
Systematics, biogeography and evolution of the endemic *Hemidactylus* geckos (Reptilia, Squamata, Gekkonidae) of the Cape Verde Islands: based on morphology and mitochondrial and nuclear DNA sequences

E. N. ARNOLD, R. VASCONCELOS, D. J. HARRIS, J. A. MATEO & S. CARRANZA

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A total of 1854 bp of mitochondrial DNA (669 bp of cytochrome *b* (*cyt b*) and 386 bp of 12S rRNA), and 804 bp of a nuclear gene (RAG2) were investigated in endemic *Hemidactylus* from eight Cape Verde Islands, and used to explore their phylogeny, biogeography and evolution. Maximum-likelihood, maximum-parsimony and Bayesian analyses based on mtDNA revealed four well-supported clades with uncorrected genetic divergences of 7.8–12.4% in the *cyt b* plus 12S rRNA genes, which were also supported by nuclear DNA. A population from the southern island of Fogo is the most divergent in both molecules and morphology and is described as *Hemidactylus lopezjuradoi* sp. n., and the populations on Sal and Boavista are also assigned species status as *H. boavistensis*. Although divergent in their DNA, the clade on S. Nicolau and that in the north-western islands are morphologically similar and both are assigned to *H. bowvieri* for the present. *Hemidactylus b. razoensis* from Raso is genetically similar to *H. b. bowvieri* and differs only in its smaller body size. A molecular clock suggests that the ancestor of the endemic *Hemidactylus* of the Cape Verde Islands colonized the archipelago approximately 10 ± 2.48 Mya, perhaps reaching the north-eastern islands first. The *H. lopezjuradoi* lineage separated soon after, and the north-western islands were colonized progressively but slowly, S. Nicolau probably being reached first, then S. Vicente and islands on the same bank, and finally Sto. Antão, which is likely to have been colonized less than 1 Mya. *Hemidactylus boavistensis* is abundant on the arid islands where it occurs, but *H. bowvieri* appears to have been uncommon at least since it was described 130 years ago, and the same may be true of *H. lopezjuradoi* sp. n. The impact of introduced *H. angulatus* and *H. mabouia* on the endemic *Hemidactylus* of the Cape Verde Islands is not clear, but the discovery of substantial genetic diversity in endemic Cape Verde *Hemidactylus* means that the conservation requirements of the group should be reassessed.

Corresponding author: Salvador Carranza, Departament de Biologia Animal, Universitat de Barcelona, Avenue. Diagonal 645, E-08028 Barcelona, Spain. E-mail: scarranza@ub.edu
E. Nicholas Arnold, Department of Zoology, The Natural History Museum, SW7 5BD, London, UK. E-mail: ena@nhm.ac.uk

Raquel Vasconcelos, CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, Campus Agrário de Vairão, R. Padre Armando Quintas, 4485-661 Vairão, Portugal; Faculdade de Ciências da Universidade do Porto Pr. Gomes Teixeira, 4099-002 Porto, Portugal. E-mail: raquel.vasconcelos@mail.icav.up.pt

D. James Harris, CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, Campus Agrário de Vairão, R. Padre Armando Quintas, 4485-661 Vairão, Portugal. E-mail: james@mail.icav.up.pt

J. Antonio Mateo, Centro de Recuperación del Lagarto Gigante de La Gomera; Antoncojo, E-38870 Valle Gran Rey, Canary Islands, Spain. E-mail: mateosaurus@terra.es

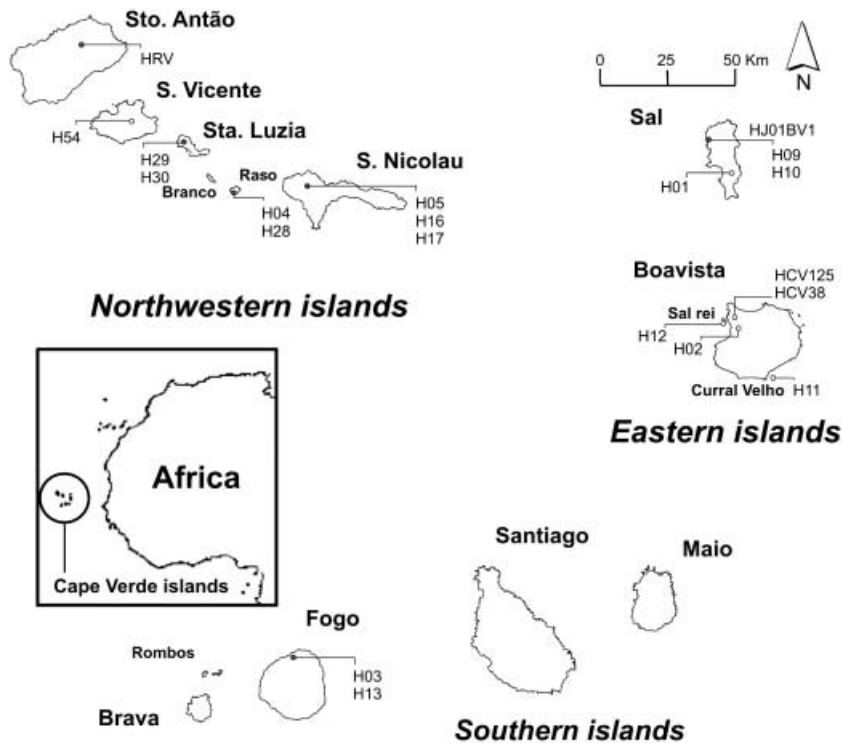


Fig. 1 Map of the Cape Verde islands showing the origins of the *Hemidactylus* samples included in the analyses. Unfilled circles indicate samples used by Jesus *et al.* (2001) and Carranza & Arnold (2006); filled circles are additional specimens used in the present study.

Introduction

Animal and plant lineages that colonize oceanic archipelagos often disperse through them and diversify on different islands. If phylogenies based on DNA sequence are available, the pattern of dispersal can sometimes be reconstructed. Phylogenies also permit reassessment of previous systematics, which are usually based only on morphology. For reptiles, this has been done in several archipelagos for a variety of taxa including the Macaronesian islands: gekkonids (Joger 1984, 1985; Nogales *et al.* 1998; Carranza *et al.* 2000, 2002; Gübitz *et al.* 2000; 2005); lacertids (Brehm *et al.* 2003; Maca-Meyer *et al.* 2003) and scincids (Brown *et al.* 2000; Carranza *et al.* 2008a). Studies focusing on the Cape Verde Islands include ones on *Tarentola* geckos (Carranza *et al.* 2000, 2002; Jesus *et al.* 2002) and *Mabuya* skinks (Brehm *et al.* 2001; Brown *et al.* 2001; Carranza *et al.* 2001; Carranza & Arnold 2003), the investigations revealing considerable cryptic variation in the taxa concerned. Here we consider a third taxon in the Cape Verde archipelago, the endemic geckos of the genus *Hemidactylus*. To date, investigation of endemic Cape Verde *Hemidactylus* has been very limited. A study of mitochondrial DNA included samples of *H. bouvieri* from just two islands, Boavista and Sal (Jesus *et al.* 2001), and a broader investigation of *Hemidactylus* added one from S. Vicente (Carranza & Arnold 2006). Both investigations revealed high genetic divergence between islands. Assessing their genetic diversity

and phylogeny, is not only helpful in elucidating their history and dispersal and comparing these with those of other taxa, but also in designing conservation strategies for these geckos. These strategies are necessary because some endemic populations of Cape Verde *Hemidactylus* are regarded as rare (*H. bouvieri bouvieri*) and in one case critically endangered (*H. bouvieri razoensis*) and in urgent need of protection (Schleich 1996).

The Cape Verde Islands are an oceanic archipelago located approximately 450 km from the West African coast. They comprise 10 main islands plus eight islets that are arranged in a deep arc with its concavity facing westwards (Fig. 1). The archipelago is volcanic (the last eruption occurred on Fogo in 1995), and has never been connected to the neighbouring mainland (Mitchell-Thomé 1976). Radiometric dating, based on potassium/argon (K/Ar) and on argon isotopes (^{40}Ar - ^{39}Ar), indicates the islands decrease in age from east to west. Sal is about 25.6 ± 1 million years (My); Maio 21.1 ± 6.3 My and Santiago 10.3 ± 0.6 My. The youngest islands at the westward tips of the arc, Sto. Antão and Brava, are about 7.56 ± 0.56 and 5.9 ± 0.1 My, respectively, and S. Vicente is about 6.1 My (dates from Griffiths *et al.* 1975; Grunau *et al.* 1975; Mitchell-Thomé 1976; Stillman *et al.* 1982; Mitchell *et al.* 1983; Carracedo 1999; Torres *et al.* 2002; Plesner *et al.* 2002). The presence of shallow banks joining some islands indicates that these would have been continuous during the

intermittent sea level falls in the last 1.6 My that have characterized the Pleistocene epoch. This is true of a group of north-western islands, including S. Vicente, Sta. Luzia, Branco and Raso, which are separated by depths of less than 50 m and may possibly also apply to the eastern islands of Boavista and Maio (Morris 1989).

