 5 kg (Fig. 10). A sample of 30 adults in Saint Lucia had a mean total length of

497 110 cm (30 cm SVL) and mass of 1.3 kg.

498

499 **Geographical distribution (Fig. 11)**

500 The distribution of native Saint Lucia horned iguanas (*Iguana insularis sanctaluciae* subsp.

501 nov.) and introduced alien iguanas (*Iguana rhinolopha*) on Saint Lucia is shown in (Fig. 16),

502 redrawn from Morton & Krauss (2011) with minor updates, after an island-wide, systematic

503 survey (Morton *et al.* 2007).

504

505 **Etymology:** The subspecific name is given in reference to Saint Lucia which is the only island

506 inhabited by this new taxon.

507

508 **Comparison to other species**

509 *Iguana insularis* sp. nov. is distinguished from *I. iguana*, *I. rhinolopha* (considered here as a

510 full species, see below) and *I. delicatissima* by the following combination of characters.

511 Because in the field there is greatest risk of confusing the new species with invasive alien *I.*

512 *rhinolopha*, which also has nasal horns, figures 9 and 10 highlight the main morphological

513 differences between the anterior parts of *I. insularis* and *I. rhinolopha*.

514

515 **Colour hue and pattern**

516 The head, body and tail are bright green in young individuals, becoming very pale greenish
517 grey or creamy white with age (unlike *I. iguana*, *I. rhinolopha* and *I. delicatissima*, which vary
518 widely in hue but are rarely as pale). The body has 6-8 thin or thick vertical black bands
519 (except in old adult *I. insularis insularis*, in which only faint traces of the vertical bands
520 remain). These vertical black bands are present on the newborn *I. i. sanctaluciae* whereas they
521 are generally absent in newborn *Iguana iguana* and *iguana rhinolopha*. According to
522 Henderson & Powell (2018), juveniles most frequently are uniform green but this point has to
523 be checked for *Iguana insularis insularis*. The tail has black bands that are conspicuous at all
524 ages (unlike *I. delicatissima*, which does not have vertical bands on the body or tail). The legs
525 are not black even in old individuals (unlike the indigenous iguanas of Saba and Montserrat).
526 Although the body of pale adults may have a pinkish hue, the body colouration of breeding
527 males is never orange as in *I. rhinolopha* from Central America (Fig. 10).

528

529 With age the dewlap changes from green to entirely creamy white (*I. insularis*
530 *insularis*) or completely black (*I. insularis sanctaluciae*) as the indigenous iguanas of Saba and
531 Montserrat, but never orange (cf. *I. rhinolopha*, Fig. 9). The dorsal crest is often high,
532 especially in males (unlike *I. delicatissima*), and of the same colour as the light part of the
533 body and often pink-orange towards the tips. The iris is dark brown, not yellow to orange, and
534 the white part of the eye is visible (unlike *I. iguana*, *I. rhinolopha* and *I. delicatissima*). There
535 is no black patch between the eye and the tympanum, and no pink on the jowls but some
536 breeding males have pale golden yellow on the jowls.

537 **Scalation**

538 Several scales between the nostrils are elongated to form horns (whereas nasal horns are absent
539 from *I. delicatissima* and *I. iguana*). There are 2 to 5 horns (usually 3-4) on the axial plane, and

1 to 3 smaller horns and sometimes up to 6 for *I. iguana insularis* on each side in adults (whereas lateral horns absent in *I. rhinolopha*). The horns are broad at their bases and the tallest are sometimes curved back (whereas the horns of *I. rhinolopha* are thin, straight and shorter). However, hatchlings and young juveniles of the new species have only very small horns.

The nostrils are prominent; their openings are from oval to circular, sometimes triangular in *Iguana insularis insularis*, looking from the side. There are some small to rarely medium conical scales on the occiput. There are 6-10 medium-sized gular spikes on the dewlap that extend to the half lower part. In adults, these spikes are triangular. A subtympenic plate is present (cf. absent in *I. delicatissima*) but it is relatively small: even in old adults the diameter of the subtympenic plate is no more than $\pm 20\%$ the height of the tympanum (cf. 2-3 times the size of the tympanum in *I. rhinolopha*).

There are 2-3 scales of decreasing size anterior to the subtympenic plate, a characteristic not found in other species systematically present in *I. i. sanctaluciae* and sometimes in *I. i. insularis*. (This trait however resembles a feature of F1 hybrids between *I. iguana* and *I. delicatissima*: Breuil 2013, 2016). There are only few tubercular nape scales: fewer than 10 in *I. i. sanctaluciae* and up to 20 in *I. i. insularis*, small, not very prominent and dispersed, *i.e.* not arranged in more or less conspicuous rows as in *I. rhinolopha* (Fig. 10) and the largely melanistic iguanas of Saba and Montserrat populations (*I. cf. iguana*). This distinguishing character is present in hatchlings and throughout life, unlike some of secondary sex characteristics noted above.

Head

The head is relatively short and flat, and the dewlap is of medium size (cf. the large dewlap in *I. rhinolopha*). The scales anterior to the subtympenic plate overlap slightly in some

567 individuals. The jowls do not appear swollen even in reproductively active males (cf. very
568 well-developed jowls in breeding male *I. rhinolopha*).

569

570 **Results of genetic analysis**

571 **Phylogeny**

572 The intra- and interspecific relationships among *Iguana* species are shown in the phylogram
573 (Fig. 12) and in the Median-Joining haplotype network (Fig. 13). Four clades can be observed:

574

575 Clade 1, the most basal, corresponds to *I. delicatissima* (GB: AF217783), which
576 clustered with mtDNA from two iguanas from Grand Anse in Saint Lucia that had been
577 identified in the field as pure endemic iguanas (see Discussion). IGU53, from the same
578 locality, shows a haplotype that was found nowhere else.

579

580 Clade 2 corresponds to the mtDNA haplotypes shared by the alien iguanas on Saint
581 Lucia, identified by their phenotypes as iguanas from Central America, likely originating from
582 the pet trade (Fig. 10). These haplotypes are close to those of the Central American clade of
583 Stephen *et al.* (2013) and Vuillaume (2012). This clade forms the sister group of the iguanas
584 from French Guiana (South America) and from the southern Lesser Antilles.

585

586 Clade 3 groups the common green iguana (*I. iguana*) from French Guiana but also
587 contains a specimen known only from a piece of shed skin (IGU74) found on Union Island (St
588 Vincent & the Grenadines).

589

590 Clade 4 is consistent with our morphological analysis and shows the existence of an
591 endemic species that inhabits Saint Lucia and the Grenadines (Grenada Bank).

592

593 **Genetic diversity**

594 No linkage disequilibrium was detected after Bonferroni correction (adjusted P-value threshold
595 = 0.0004). Only 5 of the 64 population-locus combinations deviated significantly from Hardy-
596 Weinberg expectations (adjusted P-value threshold after Bonferroni correction = 0.0008).
597 These deviations occurred for population of individuals endemic of Saint Lucia and so seem to
598 be inherent to it. All microsatellite loci were polymorphic with an allelic richness (AR) ranging
599 from 1 to 3.552 and a genetic diversity (He) ranging from 0 to 0.821 across populations (Table
600 2). Moreover, based on allelic frequencies, individuals introduced in Saint Lucia and those
601 coming from French Guiana revealed the presence of several private alleles suggesting a
602 specific genetic signature and so populations well genetically differentiated.

603

604 **Genetic structure**

605 Results revealed significant genetic differentiation between populations. After applying the
606 Bonferroni correction (adjusted P-value threshold = 0.0083), significant F_{ST} values were found
607 between several pairwise populations (mean F_{ST} value = 0.495) (Table 3). This significant
608 variation was corroborated by both FCA (Fig. 14) and the Bayesian individuals-based
609 approach. Indeed, based on the individuals' genotypes, FCA clearly distinguishes four different
610 populations and, furthermore, shows the low genetic diversity within the native Saint Lucia
611 population (only 7 circles are shown because many individuals from Louvet and one from
612 Grand Anse had the same genotypes). The STRUCTURE and STRUCTURE HARVESTER software
613 revealed a highest delta K value of 3 (Figs 15, 16). According to these results, individuals from
614 introduced iguana populations in Saint Lucia and those from French Guiana were mainly
615 assigned to the first and second genetic cluster respectively (clades 3 and 2 from the
616 phylogram, Fig. 12). Individuals native to Saint Lucia and the Grenadine islands were mainly
617 assigned to the third genetic cluster (clade 4 of the phylogram). However, we can also
618 distinguish three individuals (IGU53, IGU55, IGU56) that showed intermediate admixture
619 coefficients, even though they were assumed to be of pure native origin. These intermediate

620 admixture coefficients (Fig. 16, Table 4) and FCA results (Fig. 14) suggest hybridization has
621 occurred in Grand Anse, where three out of the four individuals sampled are considered as
622 hybrids between endemic and introduced individuals from different clades. Moreover, IGU55
623 and IGU56 have *I. delicatissima* haplotypes for ND4, and IGU53 has a unique haplotype
624 closely related to *I. delicatissima* (Fig. 13).