At present only a single endemic species of *Hemidactylus* is recognized from the Cape Verde Islands: *Hemidactylus bowvieri* Bocourt (1870). This gecko is small, the largest animals only growing to about 50 mm from snout to vent, and is characterized by its pointed snout, absence of enlarged tubercles on the dorsum of the head, body and tail, in having femoral pores in males reduced in number to one on each side in front of the vent, and in often possessing a dorsal pattern of few transverse bands that are darker than the background colour, although there is considerable variation in detail. *Hemidactylus bowvieri* has three currently recognized subspecies (Schleich 1987). *Hemidactylus bowvieri bowvieri* Bocourt (1870) described originally from S. Vicente is also recorded as occurring on Sto. Antão, Santiago, Fogo and Brava; *Hemidactylus bowvieri boavistensis* Boulenger (1906) described from Boavista is also found on Sal; and *Hemidactylus bowvieri razoensis* Gruber & Schleich (1982) is reported only from Raso and Sta. Luzia (Mateo et al. 1997). *Hemidactylus b. bowvieri* grows to less than 40 mm from snout to vent and has 3–4 scensors and enlarged scales under the first toe and 4–5 under the fourth; *H. b. boavistensis* reaches around 50 mm and has higher digital scensor counts of 5–6 and 6–8, respectively; *H. b. razoensis* is very small, not exceeding 29 mm and has similar scensor counts to *H. b. bowvieri*. It is also said to be distinctive in the first upper labial scale not reaching the lower border of the nostril. Recently, a population of *H. bowvieri* has been reported from S. Nicolau (López-Jurado et al. 2005; Köhler et al. 2007; J. A. Mateo and Ph. Geniez unpubl. data) but it has not been ascribed to any of the subspecies. A further morphologically distinctive form was found on Fogo in 1997 by J. A. Mateo and P. Geniez. Its taxonomic status is discussed later in this paper.

Two other species of *Hemidactylus* are present in the Cape Verde archipelago and are believed to have been introduced there by people, as genetically similar populations occur on the mainland of Africa, where both species have wide distributions. *Hemidactylus angulatus* Hallowell 1852 (in the sense of Carranza & Arnold 2006) is known from Boavista (Mertens 1955; López-Jurado et al. 1999), Santiago (Fea 1898; Mertens 1955; Carranza & Arnold 2006), S. Nicolau (Jesus et al. 2001), S. Vicente (Mertens 1955; Schleich 1982, 1987, 1996; Andreone 2000) Sto. Antão (Schleich 1982; Jesus et al. 2001, 2005; Carranza & Arnold 2006), and perhaps Maio (Schleich 1982) and Sta. Maria islet (Schleich 1987), while a population on Sal appears to represent an independent introduction (Carranza & Arnold 2006). It is also

reported from Fogo (Fea 1899a; Angel 1937; Schleich 1987), Brava (Mertens 1955; Schleich 1982, 1987, 1996) and Rombos islets (Mertens 1955; Schleich 1982, 1996). The second species, *H. mabouia*, was first reported from S. Vicente (Jesus et al. 2001), but is also present on the neighbouring island of Sto. Antão and on Brava (R. Vasconcelos unpubl. data).

In the present work, molecular and morphological study of endemic Cape Verde *Hemidactylus*, coverage was extended to eight islands, using fragments of two mitochondrial genes: 669 bp (base pairs) of cytochrome *b* (*cyt b*), comprising two fragments of 303 and 366 bp; and 381–386 bp of 12S rRNA. Since mitochondrial DNA (mtDNA) alone can occasionally be misleading when investigating relationships (Shaw 2002; Alves et al. 2006), an independent nuclear marker was also investigated, namely the Recombination Activating Gene 2 (RAG2). The resultant phylogenies are also used to estimate dates of events in the dispersal of endemic Cape Verde geckos.

Abbreviations. BMNH, prefix of registered numbers of specimens deposited in the reptile collection of the Natural History Museum, London. Mya, millions of years ago. My, millions of years.

Materials and methods

Samples, DNA extraction, amplification and sequencing

Identifications, localities and GenBank accession numbers of the samples used are listed in Table 1. Where voucher specimens are available, they have been deposited in the Natural History Museum, London.

Total genomic DNA was extracted from small pieces of tail using standard methods, following Carranza et al. (1999). Polymerase Chain Reaction (PCR) primers used in both amplification and sequencing were 12Sa and 12Sb for the 12S rRNA gene (Kocher et al. 1989) and *cyt b1*, *cyt b2* (Kocher et al. 1989), the forward primer of *cyt b2* (*cyt b2F*) and a modified version of CB3-3' (Palumbi et al. 1996) (5'-TGG GAT TGA TCG TAG GAT GGG GTA-3') for the *cyt b* gene. For the nuclear marker, two pairs of primers were used: 31 FN venk, LUNG 460R (Chiari et al. 2004) for the first PCR and RAG2 LUNG 35F and RAG LUNG 320R (Hoegg et al. 2004) for the second. For 12S and *cyt b*, PCR conditions were the same as those used by Harris 2001). For RAG2 an initial denaturation step of 94 °C for 2 min was used, followed by 35 cycles comprising 94 °C for 30 s, 53 °C (annealing temperature) for 40 s, 68 °C (extending temperature) for 2.5 min and then a final extension at 68 °C for 5 min. Amplified mitochondrial and nuclear fragments were sequenced from both strands on a 310 Applied Biosystems DNA Sequencing Apparatus.

Phylogenetic analyses

For the phylogenetic analyses three data sets were used. Data set 1 was used to assess the monophyly of endemic Cape

Table 1 Locality codes (see Fig. 1), taxa, location (country, region and locality) and GenBank accession numbers for the nuclear (RAG2) and mitochondrial markers (two fragments of *cyt b* plus 12S rRNA) used in the phylogenetic analyses.

Code Fig. 1	Taxon	Country	Island/Region	Locality	RAG2	<i>cyt b1</i>	<i>cyt b2</i>	12S
	<i>Tarentola americana</i>		Cuba	Guantánamo		AF184991		AF186119
	<i>T. angustimentalis</i> — 9	Spain (Canary Islands)	Fuerteventura	Fuste		AF184993		AF186121
	<i>T. b. boettgeri</i> — 3	Spain (Canary Islands)	Gran Canaria	Arinaga		AF184997		AF186125
	<i>T. b. hierrensis</i> — 7	Spain (Canary Islands)	El Hierro	Tamaduste		AF184998		AF186126
	<i>T. b. hierrensis</i> — 8	Spain (Canary Islands)	El Hierro	Los Llanillos		AF184999		AF186127
	<i>T. b. bischoffi</i> — 6	Portugal (Selvagens)	Selvagem Grande	Selvagem Grande		AF185000		AF186128
	<i>T. b. boettgeri</i> — 4	Spain (Canary Islands)	Gran Canaria	Tauro		AF184996		AF186124
	<i>T. b. boettgeri</i> — 5	Spain (Canary Islands)	Gran Canaria	Tauro		AF184995		AF186123
Hag1	<i>H. agrius</i> — 45	Brazil	Genipabu	Touros, Genipabu	EF540746	DQ120262		DQ120433
Hag2	<i>H. agrius</i> — 46	Brazil	Piauí	Dom Expedito Lopes	EF540746	DQ120261		DQ120432
Hpa	<i>H. palaichthus</i> — 44	Trinidad		Chacachaare		DQ120263		DQ120434
Hgr	<i>H. greeffi</i> — 63	S. Tomé e Príncipe	Príncipe			DQ120244		DQ120415
Bbr	<i>H. brasiliensis</i> — 50	Brazil	Piauí	Dom Expedito Lopes		DQ120257		DQ120428
Hlo	<i>H. longicephalus</i> — 61	S. Tomé e Príncipe	S. Tomé			DQ120245		DQ120416
Hpl	<i>H. platycephalus</i> — 41	Kenya	Kajiado	Rift Valley	EF540745	DQ120266		DQ120437
Hhaitl	<i>H. haitianus</i> — 92	Cuba	Cuba	Matanzas		DQ120216	EU730676	DQ120387
H03	<i>H. lopezjuradoi</i> sp. n. — 1	Cape Verde	Fogo	Ribeira Ilhéu — Atalaia	EU730681	EU730650	EU730660	EU730639
H13	<i>H. lopezjuradoi</i> sp. n. — 2	Cape Verde	Fogo	Ribeira Ilhéu — Atalaia	EU730682	EU730651	EU730660	EU730640
H05	<i>H. bouvieri</i>	Cape Verde	S. Nicolau	Cachaço	EF540737	EU730652	EU730661	EU730641
H16	<i>H. bouvieri</i>	Cape Verde	S. Nicolau	Cachaço	EF540742	EU730653	EU730662	EU730642
H17	<i>H. bouvieri</i>	Cape Verde	S. Nicolau	Cachaço	EF540743	EU730654	EU730663	EU730643
H04	<i>H. b. razoensis</i> — 2	Cape Verde	Raso	Chã do Castelo	EF540738	EU730655	EU730664	EU730644
H28	<i>H. b. razoensis</i> — 3	Cape Verde	Raso	Chã do Castelo	EF540740	EU730656	EU730665	EU730645
H29	<i>H. b. razoensis</i> — 4	Cape Verde	Sta. Luzia	Ribeira Penedo	EU730683	EU730657	EU730666	EU730646
H30	<i>H. b. razoensis</i> — 1	Cape Verde	Sta. Luzia	Ribeira Penedo	EU730684	EU730658	EU730667	EU730647
H54	<i>H. b. bouvieri</i> — 2	Cape Verde	S. Vicente	—		DQ120253	EU730668	EU730648
HRV	<i>H. b. bouvieri</i> — 1	Cape Verde	Sto. Antão	Lombo de Diogo	EF540744	EU730659	EU730669	EU730649
H01	<i>H. boavistensis</i> stat. rev. — 2	Cape Verde	Sal	Bunalema	EU730677	DQ120247	EU730670	DQ120418
H09	<i>H. boavistensis</i> stat. rev. — 3	Cape Verde	Sal	Buracona		DQ120248	EU730671	DQ120419
H10	<i>H. boavistensis</i> stat. rev. — 1	Cape Verde	Sal	Buracona		DQ120249	EU730672	DQ120420
H02	<i>H. boavistensis</i> stat. rev. — 5	Cape Verde	Boavista	Ribeira	EU730678	DQ120251	EU730673	DQ120422
H11	<i>H. boavistensis</i> stat. rev. — 4	Cape Verde	Boavista	Curral Velho islet	EU730679	DQ120251	EU730674	DQ120422
H12	<i>H. boavistensis</i> stat. rev. — 6	Cape Verde	Boavista	Sal Rei islet	EU730680	DQ120250	EU730675	DQ120421
HJ01BV1	<i>H. boavistensis</i> stat. rev. — 9	Cape Verde	Sal	—		AF324811	—	AF324812
HCV38	<i>H. boavistensis</i> stat. rev. — 7	Cape Verde	Boavista	Vila de Sal Rei		AF324809	—	AF324810
HCV125	<i>H. boavistensis</i> stat. rev. — 8	Cape Verde	Boavista	Vila de Sal Rei		AF324807	—	AF324808

Verde *Hemidactylus* and to estimate dates of divergence. It consisted of 689 bp of mtDNA (303 bp of *cyt b* — the *cyt b1* fragment — and 386 bp of 12S rRNA) from 20 individuals of Cape Verde *Hemidactylus* (including three from Jesus *et al.* 2001), seven individuals from five other members of the African-Atlantic clade of the genus (Carranza & Arnold 2006), eight individuals of three species of *Tarentola* geckos (Carranza *et al.* 2002), used to calibrate the tree, and one *Teratoscincus scincus keyserlingi*, which was used to root it. In data set 1, 380 positions were variable and 306 parsimony-informative. Data set 2 was mainly employed to assess relationships within endemic Cape Verde *Hemidactylus* and consisted of 1050 bp of mtDNA (669 bp of *cyt b* – 303 bp of the *cyt b1* and 363 bp of the *cyt b2* fragments, and 381 bp of 12S rRNA) for 17 individuals of endemic Cape Verde *Hemidactylus* from eight islands. In this data set, 332 positions were variable

and 208 parsimony-informative. *Hemidactylus haitianus* Meerwarth 1901 was used as an outgroup, in preference to closer relatives of the Cape Verde taxa in the African-Atlantic clade of *Hemidactylus*, as it proved difficult to amplify the 363 bp of the *cyt b2* fragment of *cyt b* for these. Data set 3 was used as an independent test of results from data set 2 and consisted of 804 bp of the nuclear RAG2 gene.

The most appropriate model of sequence evolution for the first data set was estimated using MODELTEST v3.06 (Posada & Crandall 1998) to be the GTR + I + Γ for the combined mtDNA genes (*cyt b* + 12S), the GTR + Γ model for the 12S rRNA, and the GTR + I + Γ model for the *cyt b*. For data set 2 the most appropriate model was K81uf + I + G for the combined mtDNA genes (*cyt b* + 12S) analyses, and the HKY + G for the 12S rRNA and the GTR + I + Γ for the *cyt b*. Genetic distances were calculated using MEGA 3.0 (Kumar *et al.* 2004).

All sequences were aligned with previously published ones for Cape Verde *Hemidactylus* and their outgroups using CLUSTALX (Thompson *et al.* 1997) with default parameters (gap opening = 10; gap extension = 02). All the *cyt b* sequences had the same length and therefore no gaps were postulated for this gene, although some were used to resolve length differences in the 12S rRNA gene fragment. All positions from both mtDNA data sets were included in the analyses.

Three methods of phylogenetic analysis, maximum-likelihood (ML), maximum-parsimony (MP) and Bayesian analysis, were employed and their results compared. The ML analysis was performed using both PAUP* (Swofford 1998) and PHYML (Guindon & Gascuel 2003) with model parameters fitted to the data by likelihood maximization. MP and ML analyses in PAUP* (Swofford 1998) included heuristic searches with TBR branch swapping and 100 random addition replicates. For the MP analyses, transitions and transversions were given the same weight and gaps were treated as a fifth state. Reliability of the ML and MP trees was assessed by bootstrap analysis (Felsenstein 1985) performed with 1000 replications.

Bayesian analyses were performed with MRBAYES v3.1.2 (Huelsenbeck & Ronquist 2001). Four incrementally heated Markov chains with default heating values were used. All analyses started with randomly generated trees and ran for 1.5×10^6 generations, with sampling occurring at intervals of 100 generations, producing 15 000 trees. After the analyses, the log-likelihood values of all trees saved from both runs were plotted against the generation time. After verifying that stationarity had been reached both in terms of likelihood scores and parameter estimation, the first 5000 trees for all three data sets were discarded from both runs, and independent majority-rule consensus trees were generated from the remaining (post burn-in) trees. The frequency of any particular clade of the consensus tree represents the posterior probability of that node (Huelsenbeck & Ronquist 2001); only values equal or above 95% were considered to indicate that nodes were significantly supported (Wilcox *et al.* 2002).

In order to assess the relations shown by the mitochondrial marker between individuals belonging to the different island groups, a network analysis based on 804 bp of RAG2 was performed for the third data set using the program TCS v2.1 (Clement *et al.* 2000). RAG2 sequences contained no indels.

Topological incongruence among partitions was tested using the incongruence length difference (ILD) test (Michkevich & Farris 1981; Farris *et al.* 1994). In this test, 10 000 heuristic searches were carried out after removing all invariable characters from the data set (Cunningham 1997). To test for incongruence among data sets, we also used a reciprocal 70% bootstrap proportion (Mason-Gamer & Kellogg 1996) or a 95% posterior probability threshold. Topological conflicts were considered significant if two different relation-

ships for the same set of taxa were both supported with bootstrap values $\geq 70\%$ or posterior probability values $\geq 95\%$.

Estimating divergence times

Divergence times were estimated for the different lineages recovered by the analysis of the first data set using the computer program r8sb v1.6.4 (Sanderson 1997, 2003). This program implements several methods for estimating absolute rates of molecular evolution, ranging from standard ML ones to more experimental semiparametric and nonparametric methods, which relax the stringency of the clock assumptions using smoothing methods. One of the advantages of this program is that, through a cross-validation test, it allows the user to explore the fidelity with which any of these methods explain the branch length variation (Sanderson 2003). This procedure removes each terminal branch in turn, estimates the remaining parameters of the model without that branch, predicts the anticipated number of substitutions on the pruned branch and reports the performance of these predictions as a cross-validation score, which allows the user to select the method that best explains the branch length variation (Sanderson 2003). To estimate absolute rates, we used a single calibration point based on the assumption that divergence between *Tarentola boettgeri hierrensis* Joger & Bischoff 1983 (endemic to the island of El Hierro) and *Tarentola boettgeri bischoffi* Joger (1984) (endemic to the Selvagens Islands) began approximately 1 Mya, soon after El Hierro was formed, and rapid colonization from Selvagens by the ancestor of *T. boettgeri hierrensis* occurred (see Carranza *et al.* 2000). These taxa are suitable for calibration as they are sisters and each is monophyletic with low intraspecific variability (Nogales *et al.* 1998).

Apart from the assumption that El Hierro was colonized rapidly, factors that could affect clock calibrations include stochastic variation at low levels of sequence divergence and the possibility of extinct or unsampled lineages (Emerson *et al.* 2000a,b; Emerson 2002), although there is no evidence, of any of these factors acting in *Tarentola* from either the Selvagens or El Hierro. The estimated dates are very provisional, as no calibration point is available within endemic Cape Verde *Hemidactylus*, or in their close relatives, and they may have been separated from *Tarentola* for as long as 100 My (Gamble *et al.* 2008a,b). However, the substitution rate inferred from r8s for the concatenated *cyt b* + 12S fragments of the present study is 1.15% per million years, which is comparable to rates calculated for exactly the same mtDNA regions for populations of non-gekkonid lizards like the lacertid lizards of the tribe Lacertini (1.35% per My; Carranza *et al.* 2004; Arnold *et al.* 2007), *Chalcides* skinks (1.35% per My; Carranza *et al.* 2008a), and even amphibians of the genus *Pleurodeles* (1.46% per My; Carranza & Arnold 2004; Carranza & Wade 2004) and *Hydromantes* (0.99% per My;