625

626 Discussion

627 Taxonomic and systematic implications

628 The presence of horns on the iguanas of Central America first prompted the description of
629 *Iguana rhinolopha*, by Wiegmann (1834), based on specimens caught in Mexico, and Duméril
630 & Duméril (1851) and Boulenger (1885) subsequently applied the same name to iguanas from
631 Saint Lucia because of their horns. No other morphological traits were used to distinguish *I.*
632 *rhinolopha* apart from a small difference in number and size of spikes on the dorsal crest,
633 identified by Duméril & Bibron (1837) based on a very small number of specimens (Figs 9,
634 10). Later, with the widespread use of the subspecies concept, Dunn (1934) proposed that
635 *rhinolopha* was merely a subspecies of *I. iguana*, and Barbour (1935) also followed this
636 position. This was the consensus until the work of Lazell (1973), who realised that the
637 presence of horns on the snout was inconsistent and, because it occurs polytopically, he
638 rejected the taxon *rhinolopha*. Lazell realised that the indigenous iguanas on Saint Lucia
639 possessed horns that were generally well developed on mature adult individuals, and this is
640 also confirmed by our observations. However, while horns can be found in Central American
641 iguanas, they differ from the arrangement of horns in *Iguana insularis* sp. nov., as we have
642 demonstrated in this work.

643 This paper describes a new species of horned iguana, *Iguana insularis* sp. nov., known
644 only from the southern Lesser Antilles. All the indigenous iguanas from Saint Lucia, St
645 Vincent & the Grenadines and Grenada, described herein as *Iguana insularis*, possess median

646 and lateral horns. Moreover *I. insularis* has a combination of morphological traits that makes it
 647 unique, including: low number and small size of nuchal tubercles, small subtympanic plate,
 648 brown iris colour with the white of the eye visible, no subtympanic swelling, colour hue and
 649 pattern of the body, etc. (Figs 4, 5, 7, 8). With about 2% divergence in the ND4-Leu sequence,
 650 *I. insularis* shows a level of differentiation from *I. iguana* from French Guiana that is within
 651 the interval of divergence of subspecies recognition among *Cyclura* (Malone & Davis 2004).
 652 So, should *insularis* be regarded as a full species, or simply a horned subspecies of *Iguana*
 653 *iguana*? In recent years, the subspecies concept has become unpopular in herpetology, and
 654 almost every subspecies in the Caribbean has now been upgraded to a full species (*e.g.* Breuil
 655 2002) in accordance with the phylogenetic species concept that treats populations as separate
 656 species if they are on separate evolutionary trajectories (see *e.g.* Torstrom *et al.* 2014), as is
 657 usually the case for animals confined to separate islands. Aside from the presence of horns, we
 658 consider there are enough distinct and consistent morphological and genetical differences to
 659 recognise the native southern Lesser Antillean iguanas as a full species, *I. insularis*.

660
 661 While the native iguanas of the Southern Lesser Antilles undoubtedly share a common
 662 ancestry (Figs 12, 13, 14, 15), consistently strong differences in colour hue and pattern have
 663 prompted us to describe the endemic iguanas of Saint Lucia as *I. insularis sanctaluciae* and
 664 those of the Grenada Bank as *I. insularis insularis*. The same basis was used by Hawlittscek
 665 *et al.* (2012) for distinguishing species and subspecies of Comoran snakes. Given that the two
 666 new subspecies are reproductively isolated on separate island banks, we cannot discount the
 667 possibility that further investigation may lead to them being further elevated into separate
 668 species. Further research is also needed on the island of St Vincent to determine whether any
 669 purebred (*i.e.* non-hybrid) native iguanas remain here, and whether they belong to either of the
 670 aforementioned subspecies or a third, undescribed subspecies.

671 When did *Iguana insularis* diverge from other species in this genus? Studies of iguana
 672 morphology (Breuil 2013, 2016) and genetics (Stephen *et al.* 2013; Valette *et al.* 2012;
 673 Vuillaume *et al.* 2015) have shown there are at least three ancient lineages (*I. delicatissima* and

the iguanas of Central America and South American) in the genus *Iguana*, with a genetic divergence approximated by a molecular clock of 1.29 million years for every 1% sequence divergence at the ND4-Leu Locus (Malone *et al.* 2000). With approximately 10% divergence (Malone & Davis, 2004) between *I. iguana* and *I. delicatissima*, the age of separation of these two species is therefore about 11-12 My; but according to Hedges *et al.* (2015), the two lineages could have diverged as much as 22.8 My ago. If we take the lower value of the molecular clock, *I. insularis* diverged about 2.2 My ago. This timeframe is compatible with the ages of Saint Lucia and Grenada, where the oldest rocks date from the Miocene and belong to the intermediate volcanic arc (Bouysse & Garrabé 1984; Germa 2008).

Evolution in isolation over millions of years does not automatically mean the taxa cannot interbreed. Even the most distantly related species in the genus *Iguana* – *I. delicatissima* and *I. iguana* – can interbreed to produce healthy, fertile offspring (Breuil 2013, 2016; Vuillaume *et al.* 2015). This is not very unusual among even more distantly related taxa: For example, even crocodiles in the genus *Crocodylus* from opposite sides of the globe can interbreed to produce fertile hybrids that have a competitive advantage (e.g. Daltry *et al.* 2016a). Judging from their nesting periods (Fig. 17), there is some overlap between the breeding seasons of *I. insularis*, *I. delicatissima* and introduced *I. iguana* from South America, which might enable these species to interbreed.

Where does this leave the horned iguanas of Central America? Stephen *et al.* (2013) recognized two well supported genetic groups in *Iguana iguana* as evolutionary significant units: Central America (México to Panamá) and South America (including Curaçao and the Lesser Antilles) but declined to propose any taxonomic changes pending further sampling across Panamá and South America and a better understanding of the basal position of the populations of Curacao (Buckley *et al.* 2016). The divergence between Central and South American clades based on ND4-Leu is about 4.3%, similar to the 4% divergence between *Cyclura* species (Malone & Davis 2004). We therefore accept *I. rhinolopha* (Wiegmann 1834)

702 as a full species native to Central America, distinguished not only by its unique arrangement of
703 nasal horns but numerous other morphological and genetical characters, as shown by Breuil
704 (2013, 2016), Stephen *et al.* (2013) and Vuillaume *et al.* (2015). This distinctive clade forms a
705 basal lineage with respect to *I. iguana* from South America and the iguanas of the Lesser
706 Antilles (Fig. 13). By sampling more areas across this region, it is likely other new cryptic
707 species will be identified (Bickford *et al.*, 2007; Buckley *et al.* 2016). Indeed, the melanistic
708 iguanas from Saba and Montserrat have been shown to be morphologically and genetically
709 distinct (Breuil 2013, 2016; Stephen *et al.* 2013; Vuillaume *et al.* 2015) and will be considered
710 in another work. Nevertheless, further studies elsewhere in this region are unlikely to change
711 our conclusions regarding the relationships of *Iguana insularis* vs *I. rhinolopha* and *I. iguana*
712 in the Lesser Antilles.

713

714 The most unexpected revelation from our genetic study is that two iguanas (IGU55,
715 IGU56) from Grand Anse, Northeast Saint Lucia, had *delicatissima* ND4 haplotypes, while a
716 third (IGU53) had an unknown haplotype that also clustered with *delicatissima* in addition to
717 the microsatellites from both *I. iguana* and *I. rhinolopha* (Figs 12, 13, 16). The samples used to
718 characterise the population of Grand Anse were juveniles caught 10 years ago, when the
719 morphological differences between *Iguana insularis*, *I. iguana*, *I. rhinolopha* and *I.*
720 *delicatissima* were less well understood, and the animals were erroneously registered as pure
721 native Saint Lucia iguanas (Table 1). As reported in our introduction, Provencher (1880) had
722 mentioned the presence of *I. delicatissima* on Saint Lucia, but the only evidence was a poorly
723 executed drawing (reproduced in Fig. 1). Our discovery of *Iguana delicatissima* haplotypes in
724 Saint Lucia may be explained by either an ancient *delicatissima* population on Saint Lucia that
725 persists only as a maternal lineage or by the recent arrival of a female with an unknown
726 haplotype from another island that has reproduced with *Iguana insularis sanctaluciaae*.
727 Currently, however, we have insufficient data to support one or other hypothesis.

728

729 **Conservation status of *Iguana insularis* sp. nov.**

730 The new species of iguana is at risk throughout its range in the southern Lesser Antilles due to
731 habitat loss, hunting (both for bushmeat and the pet trade) and invasive alien species,
732 especially alien predators and non-native *Iguana* species.

733

734 Of the two new subspecies described in this paper, the Saint Lucia horned iguana (*I.*
735 *insularis sanctaluciae*) appears to be most scarce and vulnerable to extinction. These iguanas
736 are a fully protected species under the Wildlife Protection Act (Laws of Saint Lucia 2010), but
737 they continue to be hunted and eaten at a significant level (Morton & Haynes, pers. obs.) and
738 have been illegally exported and sold to collectors overseas (J. Daltry, pers. obs.). The range of
739 the native iguana population on Saint Lucia is now restricted to that part of the island without
740 good road access (Fig. 16), putatively because of over-hunting in the more accessible areas.

741

742 Habitat conversion for development (in particular the proposed tourism developments
743 on the three large estates of Louvet, Grand Anse and Marquis, and the proposed North East
744 Corridor highway) is currently considered the most severe threat facing the remaining
745 population. Illegal mining of beach sand threatens the iguanas' nesting sites and their seasonal
746 deciduous forest habitat is also especially vulnerable to wildfires (Robbins *et al.* 2008).
747 Developments in the Northeast are also likely to exacerbate threats from introduced
748 mammalian predators: Feral cats (*Felis catus*), southern opossums (*Didelphis marsupialis*) and
749 small Asian mongooses (*Herpestes auro-punctatus*) are all known to kill hatchling iguanas in
750 Saint Lucia (Morton *et al.* 2007). Mongooses also take iguana eggs, and the mutilation of
751 hatchlings whilst still in the nest chamber has been attributed to rats (*Rattus rattus* or *R.*
752 *norvegicus*) (Morton pers. obs.). Both feral and domestic dogs (*Canis familiaris*) prey on
753 iguanas, especially nesting females that are especially vulnerable whilst on the ground (Morton
754 *et al.* 2007).