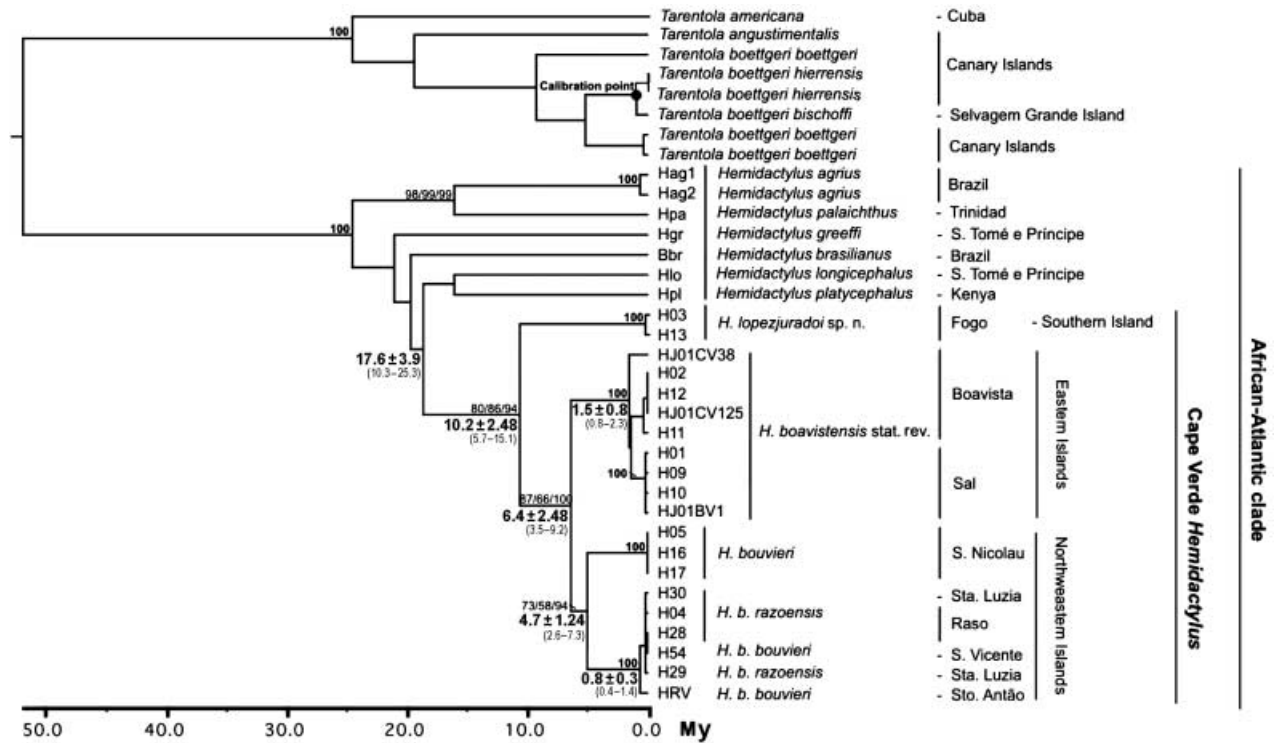


Fig. 2 Relationships and estimated times of divergence in endemic Cape Verde *Hemidactylus* and their relatives based on an analysis of 689 bp (303 bp *cyt b* and 386 bp of 12S rRNA). Output tree from r8sb program is shown, which includes other members of the African-Atlantic clade of *Hemidactylus* (*sensu* Carranza & Arnold 1996) and selected *Tarentola* geckos, is rooted using the south-west Asian gecko *Teratoscincus scincus keyserlingi*. Topologies from PHYML, MP and Bayesian analysis are similar. Figures above nodes indicate bootstrap support for ML (left), MP (centre) and Bayesian posterior probability values (right). Where the value in all three is 100, only a single figure is shown. Figures below nodes indicate the estimated age of the speciation events concerned in millions of years (My), followed by the standard deviation and 95% confidence intervals (in parenthesis below) obtained with parametric bootstrap using the original topology (see Materials and methods). For fuller locality data and GenBank accession numbers see Table 1.

Carranza *et al.* 2008b). Moreover, in order to account for the error involved in the calibration of the *Hemidactylus* phylogeny a parametric bootstrap analysis was performed in which we simulated 1000 alignments from the ML tree and recalculated dates using r8s from the same ML topology with branch lengths optimized for each simulated alignment. This allowed us to evaluate the stochastic errors of date estimates associated to sampling a finite number of base pairs (Sander-son & Doyle 2001; Lalueza-Fox *et al.* 2005). Finally, we can also test if the calibrations are appropriate by checking if the arrival of endemic Cape Verde *Hemidactylus* to particular islands is more recent than the origins of the islands themselves where this is known.

Results

The results of the ILD-test showed that the two gene partitions (*cyt b* and 12S rRNA) of data sets 1 and 2 were congruent ($P = 0.11$ and $P = 0.66$, respectively) and independent analyses of the two gene partitions in both data sets con-

firmed there were no topological conflicts (Mason-Gamer & Kellogg 1996). Therefore, the two mitochondrial fragments were combined for further analyses.

In analyses of data set 1, all three methods used (PHYML, MP and Bayesian) produced very similar estimates of relationships (Fig. 2). They show that *H. bouvieri* as presently understood and the distinctive population from Fogo form a monophyletic group within the African-Atlantic clade of *Hemidactylus*.

Data set 2, which was based on longer sequences of mtDNA, gave congruent results (Fig. 3). Samples of the recently discovered form from Fogo are sister to the populations which are currently assigned to *H. bouvieri* (uncorrected genetic divergence for the *cyt b* + 12S rRNA mtDNA genes 11–12%). Within *H. bouvieri*, as presently understood, animals from the eastern islands of Sal and Boavista (*H. bouvieri boavistensis*) are sister to the ones from the northern islands (8.3–9.8% divergence). Here the S. Nicolau sample is distinct from those from the north-western islands of S. Vicente, Sta. Luzia, Raso and Sto. Antão (7.8–8.3% divergence). The

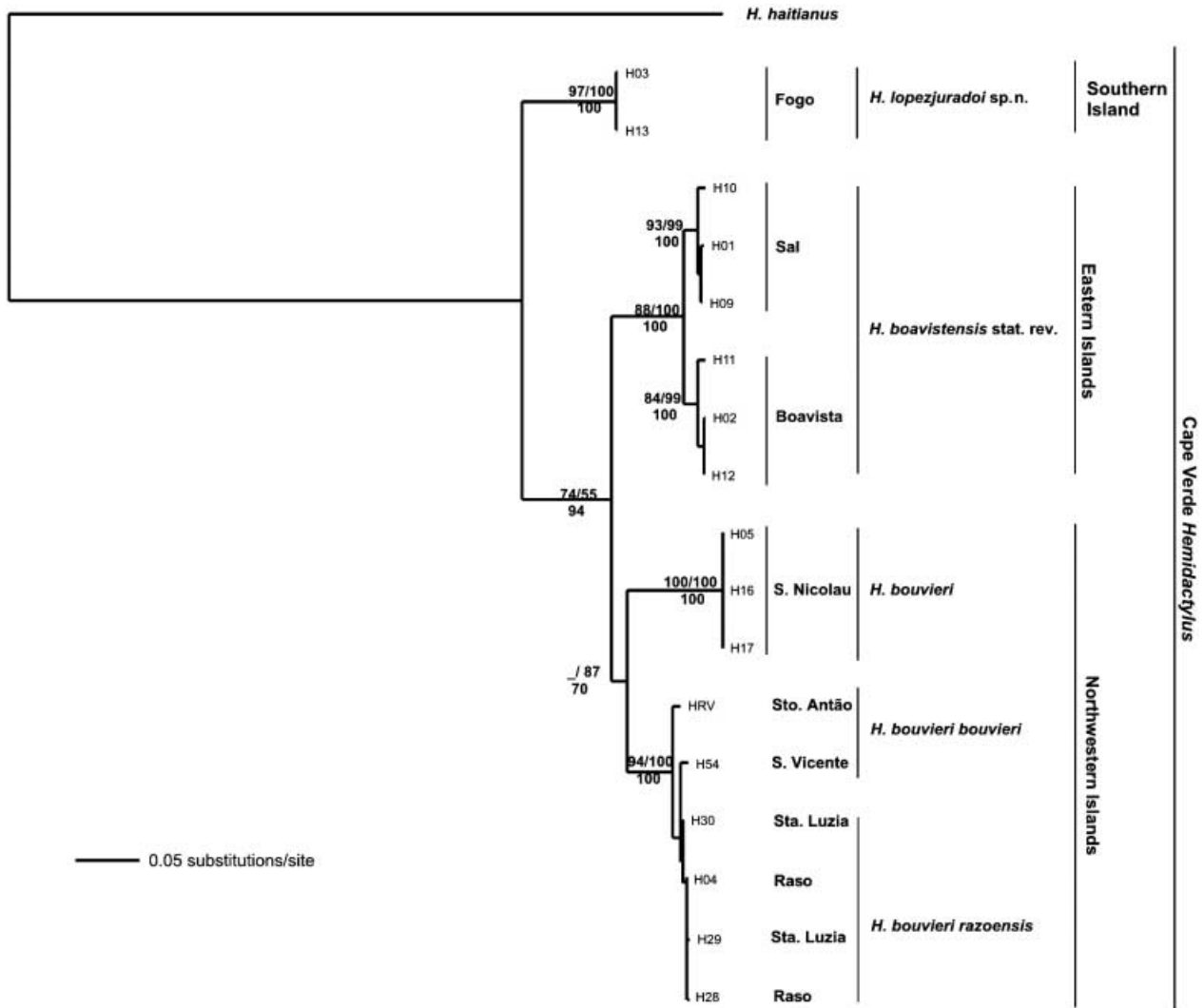


Fig. 3 Relationships within Cape Verde endemic *Hemidactylus*. ML tree based on an analysis of 1050 bp of mtDNA (669 bp *cyt b* and 381 bp of 12S rRNA), rooted using *H. haitianus* as outgroup. Topologies from ML and MP analyses were very similar. Figures above nodes indicate bootstrap support in ML (left) and MP (right) analyses; figures below node are Bayesian posterior probabilities. For fuller locality data and GenBank accession numbers of specimens, see Table 1.

first three of these north-western islands, exhibit divergences that are just 0.1–1.2%, while those between these islands and Sto. Antão are 1.3–1.7%. Divergences between Sal and Boavista animals are 2.7–3.1%.

In data set 3, six haplotypes of the independent nuclear marker, RAG2 were identified (Fig. 4). Two that differ by a single mutational step occur on Fogo and the two individuals studied are heterozygous for them. The seven individuals from the north-western islands of S. Nicolau, Raso, Sta. Luzia and Sto. Antão are all alike and differ by a further step from one of the Fogo haplotypes. The single Sal specimen investigated differed by another step more, while the three specimens from Boavista exhibited either one or two addi-

tional differences from this. The nDNA haplotypes show strong correlation with the most of the geographical units indicated by mtDNA, but do not reflect the phylogenetic topology of the mtDNA tree. When a network analysis was performed using TCS v1.21 (Clement *et al.* 2000), none of the haplotypes was identified as ancestral with high probability.

Systematics

The four geographical units among endemic Cape Verde *Hemidactylus* that are apparent from their DNA show considerable congruence with morphological variation. The Fogo animals that diverge basally from others and differ from them by 11–12% in the combined mtDNA fragments studied here,

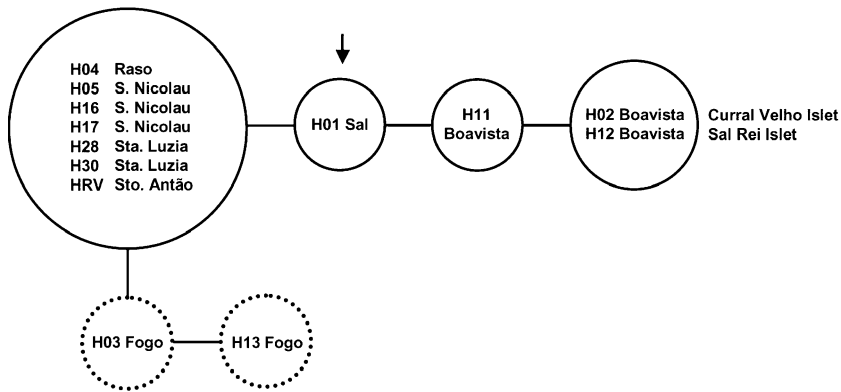


Fig. 4 Network showing RAG2 sequence variation. Lines represent mutational steps and circles represent haplotypes. The area of the circles is proportional to the number of individuals. The arrow indicates where the network is rooted to the two outgroups used (*Hemidactylus platycephalus* and *H. agrius*), which are separated by 19 and 21 mutational steps, respectively. Circles indicated by broken lines enclose heterozygote haplotypes. For fuller locality data and GenBank accession numbers of specimens, see Table 1.

also differ in several anatomical features. Similarly, the populations from Sal and Boavista that are currently assigned to their own subspecies *H. bouvieri boavistensis* have several distinctive anatomical characteristics. The remaining two units, from S. Nicolau and from the north-western islands, form a clade with distinctive morphological features but are not obviously differentiated from each other in this respect, in spite of differing by about 8% in their mtDNA. In the north-western islands most populations are assigned to *H. b. bouvieri*, the exception being those from Raso and Sta. Luzia, which have been differentiated as *H. b. razoensis*. Available specimens from Raso have a much smaller adult body size than the remaining north-western populations, but the supposedly distinctive nasal feature is not universal and also turns up occasionally in other endemic populations of *Hemidactylus* in the Cape Verde Islands (E. N. Arnold unpubl. data).

As divergences between the four DNA units are relatively high (Harris 2002), and as there are also often morphological differences, the following taxonomic changes are made. The distinctive Fogo population is described as a new species; *H. b. boavistensis* is returned to the species status originally allocated by its describer (Boulenger 1906), and remaining populations are assigned to *H. bouvieri* itself. Within this last species, the separate subspecies status assigned to the Raso and Sta Luzia populations (Gruber & Schleich 1982) is retained. The population on S. Nicolau, which is genetically distinct from other populations assigned to *H. bouvieri*, may also require formal naming and description, but material available for this study is too poorly preserved to do this.

Family GEKKONIDAE

Genus *Hemidactylus* Oken, 1817

Hemidactylus lopezjuradoi sp. n. (Fig. 5A,B)

Holotype. Adult male, CAPE VERDE ISLANDS, northern Fogo island between Ribeira Ilhéu & Atalaia 1997, Mateo & Geniez. (BMNH 2005.1632).

Paratypes. Same locality as holotype, adult male, adult female and two juveniles Mateo and Geniez (BMNH 2005.1633–1636).

Etymology. The species name, *lopezjuradoi*, honours Dr Luis Felipe López-Jurado, for his lifelong involvement in Herpetology, and for organizing the expedition during which the specimens of *H. lopezjuradoi* were collected.

Diagnosis. Small (males to about 40 mm from snout to vent); ear opening small and rounded and situated below the level of the angle of the mouth; mental scale not narrowed; one pair of short postmental scales; enlarged tubercles present on back but not on head or limbs, low and smooth or very weakly keeled, the spaces between them much larger than their diameter, in 6–10 very irregular longitudinal rows at mid-back; ventral scales of body coarse and imbricate, increasing in size posteriorly, about 20–23 across mid-belly; a total of about six small femoral pores in males; four scensors and enlarged scales under first hind toe, six to eight under fourth, six to seven under fifth; dorsal scales on tail much larger than those on body, four smooth or weakly keeled enlarged tubercles per whorl basally, subcaudal scales sometimes irregular; dorsal pattern consisting of broad dark transverse bands. Differs from other endemic *Hemidactylus* in the Cape Verde Islands, *H. bouvieri* and *H. boavistensis*, in its blunter snout with convex upper border, usually broader mental and postmental scales, presence of enlarged dorsal tubercles on body and tail, smaller but more numerous femoral pores in males, and sometimes irregular subcaudal scales.

Description

Head and body rather depressed and head not especially broad. Up to 40 mm from snout to vent; in adult males, head length about 30–33% of this, head width about 65% of head length; head depth about 45% of head length and 65–70% of head width. Nostril between rostral, supranasal and superposed postnasals, with the first upper labial scale usually also entering narrowly into its border. One or two scales separating