755

756 Invasive alien iguanas also pose a serious threat, having become well established in
757 Southwest Saint Lucia. Despite numerous efforts to catch and cull the invasive iguanas

(Morton & Krauss 2011; Krauss 2013; Krauss *et al.* 2014), it is proving prohibitively expensive and difficult to limit their spread and prevent contact with the indigenous *Iguana insularis* in Northeast Saint Lucia (Fig. 16), especially with the risk of human-mediated transport across the country. The alien iguanas (*Iguana rhinolopha*) appear to originate from the Central America clade, characterised by its greatly enlarged subtympenic plate, yellow iris, numerous and conspicuous tubercular nape scales, orange colouration in breeding male, huge dewlap with more than ten spikes but also small horns on the stout (Breuil 2013, 2016). The invasive iguanas on Saint Lucia (Fig. 9) also have larger clutches than the native species: mean clutch size for the former is 40 (n = 4 clutches) and mean clutch size for *I. insularis sanctaluciae* is only 23 eggs (n = 14 clutches). The same invasive iguanas from Central America have clutch sizes of 8-75 in Puerto Rico (Lopez-Torres *et al.* 2012) and 20–63 in Hawaii (McKeon 1996). It is very likely that the alien iguanas could hybridize as suggested by the genetic analysis (Fig. 17) with and outcompete *Iguana insularis sanctaluciae*, leading to its elimination (as occurred with *I. delicatissima* in Les Saintes, Basse-Terre and Grande-Terre: Breuil 2002, 2013, 2016; Vuillaume *et al.* 2015).

The status and threats to the Grenada Bank subspecies is less well understood because iguanas have been less closely studied and existing literature on iguanas has failed to distinguish between the native and invasive alien iguanas. Given that iguanas in general are considered to be fairly abundant and widespread on Grenada and St Vincent & the Grenadines, adult iguanas may still be lawfully hunted for several months of the year (typically October through December or January) for personal consumption and local sale (Laws of Saint Vincent & the Grenadines 1990; Laws of Grenada 1990). Unlike Saint Lucia, the national laws here do not distinguish between native and introduced or hybrid iguanas, nor define any populations that may not be hunted or moved within national borders. It is therefore not uncommon for hunters to collect iguanas from the Grenadine islands for sale on St Vincent or Grenada during the hunting season (G. Gaymes, pers. obs.). Hunting is frequent on the uninhabited island of Balliveaux, for example, where hunters from Bequia and Saint Vincent “carry away dozens of

iguanas” (Daudin & Da Silva 2011). In this context of numerous translocations, it is uncertain how many purebred populations of *Iguana insularis insularis* remain.

Not surprisingly, considering the lack of any concerted effort to prevent incursions, alien iguanas appear to have become very widespread in Grenada and St Vincent & the Grenadines, with perhaps no purebred (i.e. non-hybrid) native iguanas remaining anywhere on the main islands of St Vincent or Grenada. We suspect that the most intact native populations are restricted to some of the smallest islands in the Grenadines, including Palm Island and Union Island, where genetic samples were analysed for this study. It is noteworthy that in this context that IGU74 collected as a shed skin has a ND4 haplotype that clusters with *Iguana iguana* from South America. Like the iguanas of Saint Lucia, even these populations are at substantial risk from invasive alien predators (dogs, cats, opossums, etc.) and coastal deforestation and development (Daltry *et al.* 2016b).

Under the national laws of all three countries – Saint Lucia, St Vincent & the Grenadines and Grenada – the export of iguanas or their products is prohibited without permits from their respective chief wildlife wardens. Furthermore, on the basis that the iguanas were classified as *Iguana iguana*, listed on CITES Appendix II, exports have required an export certificate from the CITES Management Authority. Nevertheless, recent years have seen a rise in young iguanas being smuggled from these islands and sold under various trade names, including the Saint Lucia iguana, pink rhino iguana (originating from Union Island) and white zebra rhino iguana (from the Tobago Cays). Iguanas from Saint Lucia and the Grenadines have been offered for sale in the USA, Japan and Europe, for prices of up to \$10,000 per pair, with traders often claiming to have CITES permits, even though no such export permits have been issued by these countries (Noseworthy 2017).

At species level, *Iguana insularis* sp. nov. qualifies as Vulnerable, under IUCN Red List criteria B1a,b (i-v), B2 a,b (i-v) and probably C2a(i). Pure-bred (non-hybrid) individuals have

814 been confirmed only in three locations (Northeast Saint Lucia and, in St Vincent & the
815 Grenadines, on Union Island and Palm Island), giving a known extent of occurrence of less
816 than 2,000 km² and an area of occupancy of less than 30 km². Further surveys and genetic
817 analysis are needed to verify status, but it is unlikely there are as many as 10 locations with
818 non-hybrid populations of *Iguana insularis*, and no population is known to contain more than
819 1,000 mature individuals. An ongoing decline is predicted due to introgressions from invasive
820 alien iguanas, invasive alien predators, habitat loss, and over-collection for meat and the pet
821 trade. (Note that the measured extent of occurrence includes marine areas between the islands:
822 a common problem when applying this method to taxa on islands).

823

824 At subspecies level, the Saint Lucia iguana (*Iguana insularis sanctaluciae*) is Critically
825 Endangered under criteria B1ab(i-iii): Its extent of occurrence is approximately 30 km², it
826 exists in only one location (Northeast Saint Lucia), and a continuing decline is observed and
827 projected in the (i) extent of occurrence, (ii) area of occupancy, and (iii) area, extent and
828 quality of habitat due to tourism developments, sand-mining, livestock grazing and other
829 documented threats (Daltry 2009). The Grenadines horned iguana (*Iguana insularis insularis*)
830 has been less closely studied but qualifies as Vulnerable and possibly Endangered under
831 criteria B1ab(i-iii): Its area of occupancy is less than 20 km², it exists at not more than 10
832 locations (only two locations – the 9 km² Union Island and 0.55 km² Palm Island – have been
833 confirmed to have reasonably intact, non-hybrid populations) and estimates indicate continuing
834 decline, observed, inferred or projected, in the (i) extent of occurrence, (ii) area of occupancy
835 and (iii) area, extent and quality of habitat due to tourism developments, livestock grazing,
836 bushfires and other threats (Daltry *et al.* 2016).

837

838 **Recommendations**

839 International trade in horned iguanas from the Grenadine islands (specifically, Union Island,
840 Palm Island and the Tobago Cays) and Saint Lucia has been confirmed in recent years at a

level that could present a serious risk to both subspecies. By formally naming the new species and the two subspecies, we recognise that the demand from reptile collectors could increase (Auliya *et al.* 2016). We therefore recommend that as an urgent precaution the species *Iguana insularis* sp. nov., should be placed on Appendix I of CITES at the next Conference of Parties to monitor and control illegal international trade. As an interim measure, we urge Saint Lucia, Saint Vincent & the Grenadines and Grenada to jointly request the CITES Secretariat to place *Iguana insularis* on Appendix III. This is necessary to help to ensure that iguanas cannot be sold overseas without a CITES export permit from the country of origin.

Nationally, the new species is fully protected only in Saint Lucia, where the Wildlife Protection Act distinguishes between the native Saint Lucia iguana and the (non-protected) invasive alien iguanas. We recommend Grenada and St Vincent & the Grenadines also consider increased levels of protection for the native horned iguanas and ensure that any future exploitation of *I. insularis* populations is monitored closely and sustainable. Considering the outstanding importance of the apparently purebred and growing population of *I. insularis* on Palm Island (St Vincent & the Grenadines), technical assistance should be offered to the landowners to find solutions to complaints that the iguanas are causing a nuisance.

Because invasive alien iguanas have already become well established in all three countries, it is also imperative to safeguard all remaining native iguana populations from hybridisation and competition. Active biosecurity measures must be developed to prevent non-native iguanas from successfully spreading to Northeast Saint Lucia, Palm Island, Union Island and any other areas known to have purebred (non-hybrid) *I. insularis*, including monitoring these native populations regularly to ensure any incursions are detected and dealt with swiftly. Further surveys are required on St Vincent and Grenada to determine whether any purebred native iguanas remain on these islands. If alien iguanas continue to increase unchecked on Saint Lucia, it may be necessary to separate them from the native iguanas with a physical barrier. With this in mind, plans are currently being developed to create a ‘mainland island’

sanctuary for native Saint Lucian wildlife, surrounded by a pest-proof fence (Saint Lucia Forests and Land Resources Department, 2015) that could potentially conserve several hundred *I. insularis sanctaluciae* in strict isolation from alien iguanas.

To support all these recommendations, it will be necessary to develop illustrated identification materials for researchers, enforcement officials and other stakeholders to reliably distinguish both subspecies of *I. insularis* at all ages from *I. iguana*, *I. rhinolopha* and other species.

Thus, we hope that the recognition of this new species and its two subspecies will ultimately facilitate their protection and conservation.

Acknowledgements

This project was financed mainly by the Direction Régionale de l'Environnement et du Logement de Martinique to study the origin of invasive common green iguanas in Martinique and their relationships to the Saint Lucia iguana. The genetic study formed part of Barbara Vuillaume's Master's degree. The genetic analyses were initially conducted at Genindexe in La Rochelle (France) and completed by David Schikorski in Genindexe Labofarm (France), which financed part of this study.

Specimens were collected from Palm Island and Union Island, in the Grenadines, by JD and GG with kind permission from the Palm Island Resort and the St Vincent & the Grenadines Forestry Department. Fieldwork was supported with funding from the FFI Species Fund, Disney Conservation Fund, National Geographic, US Fish & Wildlife Service (#F18AP00796), and the St Vincent & the Grenadines Preservation Fund. We are most grateful to Roseman Adams, Katrina Adams and other members of the Union Island Environmental Attackers for their assistance. Special thanks also to F. Catzefis (CNRS,

896 Montpellier) and Benoît de Thoisy (Institut Pasteur, Cayenne, French Guiana), who provided
897 samples from French Guiana.

898

899 All Saint Lucia samples were collected by the Durrell Wildlife Conservation Trust and
900 the Saint Lucia Forestry Department. Many members of the Forestry Department were closely
901 involved in project work on the biology of the iguana on Saint Lucia, including especially
902 Alwin Dornelly, Timotheus Jean Baptiste, Brian James, Lyndon John, Stephen Lesmond,
903 Michael Bobb, Adams Toussaint, Michael Andrew, Fera Narcisse-Gaston, Rebecca Rock,
904 George Antoine, Mary James and Richard Regis. Martin Satney and Dunley Auguste provided
905 much appreciated support from the Ministry of Agriculture. Special thanks are due to Donald
906 Anthony (Saint Lucia Forestry Department), John Hartley and John Fa (Durrell Wildlife
907 Conservation Trust) for developing the project work on Saint Lucia, and most especially to
908 Anthony ‘Seako’ Johnny for countless hours of assistance with field work and sharing his
909 extensive local knowledge. Many hours of field assistance in Saint Lucia were also contributed
910 by Bradley Abraham, Curtis Mathurin, Neil Oculi, Nazza Gustave, Fendley Estephane,
911 Kissinger Henry and Greg Alexander from Saint Lucia, along with the tireless voluntary
912 efforts of most of the co-authors of Morton *et al.* (2007) plus Jane Huston. Catherine Stephen,
913 Bill Toone, Rich Young, Sarah Seymour, Roger Graveson, Melvin Smith, Chris Pilgrim and
914 most especially Karen Graham all provided much-valued support and insight. The farmers at
915 Sankofa Rainbow Roots Farm and Roots Farm Zimbabwe, along with the owners of Louvet
916 Estate, the Laule family, kindly facilitated access to their lands. This part of our work was
917 funded by the Balcombe Trust.

918

919 Pictures and measurements of MCZ specimens were kindly provided by Joseph
920 Martinez. We thank two anonymous reviewers for their remarks on an earlier version of this
921 manuscript.

922

923 **References**

- 924 Auliya, M., Altherr S., Ariano-Sanchez D., Baard E.H., Brown C., Brown R.M., Cantu J.C.,
925 Gentile G., Gildenhuys P., Henningheim E., Hintzmann J., Kanari K., Krvavac M.,
926 Lettink M., Lippert J., Luiselli L., Nilson G., Nguyen T.Q., Nijman V., Parham J.F.,
927 Pasachnik S.A., Pedrono M., Rauhaus A., Rueda Córdova D., Sanchez M.E., Schepp
928 U., van Schingen M., Schneeweiss N., Segniagbeto G.H., Somaweera R., Sy E.Y.,
929 Türkozan O., Vinke S., Vinke T., Vyas R., Williamson S. & Ziegler T. (2016) Trade
930 in live reptiles, its impact on wild populations, and the role of the European market.
931 *Biological Conservation*, 204, 103–119.
- 932 Bandelt, H., Forster, P. & Röhl, A. (1999) Median-joining networks for inferring intraspecific
933 phylogenies. *Molecular Biology and Evolution*, 16(1), 37–48.
934 <http://dx.doi.org/10.1093/oxfordjournals.molbev.a026036>
- 935 Barbour, T. (1914) A contribution to the zoögeography of the West Indies, with especial
936 reference to amphibians and reptiles. *Memoirs of the Museum of Comparative Zoölogy*
937 *at Harvard College*, 44, 209–359.
- 938 Barbour, T. (1930) A list of Antillean reptiles and amphibians. *Zoologica*, 11, 61–116.
- 939 Barbour, T. (1935) A second list of Antillean reptiles and amphibians. *Zoologica*, 19, 77–141.
- 940 Belkhir, K., Borsa, P., Chikhi, L., Raufaste, N. & Bonhomme, F. (1996). GENETIX 4.05,
941 logiciel sous Windows TM pour la génétique des populations. *Laboratoire Génome*,
942 *Populations, Interactions, CNRS UMR 5000, Université de Montpellier II*,
943 *Montpellier, France*.
- 944 Bickford, D., Lohman, D.J., Sodhi, N.S., Ng, P.K.L., Meier, R., Winker, K., Ingram, K. & Das,
945 I. (2007) Cryptic species as a new window on diversity and conservation. *Trends in*
946 *Ecology and Evolution*, 22, 148–155.
947 <http://dx.doi.org/10.1016/j.tree.2006.11.004>
- 948 Boulenger, G.A. (1885) *Catalogue of the Lizards in the British Museum (Natural History)*.
949 Vol. 2 (ed. 2). i-xiii, 492 pp., pl. I–XXXII. Trustees, London.

- 950 Bouysse, P. & Garrabé, F. (1984) Neogene tectonic Evolution of the Limestone Caribbees in
951 the Guadeloupe Archipelago. *Comptes Rendus Académie des Sciences Paris (série I)*,
952 298 (17), 763–766.
- 953 Breen, H.H. (1844) *St. Lucia: Historical, Statistical and Descriptive*. Longman, Brown, Green
954 and Longmans, London, xvi + 423 pp.
- 955 Breuil, M. (1999) Editorial. *West Indian Iguana Special Group Newsletter*, 2, 4.
- 956 Breuil, M. (2002) *Histoire naturelle des Amphibiens et Reptiles terrestres de l'Archipel*
957 *Guadeloupéen: Guadeloupe et dépendances, Saint-Martin, Saint-Barthélemy*.
958 Patrimoines naturels IEGB, SPN MNHN, 54, 1–339.
- 959 Breuil, M. (2003) In the footsteps of French Naturalists, a “Battle” of Iguanas and
960 “Improvements” in Biodiversity. In Henderson R. W. & Powell R. (eds) *Islands and*
961 *the Sea: Essays on Herpetological Exploration in the West Indies*. Society for the
962 Study of Amphibians and Reptiles, Ithaca (New York). Contributions to
963 Herpetology, 20. pp. 255–270.
- 964 Breuil, M. (2009) The terrestrial herpetofauna of Martinique: Past, present, future. *Applied*
965 *Herpetology*, 6, 123–149.
966 <http://dx.doi.org/10.1163/157075408x386114>
- 967 Breuil, M. (2011) The terrestrial herpetofauna of Martinique: Past, present, future. In: Hailey
968 A., Wilson, B.S. & Horrocks, J.A. (eds). *Conservation of Caribbean Island*
969 *Herpetofaunas, Vol. 2, Regional Accounts of the West Indies*, pp. 311–338. Leiden,
970 Brill.
- 971 Breuil, M. (2013) Caractérisation morphologique de l'iguane commun *Iguana iguana*
972 (Linnaeus, 1758), de l'iguane des Petites Antilles *Iguana delicatissima* Laurenti,
973 1768 et de leurs hybrides. *Bulletin Société Herpétologique de France*, 147, 309–346.
- 974 Breuil, M. (2016) Morphological characterization of the common iguana *Iguana iguana*
975 (Linnaeus, 1758), of the Lesser Antillean iguana *Iguana delicatissima* Laurenti, 1768
976 and of their hybrids. (Same paper as Breuil 2013, translated into English, by the
977 *International Reptile Conservation Foundation, IRCF*).

- 978 Breuil, M., Guiougou, F., Questel, K. & Ibéné B. 2010 (2009) Modifications du peuplement
979 herpétologique dans les Antilles françaises: Disparitions et espèces allochtones. 2e
980 partie: Reptiles. *Le Courrier de la Nature*, 251, 36–43.
- 981 Buckley, L.J., De Queiroz, K., Grant, T.D., Hollingsworth, B.D., Iverson, J.B., Pasachnick,
982 S.A. & Stephen, C.L. (2016) A checklist of the iguanas of the World. pp. 4–46 *In*
983 Iverson J.B., Knapp C.R. & Pasachnick S.A. (eds) *Iguanas: Biology, Systematics,*
984 *and Conservation*. Herpetological Conservation and Biology, 11 (Monograph 6).
- 985 Censky, E.J., Hodge, K. & Dudley, J. (1998) Overwater dispersal of lizards due to hurricanes.
986 *Nature*, 395, 556.
- 987 Daltry, J.C. (2009) *The Status and Management of Saint Lucia's Forest Reptiles and*
988 *Amphibians*. Technical Report No. 2 to the National Forest Demarcation and Bio-
989 Physical Resource Inventory Project, FCG International Ltd, Helsinki, Finland.
- 990 Daltry, J.C., Langelet, E., Solmu, G.C., van der Ploeg, J., van Weerd, M. & Whitaker, R.
991 (2016a) Successes and failures of crocodile harvesting strategies in the Asia Pacific.
992 *In: Aguirre, A.A. & Sukumar, R. (eds) Tropical Conservation*, pp. 345–362. Oxford
993 University Press, New York, USA.
- 994 Daltry, J.C., Adams, R., Gaymes, G., Providence, F. & Sweeney, R. (2016b) *Union Island*
995 *Gecko: Conservation Action Plan, 2016–2021*. Report to the Saint Vincent & the
996 Grenadines Forestry Department, Fauna & Flora International, Union Island
997 Environmental Attackers and Virginia Zoo.
- 998 Darriba, D., Taboada, G.L., Doallo, R. & Posada, D. (2012) JModelTest 2: more models, new
999 heuristics and parallel computing. *Nature Methods*, 9(8), 772.
1000 <http://dx.doi.org/10.1038/nmeth.2109>
- 1001 Daudin, J. & de Silva, M. (2011) An annotated checklist of the amphibians and terrestrial
1002 reptiles of the Grenadines with notes on their local natural history and conservation.
1003 *In: Hailey A., Wilson B.S. & Horrocks J.A. (eds) Conservation of Caribbean Island*
1004 *Herpetofaunas, Vol. 2 Regional Accounts of the West Indies: Conservation Biology*
1005 *and the Wider Caribbean*, pp. 259–271. Leiden, Brill. Reprinted from *Applied*