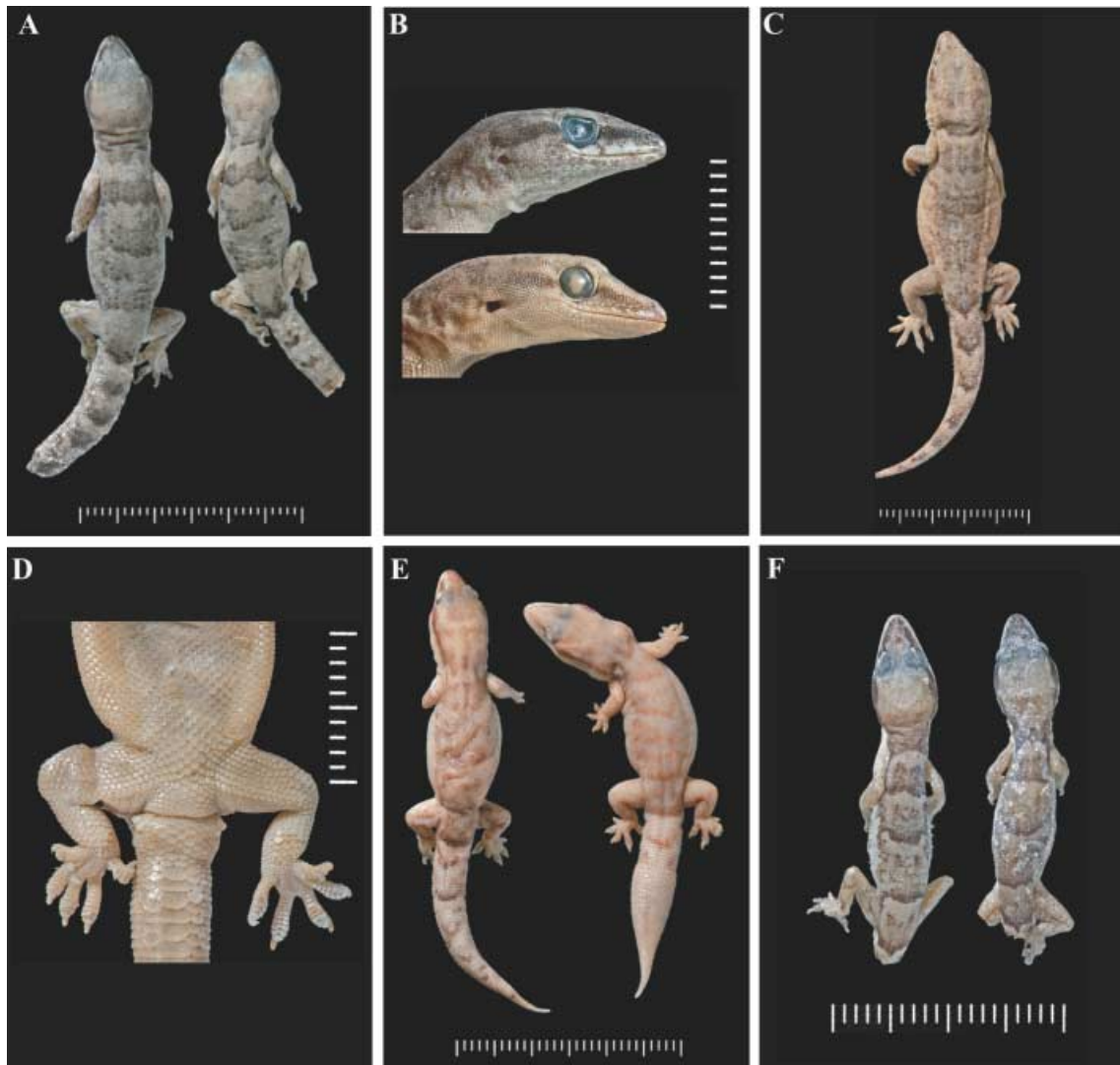


Fig. 5 A–F. Endemic *Hemidactylus* from the Cape Verde Islands. —A. *Hemidactylus lopezjuradoi* sp. n. Holotype (left) and one of the paratypes (BMNH 2005.1633–1634), both males, from between Ribeira Ilhéu and Atalaia, northern Fogo; —B. *H. lopezjuradoi* sp. n. (holotype) and *H. boavistensis* from Boavista, showing difference in upper profile of snout; —C. *H. boavistensis*, male (BMNH 1946.8.25.70) from Boavista, one of the type series; —D. *H. boavistensis*. Underside of male, showing the narrow toes pads characteristic of endemic Cape Verde *Hemidactylus*, and the two well-developed femoral pores in males and regular, laterally expanded subcaudals scales typical of *H. boavistensis* and *H. bouvieri*; also visible are the rather elongated ventral scales found in many *H. boavistensis*; —E. *H. bouvieri*. Left: male from Santiago (BMNH 1875.4.26.10); right: female from S. Vicente with a regenerated tail (BMNH 1866.4.12.3); —F. *H. bouvieri*. Two apparently adult animals from Raso, the type locality of *H. b. razoensis*, right: female, left: male (BMNH 2005.1666–1667). All scales in mm.

supranasal scales on midline, 11–14 scales in a straight line from postnasal scales to edge of orbit. No enlarged tubercles on head. Ear opening usually round rather than diagonally elongated, smooth edged, only 20–25% of diameter of eye, the upper part of the ear drum hidden by a downwardly directed fold of skin. Upper labial scales 8, lower labial scales 6–7. Sides of mental scale converging posteriorly to form a right angle (or a slightly more acute one), two large postmental scales that are broader than long, and meet in a short

suture; these and lower labial scales bordered by more irregular and smaller though still enlarged scales. Gular scales small and granular as far back as about the level of the ear openings. Enlarged tubercles present on dorsal surface of body but relatively small (about twice diameter of surrounding scales), low, round and unkeeled or only very weakly so, arranged in about 6–10 very irregular longitudinal rows at mid-back and about six rows between hind legs; tubercles rather larger laterally, either not extending forward beyond

forelimbs or very few present on neck, tending to be rather larger laterally, spaces between them much greater than their own diameter. Ventral scales under neck and body larger than gulars and dorsal scales with which they gradually merge, imbricate with rounded borders, increasing in size posteriorly, about 20–23 in a transverse row at mid-body. Available males with three small femoral pores on each side, separated by a single central scale. Usually two cloacal tubercles on each side, larger in males. No enlarged tubercles on limbs. Scales on forelimb small and juxtaposed, though rather larger and somewhat imbricate on anterior surface and on dorsal surface of upper limb. Dorsal scales on hindlimb small and juxtaposed; scales on front of thigh and underside of limb large and imbricate but smaller than those on posterior belly. Distal sections of digits extending well beyond adhesive pad, the maximum width of which on the fourth hind toe is much narrower than its length in adults; four scensors and enlarged scales under first hind toe, six to seven under third, six to eight under fourth and six to seven under fifth. Whorls of tail poorly defined, its dorsal scales larger than those on body, being about twice as long; about five to six scales in longitudinal row on fourth whorl after vent. Four enlarged smooth rounded tubercles on dorsal surface of each whorl that are twice as long as those on body, and about a third the length of the whorls themselves; about one to three small scales between tubercles on fourth and fifth whorls. Scales increase in size ventrally, so underside of tail is covered by about five longitudinal rows of large scales, with sometimes the medial row laterally expanded beginning just after the hemipenial bulge in males, or large ventral scales of tail may be tessellated.

Colouring. Grey brown to brown above; a dark brown streak running from nostril through eye and above ear, sometimes joining a broad transverse band on neck; three similar broad transverse bands present on body and one on tail base; edges of bands often wavy or jagged, posterior margin often remaining dark in pale animals; a series of dark blotches on upper surface of tail, spaced every two whorls. Dorsal pattern stronger in juveniles, which may have dark blotches on upper surface of head including a dark transverse bar in occipital region. Underside pale greyish; mental and labial scales blotched light brown; underside sometimes with a light brown stipple especially at sides of belly, accompanied or replaced by tiny blackish punctuations, which may also occur under the tail; dorsum of tail orange in life.

Distinctive features of the holotype. 40 mm from snout to vent; tail broken off at base, truncated separated section 12 mm long. Lower labial scales seven; four scensors and enlarged scales under first hind toe, six under fourth and six under fifth; scales under tail tessellated.

Distribution. Known only from the north of Fogo island.

Conservation status. *Hemidactylus b. bouvieri* was listed as being rare on Fogo and so in need of urgent protection under the criteria of the First Red List of Cape Verde (Schleich 1996). Later, the Cape Verde authorities considered the status of this population as Indeterminate (Anonymous 2002). Whether either of these assessments actually refers to *Hemidactylus lopezjuradoi* is unknown.

Hemidactylus boavistensis stat. rev. Boulenger (1906) (Fig. 5B–D)

Hemidactylus bouvieri Bocage (part), (1902: 209);

Hemidactylus boavistensis Boulenger (1906): 198. Type locality: Boa Vista island, Cape Verde Islands;

Hemidactylus chevalieri Angel (1935): 166. Type locality: 'le Sal, Cape Verde Islands;

Hemidactylus bouvieri boavistensis Loveridge (1947): 121;

Hemidactylus bouvieri chevalieri Loveridge (1947): 121.

Material examined. Sal (BMNH 1946.8.25.68–73, originally BMNH 1906.3.3.4–9), types donated by L. Fea.

Diagnosis. Up to about 50 mm from snout to vent; head relatively broad posteriorly, snout narrow with concave or straight upper profile; mental often narrowed posteriorly, postmentals frequently longer than wide; no enlarged tubercles on dorsum; ventral scales small, often some longer than wide, about 35–40 across mid-belly; two large femoral pores in males; five scensors and enlarged scales under first hind toe, seven to nine under fourth; five to seven under fifth; medial subcaudal scales regular and expanded laterally; dorsal pattern often consisting of broad transverse bands, but these may be divided on the midline, or the anterior ones broken in to several sections, or animals may be more uniform without bands.

Distribution. Sal and Boavista islands

Conservation status. Populations considered at Low Risk, following the criteria of the First Red List of Cape Verde (Schleich 1996).

Hemidactylus bouvieri (Bocourt 1870) (Fig. 5E,F)

Emydactylus bouvieri Bocourt (1870): 17. Saint Vincent, Cape Verde Islands

Hemidactylus Cessacii Bocage (1873): 210. Saint Iago, Cape Verde Islands

Hemidactylus bouvieri Rochebrune (1884): 76.

Diagnosis. Up to about 40 mm from snout to vent; head not broad posteriorly, snout narrow with a concave or straight

upper profile; mental often narrowed posteriorly, postmentals frequently longer than wide; no enlarged tubercles on dorsum; ventral scales moderate, not longer than wide, about 20 across mid-belly, two large femoral pores in males; three to four scapulars and enlarged scales under first hind toe, four to five under fourth; four to six under fifth; medial subcaudal scales regular and expanded laterally; dorsal pattern usually consisting of broad transverse bands.

Distribution. S. Vicente, Sto. Antão, St. Luzia, Raso, S. Nicolau, Santiago; also possibly Brava (Fea 1899b; Angel 1937; Loveridge 1947; Mertens 1955). Although it has also been reported from Fogo by Angel (1935, 1937), Loveridge (1947), Mertens (1955) Schleich (1982, 1996), Joger (1993) and López-Jurado *et al.* (2005); at least some of these reports may actually refer to *H. lopezjuradoi*.

Hemidactylus bouvieri bouvieri (Bocourt 1870) (Fig. 5E)
Emydactylus bouvieri Bocourt (1870): 17. Saint Vincent, Cape Verde Islands
Hemidactylus Cessacii Bocage (1873): 210. Saint Iago, Cape Verde Islands
Hemidactylus bouvieri Rochebrune (1884): 76.
Hemidactylus bouvieri bouvieri Loveridge (1947): 122

Material examined. S. Vicente (BMNH 1866.4.12.3–4); Santiago (BMNH 1875.4.26.10) and S. Nicolau (BMNH 2005.1638–1640).

Distinctive features. Differs from *H. b. razoensis* in its larger size (adults up to about 40 mm from snout to vent).

Distribution. S. Vicente (Bocourt 1970; Bocage 1902; Angel 1937; Loveridge 1947; Mertens 1955; Schleich 1982; Andreone 2000; Carranza & Arnold 2006) Sto. Antão (Bocage 1902; Angel 1937; Mertens 1955), Santiago (Bocage 1902; Angel 1937; Mertens 1955) and possibly Brava (Fea 1899b; Angel 1937; Mertens 1955).