- 1006 *Herpetology*, 4, 163–175 (2007).
- 1007 Des Vœux, G.W. (1903) *My Colonial Service in British Guiana, St. Lucia, Trinidad, Fiji,*
- 1008 *Australia, Newfoundland, and Hong Kong with Interludes: Volume 1.* John Murray,
- 1009 London, 460 pp.
- 1010 Drummond, A.J. & Rambaut, A. (2007) BEAST: Bayesian evolutionary analysis by sampling
- 1011 trees. *BMC Evol. Biol.*, 7, 214.
- 1012 <http://dx.doi.org/10.1186/1471-2148-7-214>
- 1013 Duméril, A.-M.-C. & Bibron, G. (1837) *Erpétologie Générale ou Histoire Naturelle Complète*
- 1014 *des Reptiles. T. IV.* Lib. encycl. Roret, Paris, 572 pp.
- 1015 Duméril, A.-M.-C. & Duméril, A.H.A. (1851) *Catalogue Méthodique de la Collection des*
- 1016 *Reptiles du Muséum National d'Histoire Naturelle.* Gide et Baudry, Paris. 224 pp.
- 1017 Dunn, E.R. (1934) Notes on *Iguana*. *Copeia*, 1934, 1–4.
- 1018 <http://dx.doi.org/10.2307/1436422>
- 1019 Earl, D.A. & VonHoldt, B.M. (2011) STRUCTURE HARVESTER: a website and program for
- 1020 visualizing STRUCTURE output and implementing the Evanno method.
- 1021 *Conservation Genetic Resources*, 4, 359–361.
- 1022 <http://dx.doi.org/10.1007/s12686-011-9548-7>
- 1023 Evanno, G., Regnaut, S. & Goudet, J. (2005) Detecting the number of clusters of individuals
- 1024 using the software structure: a simulation study. *Molecular Ecology*, 14, 2611–2620.
- 1025 <http://dx.doi.org/10.1111/j.1365-294x.2005.02553.x>
- 1026 Falcón, W., Ackerman, J.D. & Daehler, C.C. (2012) March of the green iguana: Non-native
- 1027 distribution and predicted geographic range of *Iguana iguana* in the Greater
- 1028 Caribbean Region. *IRCF Reptiles & Amphibians*, 19(3), 150–160.
- 1029 <http://dx.doi.org/10.2984/67.2.2>
- 1030 Falcón, W., Ackerman, J.D., Recart, W. & Daehler, C.C. (2013) Biology and impacts of Pacific
- 1031 island invasive species: *Iguana iguana*, the green iguana (Squamata: Iguanidae).
- 1032 *Pacific Sciences*, 67(2), 157–186.
- 1033 <http://dx.doi.org/10.1007/bf02101694>

- 1034 Garmann, S. (1887) On the West Indian reptiles. Iguanidae. *Bull. Essex. Inst.*, 19: 17–24.
- 1035 Germa, A., (2008) *Évolution volcano-tectonique de l'île de la Martinique (Arc insulaire des*
1036 *Petites Antilles): Nouvelles contraintes géochronologiques et géomorphologiques.*
1037 Thèse de Doctorat (PhD), version 1, 2010, Université Paris Sud 11, 360 pp.
- 1038 Goudet, J. (2001) FSTAT, a program to estimate and test gene diversities and fixation indices
1039 (version 2.9.3). Available at <http://www2.unil.ch/popgen/softwares/fstat.html>.
- 1040 Hawlitschek, O., Nagy, Z.T. & Glaw, F. (2012) Island evolution and systematic revision of
1041 Comoran snakes: why and when subspecies still make sense. *PLoS ONE* 7(8):
1042 e42970.
1043 <http://dx.doi.org/10.1371/journal.pone.0042970>
- 1044 Hedges, S.B. (2018) Caribherp: West Indian amphibians and reptiles. Temple University,
1045 Philadelphia, Pennsylvania.
1046 <http://www.caribherp.org>
- 1047 Hedges, S.B., Marin, J., Suleski, M., Paymer, M. & Kumar, S. (2015) Tree of Life reveals
1048 clock-like speciation and diversification. *Molecular Biology and Evolution*, 32, 835–
1049 845.
1050 <http://dx.doi.org/10.1093/molbev/msv037>
- 1051 Henderson, R.W. & Breuil, M. (2012) Island lists of West Indian amphibians and reptiles:
1052 Lesser Antilles. *Bulletin of the Florida Museum of Natural History*, 51(2), 148–159.
- 1053 Henderson, R.W. & Powell, R. (2018) *Amphibians and Reptiles of the St. Vincent and*
1054 *Grenada Banks, West Indies*. Edition Chimaera, Frankfurt, Germany, 448 pp.
- 1055 Hodge, K.V.D., Powell, R. & Censky, E.J. (2011) Conserving the herpetofauna of Anguilla.
1056 In: Hailey, A., Wilson, B.S. & Horrocks, J.A. (eds), *Conservation of Caribbean*
1057 *Island Herpetofaunas, Vol. 2 Regional Accounts of the West Indies: Conservation*
1058 *Biology and the Wider Caribbean*, pp. 2–13. Leiden, Brill.
- 1059 Katoh, K., Kuma, K., Toh H. & Miyata, T. (2005) MAFFT version 5: improvement inaccuracy
1060 of multiple sequence alignment. *Nucleic Acids Research*, 33(2), 511–518.
1061 <http://dx.doi.org/10.1093/nar/gki198>

- 1062 Kraus, F. (2009) *Alien Reptiles and Amphibians: a Scientific Compendium and Analysis*.
1063 Invading Nature: Springer Series In Invasion Ecology, Volume 4., i-x, 1-563.
- 1064 Krauss, U. (2013) Invasive alien species management in St. Lucia and Caribbean partner
1065 countries. In: Vernier, J.-L. & Burac, M. (eds), *Actes du Colloque Biodiversité*
1066 *Insulaire: la Flore, la Faune et l'Homme dans les Petites Antilles, Martinique, 2010*,
1067 pp. 196–206.
- 1068 Krauss, U., Isidore, L. Mitchel, Nerius. Seely, L., Alfred, P., Ramessar, A., Johnny, A., Joseph,
1069 B., James, M., Dornelly, A., Breuil, M., Vuillaume, B., Morton, M., John, L.& Bobb,
1070 M. (2014) An assessment of control methods for invasive alien iguanas in Saint
1071 Lucia. *Workshop on Policies, Strategies and Best Practices for Managing Invasive*
1072 *Alien Species (IAS) in the Insular Caribbean*, Port of Spain, Trinidad, 27 pp.
- 1073 Laurenti, J.N. (1768) *Specimen Medicum Exhibens Synopsis Reptilium*. Joan Thom, Vienna,
1074 215 pp., 5 pls ht.
- 1075 Laws of Grenada (1990) Birds and Other Wild Life (Protection of)(Amendment) Ordinance,
1076 1964 (No. 26 of 1964). Revised Edition 1990.
- 1077 Laws of Saint Lucia (2010) Wildlife Protection Act (No. 6.03). Revised Edition 2010.
- 1078 Laws of Saint Vincent & the Grenadines (1990) Wildlife Protection Act, 1964 (No. 26 of
1079 1964). Revised Edition 1990.
- 1080 Lazell, J.D. (1973) The lizard genus *Iguana* in the Lesser Antilles. *Bulletin Museum*
1081 *Comparative Zoology*, 145, 1–28.
- 1082 Leigh, J.W. & Bryant, D. (2015) PopART: Full-feature software for haplotype network
1083 construction. *Methods in Ecology and Evolution*, 6(9), 1110–1116.
1084 <http://dx.doi.org/10.1111/2041-210x.12410>
- 1085 Leighton, R.M.G., Hugo, P.S., Roulin, A. & Amar, A. (2016) Just Google it: assessing the use
1086 of Google Images to describe geographical variation in visible traits of organisms.
1087 *Methods in Ecology and Evolution*, 7, 1060–1070.
1088 <http://dx.doi.org/10.1111/2041-210X.12562>

- 1089 Levacher, M.G. (1834) *Guide Médical des Antilles, ou Études sur les Maladies des Colonies*
1090 *en Général et Sur Celles Qui Sont Propres à la Race Noire*. J.B. Baillières, Paris, 251
1091 pp.
- 1092 Linnaeus, C. (1758) *Systema Naturae per Regna tria Naturae, secundum Classes, Ordines,*
1093 *Genera, Species, cum characteribus, differentiis, synonymus, locis. T.1.* Editio
1094 decimata reformata. Laurentii Salvii, Holmiae. 4 + 824 pp.
- 1095 Lopez-Torres, A.L., Claudio-Hernandez, H.J., Rodriguez-Gomez, C.A., Longo, A.V. & Joglar,
1096 R.L. (2012) Green iguanas (*Iguana iguana*) in Puerto Rico: is it time for
1097 management? *Biological Invasions*, 14, 35-45
- 1098 Malone, C.L. & Davis, S.K. (2004) Genetic contributions to Caribbean iguana conservation.
1099 *In: Alberts, A.C., Carter, R.L., Hayes, W.K. & Martins, E.P. (eds), Iguanas: Biology*
1100 *and Conservation*, University of California Press, US, pp. 45–57.
- 1101 Malone, C.L., Wheeler T., Taylor J.F. & Davis S.K. (2000) Phylogeography of the Caribbean
1102 rock iguana (*Cyclura*): Implications for conservation and insights on the
1103 biogeographic history of the West Indies. *Molecular Phylogenetics and Evolution*,
1104 17, 269–279.
1105 <http://dx.doi.org/10.1006/mpev.2000.0836>
- 1106 Martin, J.L., Knapp, C.R., Gerber, G.P., Thorpe, R.S. & Welsh, M. (2015) Phylogeography of
1107 the Endangered Lesser Antillean iguana, *Iguana delicatissima*: A recent diaspora in
1108 an archipelago known for ancient herpetological endemism. *Journal of Heredity*,
1109 2015, 315–321.
1110 <http://dx.doi.org/10.1093/jhered/esv004>
- 1111 Massemin, D., Fouquet, A. & Breuil, M. (2012) Les amphibiens et reptiles du littoral guyanais:
1112 un peuplement particulier et méconnu. In: Guiral D. & Le Guen R. (eds), *Guyane*
1113 *Océane*, IRD-Roger Leguen éditions, Marseille pp. 294–320.
- 1114 McKeon, S. (1996) *A Fieldguide to Reptiles and Amphibians in the Hawaiian Islands*.
1115 Diamond Head Publishing, Inc., Los Osos, California, USA. 173 pp.
- 1116 Morton, M.N. & Krauss, U. (2011) Native and alien iguanas on Saint Lucia, West Indies.

- 1117 *IRCF Reptiles & Amphibians*, 18(1), 19–25.
- 1118 Morton, M.N., Anthony, D., Besné Garcia, G.G., Corry, E., Dornelly, A., Dröge, E.D., Harley,
1119 S., Jean Baptiste, T., Johnny, A., Kelly, A., McGowan, D., McPharlin, M., Mitchel,
1120 N., O’Kelly, H., Ogrodowczyk, A., Perrett, E. S., Takács, R. & Graham, K.S. (2007)
1121 St. Lucia Iguana Project Report 2002-07. Unpublished report to Saint Lucia Forestry
1122 Department and Durrell Wildlife Conservation Trust.
- 1123 Moss, J.B., Welch, M.E., Burton, F.J., Vallee, M.V., Houlcroft, E.W., Laaser, T. & Gerber,
1124 G.P. (2017) First evidence for crossbreeding between invasive *Iguana iguana* and the
1125 native rock iguana (Genus *Cyclura*) on Little Cayman Island. *Biological Invasions*.
1126 <https://doi.org/10.1007/s10530-017-1602-2>.
- 1127 Nellis, D.W. & Everard, C.O.R. (1983) The biology of the mongoose in the Caribbean *Studies*
1128 *on the Fauna of Curaçao and other Caribbean Islands*, 1, 1-162.
- 1129 Noseworthy, J. (2017) *Cold-blooded conflict: tackling the illegal trade in endemic Caribbean*
1130 *island reptiles*. MPhil thesis, University of Cambridge, UK.
- 1131 Nylander, J.A.A., Wilgenbusch, J.C., Warren, D.L. & Swofford, D.L. (2008). AWTY (are we
1132 there yet?): a system for graphical exploration of MCMC convergence in Bayesian
1133 phylogenetics. *Bioinformatics*, 24(4), 581–583.
- 1134 Pasachnik, S.A., Breuil, M. & Powell R. (2006) *Iguana delicatissima*. *Catalogue of American*
1135 *Amphibians and Reptiles*, 811, 1–14.
- 1136 Pasachnik, S.A., De León R.C., Reynoso, V.H., Rupp E., León Y.M. & Incháustegui, S.J.
1137 (2012) Green Iguanas in the Dominican Republic. *IRCF Reptiles and Amphibians*,
1138 19(2), 132–134.
- 1139 Pritchard, J.K., Stephens M. & Donnelly, P. (2000) Inference of population structure using
1140 multilocus genotype data. *Genetics*, 155, 945–959.
- 1141 Provancher, L. (1890) *Une excursion aux climats tropicaux. Voyage aux îles du Vent : St-Kitts*,
1142 *Névis, Antigue, Montserrat, La Dominique, La Guadeloupe, Ste-Lucie, La Barbade*,
1143 *Trinidad*. J.A. Langlais, Québec, 353 pp.

- 1144 Rand, A.S. & Greene, H.W. (1982) Latitude and climate phenology of reproduction in the
1145 green iguana, *Iguana iguana*. In: Burghardt, G.M. & Rand, A.S. (eds.) *Iguanas of*
1146 *The World: Their Behavior, Ecology and Conservation*. Noyes Publications, Park
1147 Ridge, New Jersey, pp. 142–149.
- 1148 Rice, W.R. (1989) Analyzing tables of statistical tests. *Evolution*, 43, 223–225.
1149 <http://dx.doi.org/10.1111/j.1558-5646.1989.tb04220.x>
- 1150 Robbins, A.M.J., Eckelmann, C.-M. & Quinones, M. (2008) Forest fires in the insular
1151 Caribbean. *Ambio*, 37 (7/8), 528-534.
- 1152 Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D.L., Darling, A., Höhna, S., Larget, B.,
1153 Liu, L., Suchard, M.A. & Huelsenbeck, J.P. (2012) MrBayes 3.2: efficient Bayesian
1154 phylogenetic inference and model choice across a large model space. *Systematic*.
1155 *Biology*, 61(3), 539–542.
- 1156 Rosenberg, N.A. (2004) DISTRUCT: a program for the graphical display of population
1157 structure. *Molecular Ecology Notes*, 4, 137-138.
- 1158 Saint Lucia Forests and Lands Resources Department (2015) *Strategy 2015–2025*. Saint Lucia
1159 Forests and Lands Resources Department, Union, Saint Lucia.
- 1160 Stephen, C.L., Reynoso, V.H., Collett, W.S., Hasbun, C.R. & Breinholt, J.W. (2013).
1161 Geographical structure and cryptic lineages within common green iguanas, *Iguana*
1162 *iguana*. *Journal of Biogeography* 1–13. doi: 10.1111/j.1365- 2699.2012.02780.x
- 1163 Tamura, K., Stecher, G., Peterson, D., Filipski A. & Kumar S. (2013) MEGA6: Molecular
1164 Evolutionary Genetics Analysis version 6.0. *Molecular Biology and Evolution*, 30,
1165 2725–2729.
1166 <http://dx.doi:10.1093/molbev/mst197>
- 1167 Torstrom, S.M., Pangle, K.L. & Swanson B.J. (2014) Shedding subspecies: The influence of
1168 genetics on reptile subspecies taxonomy. *Molecular Phylogenetics and Evolution*, 76,
1169 134–143.
1170 <http://dx.doi.org/10.1016/j.ympev.2014.03.011>
- 1171 Treglia, M.L. (2006) An annotated checklist of the amphibians and reptiles of St. Vincent,

1172 West Indies. *Iguana* 13: 251–262.

1173 Underwood, G. (1962) Reptiles of the Eastern Caribbean. *Caribbean Affairs* (N. S.), 1, 1–192.

1174 Valette, V., Filipova L., Vuillaume, B., Cherbonnel, C., Risterucci, A.M., Delaunay, C.,
1175 Breuil, M. & Grandjean, F. (2012) Isolation and characterization of microsatellite
1176 loci from *Iguana delicatissima* (Reptilia: Iguanidae), new perspectives for
1177 investigation of hybridization events with *Iguana iguana*. *Conservation Genetic*
1178 *Resources*, 5 (1), 173–175.
1179 <http://dx.doi.org/10.1007/s12686-012-9761-z>

1180 van den Burg, M., Breuil, M. & Knapp, C. (2018) *Iguana delicatissima*. The IUCN Red List of
1181 Threatened Species 2018: e.T10800A122936983.
1182 <http://dx.doi.org/10.2305/IUCN.UK.2018-1.RLTS.T10800A122936983.en>

1183 Vuillaume, B. (2012) Origine, différenciation et hybridation entre deux espèces d’iguane
1184 (*Iguana delicatissima* et *Iguana iguana*) dans les Petites Antilles. Master II
1185 ingénieur, Institut Supérieur Agronomique, Dijon, 51 pp.