Conservation status. *Hemidactylus b. bouvieri* was listed as being rare and so in need of urgent protection under the criteria of the First Red List of Cape Verde (Schleich 1996).

Later, the Cape Verde authorities considered the status of this form as Indeterminate (Anonymous 2002).

Hemidactylus bouvieri razoensis Gruber & Schleich (1982) (Fig. 5F)

Material examined. Raso (BMNH 2005.1666–1667).

Distinctive features. Differs from *H. b. bouvieri* in its small size (adults only to 29 mm from snout to vent). Also said to be distinctive in having first upper labial scale separated from nostril. However, this does not apply to all animals and the condition sometimes occurs in *H. b. bouvieri* and *H. boavistensis*.

Distribution. Raso (Gruber & Schleich 1982; Mateo *et al.* 1997) and Sta. Luzia (Mateo *et al.* 1997).

Conservation status. *Hemidactylus b. razoensis* was listed as being critically endangered, following the criteria of the First Red List of Cape Verde (Schleich 1996), an assessment also later made by the Cape Verde authorities (Anonymous 2002). Without intervention, these populations are likely soon to become extinct, as they appear to have already done on the nearby island of S. Vicente (Schleich 1987).

Hemidactylus bouvieri, S. Nicolau population

Material examined. S. Nicolau, Cachaço (BMNH 2005.1637–1640).

Distinctive features. The four desiccated specimens available appear distinctive only in one of them having a scattering of slightly enlarged scales on the dorsum of the body. More importantly this population shows an uncorrected genetic divergence from others analysed in the present study of 14.2–16.1% for the *cyt b* and 4.5–8.8% for the 12S rRNA mitochondrial gene fragments used (GenBank accession numbers: EU730652–4, EU730661–3, EU730641–3).

Distribution. S. Nicolau island (López-Jurado *et al.* 2005; Köhler *et al.* 2007; J.A. Mateo and Ph. Geniez unpubl. data).

Key to *Hemidactylus* geckos in the Cape Verde archipelago

- 1a Enlarged, raised, keeled or trihedral tubercles present on upper surface; males with 20–54 femoral pores.....2
- 1b Enlarged tubercles on upper surface absent or, if present, low, not strongly keeled and confined to body and tail; femoral pores few, perhaps not exceeding six.....3
- 2a Enlarged scales under fourth hind toe reaching base of the digit; femoral pores in males 20–46 (Sal, Boavista, Fogo, Santiago, Sto. Antão, S. Vicente, S. Nicolau, Brava and Rombos and perhaps Maio and Santa Maria islet).....***H. angulatus***
- 2b Enlarged scales under fourth hind toe not reaching base of the digit; femoral pores in males 24–54 (S. Vicente, Sto. Antão and Brava).....***H. mabouia***

- 3a Low, smooth or weakly keeled enlarged tubercles present on upper surface; femoral pores in males small, more than 2; snout relatively blunt with a convex upper profile; large scales under tail may be irregular (Fogo)..... *H. lopezjuradoi*
- 3b No enlarged dorsal tubercles on upper surface (or just a few weakly enlarged scales); males with two relatively large femoral pores; snout pointed with a concave or straight upper profile; a regular row of large broad scales on underside of tail..... 4
- 4a Relatively large, up to 50 mm from snout to vent; head broad, ventral scales fine and often longer than wide, about 35–38 across mid-belly; usually 5 enlarged scales under first hind toe and 7–9 under fourth; head broad (Sal and Boavista)..... *H. boavistensis*
- 4b Relatively small, up to 40 mm from snout to vent; ventral scales coarse, about 20–25 across mid-belly; usually 3–4 scales under first hind toe and 4–5 under fourth; head narrow..... *H. bouvieri*.5
- 5a Up to about 40 mm (Sto. Antão, S. Vicente, Santiago and possibly Brava)..... *H. b. bouvieri*
- 5b Up to 30 mm; (Raso, Sta. Luzia)..... *H. b. razoensis*
- 5c Up to 40 mm; sometimes with a few weakly enlarged scales on back mitochondrial DNA sequence distinctive (S. Nicolau)..... *H. bouvieri*, S. Nicolau population

Discussion

Morphological evolution

The main morphological changes in the Cape Verde clade of endemic *Hemidactylus* are shown in Fig. 6. Clearly, the ancestor of the group evolved a syndrome of features, some of which are uncommon or not found among close relatives in the African-Atlantic clade of the genus. *Hemidactylus lopezjuradoi* sp. n. is relatively primitive in its morphology, but the remaining forms all share additional synapomorphies including loss of enlarged tubercles, presence of a very pointed snout, and reduction of the femoral pores in males to two. It is unknown whether the distinctive features of endemic Cape Verde *Hemidactylus* are functionally related to their mode of life.

All the populations of endemic Cape Verde *Hemidactylus* have adult body sizes that are much smaller than other members of the African-Atlantic group of species, suggesting that their ancestral lineage underwent size reduction after arrival in the archipelago. This contrasts with the frequent increase in body size that occurs in other lizard groups in oceanic islands, such as some *Tarentola* geckos and *Mabuya* skinks in the Cape Verde archipelago; Carranza *et al.* 2000, 2001), and some *Phelsuma* geckos and *Leiolopisma* skinks on Mauritius (Austin *et al.* 2004; Austin & Arnold 2006). However, size reduction in Cape Verde *Hemidactylus* is not unique and has occurred in the ancestor of the gecko *Nactus coindemerensis* Bullock, Arnold & Bloxam 1985 on Mauritius and its likely relative on the neighbouring island of Reunion (Arnold 2000; Arnold & Bour 2008).

History and phylogeny of endemic Cape Verde Hemidactylus

The internal relationships of the African-Atlantic clade of *Hemidactylus* to which the endemic Cape Verde species belong, together with its relationships to the other main clades of *Hemidactylus*, indicate that it originated in tropical Africa but has made several excursions into the Atlantic: at least twice to islands in the Gulf of Guinea (Jesus *et al.* 2005), twice to Southern America (Carranza & Arnold 2006), and

once to the Cape Verde Islands. As Cape Verde endemic *Hemidactylus* are not especially closely related to any of the other trans-Atlantic migrants, their colonization of the Cape Verde archipelago is likely to have been independent of these. Also, the pattern of water circulation in the Atlantic Ocean suggests the ancestor of Cape Verde endemics reached the archipelago from extreme West Africa, while ancestors of the South American forms travelled with the west-running Equatorial current, which arises further south and east in the Gulf of Guinea.

If the results of the molecular clock are accepted, the ancestor of the endemic Cape Verde *Hemidactylus* could have reached the archipelago between 10 ± 2.48 and 18 ± 3.9 Mya (Fig. 2). Prevailing south-westerly currents suggest the first landfall may have been in the north-east of the archipelago, possibly on Sal. From here, there was an early migration, presumably with the same current, to the southern island of Fogo perhaps about 10 ± 2.48 Mya. Topology suggests later movement occurred from the initial area of colonization along the northerwestern island chain: first to S. Nicolau then somewhat later to the group of islands including S. Vicente, Sta. Luzia and Raso, and finally to Sto. Antão, perhaps arriving there less than only 1 Mya. Spread to the north-west was apparently very slow, perhaps because the prevailing south-west-running currents in the area run transversely across the line of islands making movement between them difficult. A similar situation exists in *Gallotia* lacertids in the Canary Islands, where spread westwards through the archipelago to Gomera, again across the prevailing current, may have taken several million years (Maca-Meyer *et al.* 2003). Even taking the effects of currents into account, the long period of possibly 4 My or more between *H. bouvieri* reaching the S. Vicente group of islands and the colonization of Sto. Antão is surprising, given that the gap between these islands is less than 15 km. One possibility is that *H. bouvieri* did colonize earlier but the resultant populations were eliminated by volcanic activity, which has been extensive at times on Sto. Antão since its origin 7.6 Mya (Plesner *et al.* 2002). If

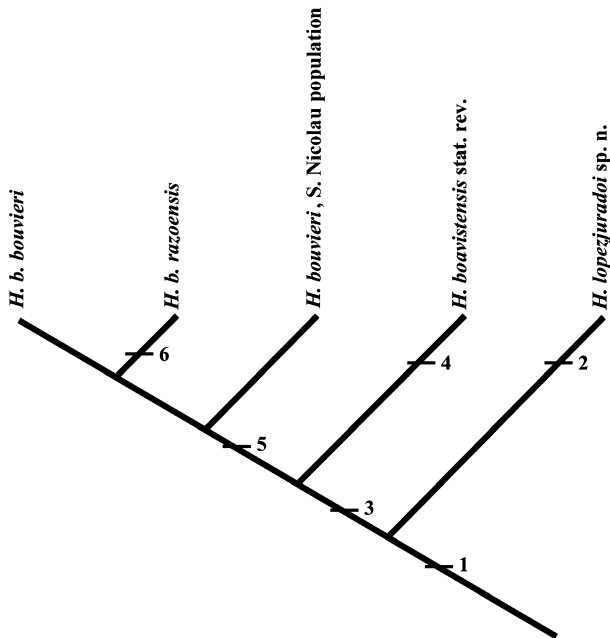


Fig. 6 Some morphological changes in the history of endemic Cape Verde *Hemidactylus* geckos. Where parsimony does not indicate direction of change, as for example with size, size of ventral scales and scansors under toes, values are given for more than one taxon. (1) Small size (only up to about 50 mm from snout to vent); ear opening small and rounded; at least some reduction of dorsal tubercles; femoral pores in males reduced in number (perhaps to six or fewer); dorsal scales on tail markedly larger than those on body; dorsal pattern often consisting of broad dark transverse bands. (2) Comparatively small (up to 40 mm from snout to vent), ventral scales large (about 20–23 across mid-belly), femoral pores reduced in size; scaling beneath tail sometimes irregular. (3) Snout narrow, its upper profile concave or straight, mental often constricted posteriorly; postmentals narrow; no enlarged dorsal tubercles; number of femoral pores reduced to two. (4) Comparatively large (up to about 50 mm); posterior head broad; ventral scales often longer than wide and fine (about 35–40 across mid-belly); 7–9 scansors and large scales under fourth hind digit; dorsal pattern variable with transverse bands sometimes broken up anteriorly, divided on midline or absent. (5) Comparatively small (less than 40 mm); ventral scales relatively large (about 20–23 across mid-belly); 4–5 scansors and large scales under fourth hind digit. (6) Very small adult size (under 30 mm).