1186 Vuillaume, B., Valette, V., Lepais, O., Grandjean, F. & Breuil, M. (2015) Genetic evidence of
1187 hybridization between the Endangered native species *Iguana delicatissima* and the
1188 invasive *Iguana iguana* (Reptilia, Iguanidae) in the Lesser Antilles: Management
1189 implications. *PLoS ONE* 10(6): e0127575. doi:10.1371/journal.pone.0127575.
1190 <https://doi.org/10.1371/journal.pone.0127575>

1191 Weir, B.S. & Cockerham, C.C. (1984) Estimating F-statistics for the analysis of population
1192 structure. *Evolution*, 38, 1358–1370.
1193 <http://dx.doi.org/10.2307/2408641>

1194 Wiegmann, A.F.A (1834) *Herpetologica Mexicana, seu Descriptio Amphibiorum Nova*
1195 *Hispaniae*. Berolini: Vol. 1, vi + 54 pp.

1196

1197 **Tables**

1198 **Table 1.** Genetic samples

1199

Locality/Status	Microsatellites	ND4	Genbank
SAINT LUCIA			
Soufriere/ Alien iguanas from Central America	IGU43		
	IGU44	IGU44	
	IGU45		
	IGU46	IGU46	
	IGU47	IGU47	
	IGU49		
		IGU50	
	IGU51		
Grand Anse/ Native iguanas	IGU52	IGU52	
	IGU53	IGU53	
	IGU55	IGU55	
	IGU56	IGU56	
Louvet/ Native iguanas	IGU57	IGU57	
	IGU58	IGU58	
	IGU59		
	IGU60		
	IGU61		
	IGU62		
	IGU63	IGU63	
	IGU64		
		IGU65	
	IGU67		
	IGU68		
	IGU69		
	IGU70		
	IGU71		
	IGU72		
ST VINCENT & THE GRENADINES			
Union Island/ Native iguanas	IGU73	IGU73	
		IGU74 (skin)	
Palm Island/ Native iguanas	IGU75	IGU75	
	IGU76	IGU76	
	IGU77	IGU77	
FRENCH GUIANA			
Trois-Sauts/ Native	IGU78	IGU78	
	IGU79	IGU79	
	IGU81		
French Guiana/ Native	IGU82	IGU82	
	IGU83		
	IGU84	IGU84	
	IGU85		

1200

1201

Table 2. Genetic diversity parameters for each locus

Expected heterozygosity (He); number of private alleles (PA); allelic richness (AR); and inbreeding coefficient (Fis) have been computed for each population and each locus using FSTAT ver. 2.9.3.2 software (Goudet 2001). In italics and bold: the Fis with significant departures from Hardy-Weinberg expectations (i.e. significantly different from 0; $P < 0.0008$ after Bonferroni adjustment).

		Saint Lucia Introduced <i>Iguana rhinolopha</i>	Saint Lucia endemic <i>Iguana insularis sanctaluciae</i>	Grenadines endemic <i>Iguana insularis insularis</i>	French Guiana <i>Iguana iguana</i>	All populations
	n	8	17	4	7	36
L2	He	0	0.265	0	0.262	0.132
	PA	0	0	0	0	-
	AR	1	1.647	1	1.692	1.91
	Fis	NA	0.778	NA	-0.091	0.343
L3	He	0.125	0	0	0	0.031
	PA	1	0	0	0	-
	AR	1.375	1	1	1	1.768
	Fis	0	NA	NA	NA	0
L5	He	0.690	0.272	0	0.524	0.371
	PA	2	0	0	0	-
	AR	2.874	1.779	1	1.99	2.738
	Fis	-0.448	0.351	NA	-0.091	-0.063
L6	He	0.429	0.217	0	0.524	0.2925
	PA	0	0	0	1	-
	AR	1.930	1.559	1	1.972	2.299
	Fis	-0.333	0.458	NA	0.727	0.284
L8	He	0.667	0	0	0.262	0.232
	PA	1	0	0	1	-
	AR	2	1	1	1.692	1.453
	Fis	0.5	NA	NA	-0.091	0.204
L9	He	0.652	0.217	0.75	0.607	0.556
	PA	0	0	0	1	-
	AR	2.604	1.559	2.929	2.692	2.972
	Fis	0.233	0.458	0.333	-0.412	0.153
L13	He	0	0.217	0.5	0	0.179
	PA	0	0	0	0	-
	AR	1	1.559	1.964	1	1.975
	Fis	NA	0.458	1	NA	0.729
L14	He	0.125	0.116	0	0.143	0.096
	PA	0	1	0	1	-
	AR	1.375	1.353	1	1.429	1.959
	Fis	0	-0.016	NA	0	-0.005
L15	He	0.393	0.059	0	0.679	0.28275
	PA	1	0	0	1	-

	AR	1.885	1.176	1	2.774	1.893
	Fis	-0.273	0	NA	0.158	-0.038
L16	He	0.81	0	0.25	0.143	0.301
	PA	2	0	1	0	-
	AR	3.375	1	1.75	1.429	2.06
	Fis	0.824	NA	0	0	0.275
L17	He	0.548	0.224	0	0.488	0.315
	PA	1	0	0	2	-
	AR	1.99	1.652	1	2.275	3.055
	Fis	0.478	0.475	NA	0.415	0.456
L18	He	0.339	0	0	0.533	0.218
	PA	1	0	0	1	-
	AR	1.786	1	1	1.998	1.667
	Fis	0.632	NA	NA	-0.25	0.191
L19	He	0.125	0.272	0	0.524	0.230
	PA	0	0	0	0	-
	AR	1.375	1.779	1	1.995	2.439
	Fis	0	0.351	NA	-0.364	-0.004
L20	He	0.571	0.224	0	0.655	0.3625
	PA	1	0	0	3	-
	AR	2.348	1.652	1	2.827	3.213
	Fis	-0.094	0.475	NA	-0.091	0.097
L23	He	0.4	0.272	0	0.821	0.373
	PA	0	0	0	3	-
	AR	1.909	1.779	1	3.552	3.071
	Fis	-0.25	0.351	NA	0.304	0.135
L24	He	0	0	0	0	0
	PA	0	0	0	0	-
	AR	1	1	1	1	1
	Fis	NA	NA	NA	NA	NA
All loci	He	0.367	0.147	0.094	0.385	0.248
	PA	10	1	1	14	-
	AR	1	1	1	1	1
	Fis	0.156	0.425	0.5	0.034	0.279

1208
1209

Table 3. Pairwise Fst values for each population comparison (below diagonal) and their significance level (above diagonal).

P-value threshold is adjusted with the Bonferroni correction, P= 0.0083.

	Saint Lucia Introduced <i>Iguana rhinolopha</i>	Saint Lucia endemic <i>Iguana insularis sanctaluciae</i>	Grenadines endemic <i>Iguana insularis insularis</i>	French Guiana <i>Iguana iguana</i>
Introduced Saint Lucia	-	0.0083	0.1083	0.0667
Saint Lucia endemic	0.6846	-	0.0583	0.0083
Grenadines endemic	0.6448	0.1051	-	0.0083
French Guiana	0.5048	0.5472	0.4832	-

Table 4. Admixture coefficient inferred by STRUCTURE software for the four studied populations.

	Cluster 1	Cluster 2	Cluster 3
Introduced Saint Lucia <i>Iguana rhinolopha</i>	0.941 (±0.153)	0.056 (±0.151)	0.003 (±0.002)
Saint Lucia endemic <i>Iguana insularis sanctaluciae</i>	0.064 (±0.142)	0.072 (±0.196)	0.864 (±0.324)
Grenadines endemic <i>Iguana insularis insularis</i>	0.011 (±0.015)	0.025 (±0.025)	0.964 (±0.037)
French Guiana <i>Iguana iguana</i>	0.003 (±0.001)	0.994 (±0.001)	0.003 (±0.001)

1221 Figures

1222 FIGURE 1. Drawing by Provancher (1890) of a stuffed iguana on Saint Lucia.

1223 Provancher identified it as *Iguana delicatissima* (see text), but the body and tail seem to have vertical
 1224 black stripes, and there are small and scattered tubercular nape scales, and no subtympanic plate. There
 1225 is no tympanum and no nasal horns on this drawing, which also shows a forked tongue.
 1226

1227
 1228

FIGURE 2. Distribution of the three iguana groups identified by Lazell (1973).

Based on a clinal variation of their morphology, Lazell (1973) identified at the beginning of the Sixties 3 groups of the Common Iguana *Iguana iguana* that he thought to be native in Lesser Antilles. At that time, the central group was known to be present only in Guadeloupe (Les Saintes, Basse-Terre and Grande-Terre). This group is not native and is the descent of invasive common iguanas from French Guiana Breuil 2016; Vuillaume *et al.* 2015). Now, however, alien iguanas from Central and South America are present throughout most of this region (van den Burg *et al.* 2018) except Saint Christopher and Nevis, Dominica, Petite Terre and some satellites of Saint Barthélemy, Anguilla, and Martinique. The Southern Group is described in this work as a new species *Iguana insularis*.

1241 **FIGURE 3. Holotype of *Iguana insularis insularis* ssp. nov.**

1242 MCZ X-17620/R-79057 © Museum of Comparative Zoology, Harvard University. Specimen in alcohol
1243 with discolouration. Annotations: 1. Small size of subtympenic plate $\pm$ 10-20% of the eardrum. 2. Two
1244 to three scales of decreasing size anterior to subtympenic plate. 3. Juxtaposed elongated sublabial scales
1245 5. Median and lateral horns on the snout. 6. Horns with enlarged bases. 7. Oval and prominent nostrils.
1246 9. Flat and triangular gular spikes. 10. Six gular spikes. 11. Scattered nuchal tubercles. 12. Low number
1247 of nuchal tubercles. 13. Small size of nuchal tubercles. 15. Dewlap of medium size.
1248

1249
1250
1251

FIGURE 4. Examples of adult male *Iguana insularis insularis* ssp. nov.

Top left. Adult male sequenced under the number IGU75 (SVL 41 cm); Top right and bottom, adult male sequenced under the number IGU77 (SVL 45 cm). Annotations: 1. Small size of subtympenic plate $\pm 10\text{-}20\%$ of the eardrum. 2. Two or three scales of decreasing size anterior to subtympenic plate. 3. Juxtaposed elongated sublabial scales. 4. No apparent swelling of the jowls in breeding males. 5. Median and lateral horns on the snout. 6. Horns with enlarged bases. 7. Oval and prominent nostrils. 8. Brown eyes with visible white. 9. Flat and triangular gular spikes. 10. Seven or eight gular spikes. 11. Scattered nuchal tubercles. 12. Low number of nuchal tubercles. 13. Small size of nuchal tubercles. 14. Orange in dorsal scales in breeding animals. 15. Creamy white dewlap of medium size. 16. Creamy white body with faint to no black banding in old individuals.

1266 **FIGURE 5. Nasal horns of *Iguana insularis insularis* ssp. nov.**

1267 View of the snout of IGU75 (left) and IGU77 (right) from Palm Island (same individuals as Fig. 4).
 1268 Annotations: 0. Frontal scale not developed into a horn. 1. Median horns with enlarged bases. 2. Lateral
 1269 horns. 3. Oval prominent nostril. Note the differing forms and disposition of cephalic scales, and that
 1270 IGU75 (a younger male) has flat scales whereas IGU77 (an older, larger male) has more prominent
 1271 scales.
 1272

1273
 1274

FIGURE 6. Distribution of iguanas in the Grenadine islands.

Locations are mapped to the nearest 2x2 km square representing groups of islands in the Grenadines. We have deliberately avoided being specific to protect the animals (see Auliya *et al.* 2016). Note that there are alien iguanas on some islands and not all of the island clusters shown here have purebred populations of *Iguana insularis insularis*. We have no confirmed specific localities for the main island of Grenada, although a museum specimen (MCZ R-79747) confirms this subspecies occurred here. Henderson & Breuil (2012), Henderson & Powell (2018), Baldwin (2012) and Baldwin & Mahon (2011), G. Gaymes and J. Daltry (pers. obs.; the Grenadines). While iguanas are present on St. Vincent, these have not been identified to subspecies level and cannot be assumed to be identical to those on the Grenada Bank. The grey line just south of St Vincent marks the brake between the St. Vincent Bank to the north and the Grenada Bank to the south. The black line between Petit Saint Vincent and Petit(e) Martinique shows the political boundary between St. Vincent and the Grenadines to the north and Grenada to the south. The Grenadine islands form an archipelago from the south of St. Vincent to the north of Grenada.

1292 **FIGURE 7. Holotype and paratype of *Iguana insularis sanctaluciae***

1293 The holotype MNHN2362 is top left and the paratype MNHN 1996.8276 is top right. Both specimens
 1294 collected by Bonnecour(t) in 1850-51 in Saint Lucia. Note the nasals (median and lateral horns), the
 1295 small subtympanic plate, the low number of small nuchal tubercles, the 7 gular spikes, the prominent
 1296 oval nostril, the banded body.
 1297

1298
 1299
 1300

FIGURE 8. Ontogenetic change in colour of *Iguana insularis sanctaluciaae*

Young male (left), old male (right). Annotations: 1. Small subtympnic plate $\pm 10\%$ of the eardrum. 2. Two or three scales of decreasing size anterior to subtympnic plate. 3. Low number of sublabial scales with black margins. 4. No swelling of the jowls in breeding males. 5. Lateral and median horns. 6. Median horns with enlarged bases. 7. Oval to rounded nostril. 8. Brown eye with the white of the eye visible. 9. Triangular gular spikes. 10. 7 gular spikes. 11. Dispersed nuchal tubercles. 12. Low number of nuchal tubercles. 13. Small size of nuchal tubercles. 14. Orange in first dorsal spikes in breeding animals. 15. Entirely black dewlap in old adults. 16. Body and tail black and bright green in young individuals and very light green to almost pale greenish grey in old adults. Old individuals may look nearly “black and white”.

FIGURE 9. Horned iguanas from the Central American clade of the “*rhinolopha*” phenotype

Photographed from invasive introduce populations in the Lesser Antilles: young male caught on Saint Maarten (left); old male caught in Saint Lucia (right). Annotations: 1. Huge subtympenic plate, 2 to 3 times the size of the eardrum. 2. A half crown of sublabial scales around the subtympenic plate and the first scale anterior to subtympenic plate. 3. Mosaic of sublabial scales. 4. Swelling of the jowls in breeding male. 5. Generally 2-3 small median horns and no lateral horns. 6. Flat small horns. 7. Triangular nostril. 8. Yellow to dark orange eye with not the white visible. 9. Triangular gular spikes. 10. Number of gular spikes ≥ 10 . 11. Nuchal tubercles appear to be organised in rows. 12. High number of nuchal tubercles. 13. Very large nuchal tubercles. 14. Yellow, orange to red dorsal scales on the whole body in breeding males. 15. Variable size and colour of the dewlap but often large and not uniform black (cf. *I. insularis sanctaluciae*) or creamy white (cf. *I. insularis insularis*). 16. Body orange to red in breeding males, green in other individuals, and not heavily banded. This phenotype is recognised in this paper as a full species, *I. rhinolopha*, native to Central America (see text).

FIGURE 10. Adult breeding males *I. insularis sanctaluciae* and *I. rhinolopha*.

The endemic Saint Lucia horned iguana (*I. insularis sanctaluciae*, photo from Grand Anse, top) is clearly different from the Central America horned iguana (*I. rhinolopha*: this specimen was photographed from an introduced population on Sint Maarten by M. Yokoyama, bottom) by size, body proportion, body colour, size and form of the horns, eye colouration, scalation of the jowls, and dewlap size, colour and form.

FIGURE 11. Distribution of iguanas on Saint Lucia.

Locations are mapped to the nearest 1x1 km square. Data come from Morton *et al.* (2007; Saint Lucia). Black squares, Saint Lucia endemic iguana, Grey squares, alien iguana from Central America clade. “False absences” were minimized by interviewing persons about iguana presence in grid squares confirmed independently, through sightings and captures by us, to have iguanas present. We rejected some reported sightings of native iguanas, shown here as open grid squares, as being iguanas captured for food or pets or reports based on misidentification (for example on the islet of Maria Major off the far south of Saint Lucia; J. Lazell, *in litt.* 2010). Some of the reports that were accepted from the interior of the northern half of Saint Lucia may also be suspect, though they are all below 300 m ASL. These patterns of distribution suggest that the mountainous interior of Saint Lucia may create at least a partial barrier to direct east-west movements of iguanas.

FIGURE 12. Phylogenetic tree

Based on mtDNA of 23 iguanas (21 from this study, 2 from GenBank). Four clades are identified. *Iguana delicatissima* (AF217783) serves as the outgroup. The monophyly of Lazell's Southern Lesser Antilles group, characterised by horns, is described here as a new species *Iguana insularis*. The horned iguanas from Central America are also considered here as a full species *I. rhinolopha*. The sister group of *I. insularis* is *I. iguana* (based on specimens shown here from French Guiana). This phylogenetic tree shows that *I. iguana* is present as an invasive alien species in the Grenadines (IGU74) and that there is *I. delicatissima* mitochondrial DNA in some samples of *I. insularis sanctaluciae*. The ML tree with the highest log likelihood is shown. Node supports were indicated by bootstrap values from ML (>70) and posterior probability from BI (>0.95).

1370 **FIGURE 13. Median-Joining haplotype network**

1371 Based on 23 mtDNA sequences of *Iguana* (21 from this study, 2 from GenBank). Black circles are
 1372 median vectors that represent extinct or unsampled haplotypes. Numbers of mutational steps are
 1373 indicated by hatch marks.

1374

1375

1376

FIGURE 14. Factorial Correspondence Analysis (FCA) of the genotypes of samples from four populations

Black squares: individuals introduced in Saint Lucia (*Iguana rhinolopha*) [n=8] circles: individuals endemic to Saint Lucia (*Iguana insularis sanctaluciaae*), with white circles for individuals from Louvet (n=13) and hatched circles for individuals from Grand Anse (n=4); white triangles: individuals endemic to Grenadines (*Iguana insularis insularis*), [n=4]; and grey stars: individuals from French Guiana (*Iguana iguana*) [n=7]. Only 7 circles are shown for the 17 'native' individuals from Saint Lucia because many individuals from Louvet and one from Grand Anse had the same genotypes.

FIGURE 15: Results from the Evanno's Method using the STRUCTURE HARVESTER software.

This analysis reveals a maximum likelihood for K=3.

FIGURE 16. STRUCTURE bar plot

Showing admixture coefficient of each individual to the three inferred genetic clusters. This bar plot was produced using the DISTRUCT program (Rosenberg 2004).

FIGURE 17. Nesting periods of various iguana populations.

Monthly mean precipitation is indicated in mm. Precipitation varies according to altitude and aspect, but the important point is that after a 3 months incubation period, the eclosions occur at the beginning or during the rainy season. The brackets indicate the main laying period for the different species at different insular and continental locations. Note that the nesting period of *Iguana insularis sanctaluciaae* overlaps the laying periods of both *Iguana delicatissima* and *Iguana iguana*, which suggests that mating periods could also overlap, potentially enabling all three species to interbreed.