such extermination took place, the present populations would represent a later recolonization. Genetic uniformity in the populations of *H. bouvieri* from S. Vicente, Sta. Luzia and Raso is probably because these islands all occur on a shallow bank and have been connected during the seal-level falls that characterized the Pleistocene epoch. The *H. bouvieri* on the southern island of Santiago probably colonized it from the more northern islands where this species is found with

the prevailing current. As no DNA sequence is available from Santiago, it is not possible to say whether this population originated in the north-western islands or on S. Nicolau. A relatively recent movement also occurred in *H. boavistensis* between the islands of Sal and Boavista, an estimated 1.6 ± 0.85 Mya. As expected, estimated dates of dispersal of endemic Cape Verde *Hemidactylus* to particular islands are more recent than the origins of the islands themselves where this is known.

The Cape Verde endemic *Hemidactylus* clade shows both similarities and differences in its history compared to the other lizard groups in the archipelago, namely *Tarentola* geckos and *Mabuya* skinks (Carranza *et al.* 2000, 2001; Brehm *et al.* 2001; Jesus *et al.* 2002). These are estimated to have diversified, respectively, around 4 and 6 Mya, perhaps rather later than the endemic *Hemidactylus*. They are similar in having a strong division between the northern and southern groups and probably making their initial landfall in the north-east and moving slowly to the north-west, but again did so rather later and were also different in each having more than one lineage there. As with the *Hemidactylus*, their populations on islands on the S. Vicente bank exhibit little divergence, and those on Sto. Antão are also similar, again suggesting recent colonization of this relatively old and long-separated island. *Tarentola* twice colonized the southern islands from the northern ones an estimated 2–4 Mya. In *Mabuya*, the ancestor of the clade formed by *M. delalandii* and *M. vaillanti* probably moved to the southern islands from the north approximately 6 Mya, as did *M. spinalis* at a later stage, perhaps 2 Mya. In all these cases, the lineages concerned may parallel the origin of the *H. bouvieri* population of Santiago, although no timing is yet available for this. The relatively late arrival of *Tarentola* and *M. spinalis* on the southern islands of the Cape Verdes has been tentatively attributed to extinction of previous populations by volcanic action there (Carranza *et al.* 2001), as is postulated here for Sto. Antão. But the presence on Fogo of the very distinct *H. lopezjuradoi* sp. n., which separated from its relatives over 10 ± 2.48 Mya, and the long persistence of the representatives of the *M. delalandii* – *M. vaillanti* clade on the southern islands makes this less likely.

Interestingly, other Cape Verde vertebrates exhibit a similar pattern of differentiation to the endemic *Hemidactylus*. For example, although the kestrel *Falco tinnunculus* has only two presently recognized subspecies in the archipelago, DNA indicates there are three geographical units: in the north-western, eastern and southern islands, respectively (Hille *et al.* 2003). However, it is likely that this pattern originated much later than in *Hemidactylus*.

Abundance and conservation status of endemic Cape Verde *Hemidactylus*

Of the endemic *Hemidactylus* geckos in the Cape Verde archipelago, *H. boavistensis* appears to have been abundant at least

since it was first noted by scientists. L. Fea collected specimens on Boavista in 1898, depositing 10 in the Natural History Museum, London and 25 in the Museo Civico 'G. Doria' di Storia Naturale, Genoa. Mertens (1955) mentions 11 collected on this island by H. Lindberg in 1954, and the species was still abundant there in 1997 (López-Jurado *et al.* 1999). On Sal, Angel (1935) recorded a sample of 13 animals, and Mertens (1955) one of 22, also collected by H. Lindberg; again it was found to be common in 1997 (J. A. Mateo unpubl. data).

Although known for much longer, *H. bouvieri* has also never been recorded as abundant. The original description of the species from S. Vicente was based on just three animals (Bocourt 1870), although two had already been collected by Rev. T. Lowe before 1865, and one much more recently (Andreone 2000). On Sto. Antão, an unspecified small number were collected by Dr Hopffer (Bocage 1897, 1902) and one was encountered in 2007 by R. Vasconcelos, S. Rocha and S. Martins. The Raso population was first discovered in 1981 when five animals were collected by Gruber & Schleich (1982), and a further four were found in 1997 (Mateo *et al.* 1997). On S. Nicolau and Sta. Luzia, *H. bouvieri* was first noted only in 1997, when, respectively, four and two animals were encountered (J. A. Mateo and Ph. Geniez unpubl. data; Mateo *et al.* 1997; López-Jurado *et al.* 2005) plus one in 1997 by Köhler *et al.* (2007) in S. Nicolau.

On Santiago, the description of *Hemidactylus cessacii*, a synonym of *H. bouvieri*, was based on a single animal (Bocage 1873), although Bocage presented another specimen from the island to the Natural History Museum, London & in 1875. An unspecified number was collected there by Cessac and F. Borges (Bocage 1897, 1902) and a further single animal is recorded by Mertens (1955). Only one individual has been reported from Brava, collected by L. Fea in 1899 (Fea 1899b; Andreone 2000).

The records listed above indicate that *H. bouvieri* has never been encountered in large numbers in the past 140 years, so there may not have been recent decline. This may possibly have occurred earlier in the period since the Cape Verde islands were first occupied by people, with associated extensive habitat destruction, or *H. bouvieri* may have been uncommon even before this. The species may also be secretive, or occurs in habitats that are rarely searched by herpetologists. There is some evidence that *H. lopezjuradoi* sp. n and *H. bouvieri* may have specialized habitats, perhaps in the restricted relatively humid places in the Cape Verde Islands. While *H. boavistensis* is abundant in very arid open areas with few plants, *H. lopezjuradoi* sp. n. was found under stones in deep valleys on Fogo with lots of vegetation, and *H. bouvieri* was encountered on S. Nicolau (J. A. Mateo unpubl. data) and on S. Antão (R. Vasconcelos unpubl. data) on the tops of mountains, where humidity was high due to condensation.

One possible cause of decline of endemic Cape Verde *Hemidactylus* is the introduced species of this genus. At least one of the introduced species, *H. mabouia*, is known to be an aggressive species capable of displacing and eating other geckos, as has been reported in Venezuela where it seems to be increasing dramatically in numbers (Rivas *et al.* 2005). Elsewhere, *H. frenatus* has had a deleterious effect on endemic gecko populations in other parts of the world. Its introduction to islands in the Pacific has often been associated with decline in the endemic *H. garnotii* (Case *et al.* 1992). This species also appears to be responsible for the ongoing extermination of a radiation of seven species of *Nactus* in the Mascarene Islands (Arnold 2000), something that may have been mediated through competition for refugia (Cole *et al.* 2005). However, *H. boavistensis* appears to survive well in the presence of *H. angulatus* on Sal and Boavista, even though the latter species has been there for a long time, having been collected by L. Fea over a century ago (Andreone 2000). Nevertheless, the two species do not coexist widely, *H. angulatus* tending to occur in different habitats from *H. boavistensis*, being mainly found in anthropogenic situations like airport and village buildings, and neighbouring field walls and ruins. Moreover, where *H. angulatus* is really abundant, as in Ribeira do Norte, Boavista, *H. boavistensis* is not present (López-Jurado *et al.* 1999). Introduced *Hemidactylus* species could conceivably have some potential effect on *H. lopezjuradoi* sp. n and *H. bouvieri*, but this cannot apply to the highly endangered population of *H. bouvieri* on Raso and Sta. Luzia, as neither *H. angulatus* nor *H. mabouia* have been recorded on these islands. Although *H. angulatus* is said to have been collected on Fogo by L. Fea (Fea 1899a; Andreone 2000) and Schleich (1987), and on Brava and Rombos by H. Lindburg (Mertens 1955), these records have to be confirmed, especially as the species was not encountered on these islands in 1997 (J. A. Mateo unpubl. data), 1998 (S. Carranza unpubl. data) or in 2007 (R. Vasconcelos, unpubl. data). However, it seems that its presence has been increasing through time and presently was recorded on almost all of the islands, except the desert islands and islets of Santa Luzia, Raso and Branco. The other introduced reptile, *H. mabouia*, may be expanding its range, as it was originally identified from S. Vicente (Jesus *et al.* 2001) and has been found more recently on Sto. Antão and Brava (R. Vasconcelos unpubl. data). *Hemidactylus mabouia* has also expanded rapidly in many other areas where it has been introduced, especially in the Americas (Carranza & Arnold 2006). Another threat to endemic *Hemidactylus* species and other reptiles in the Cape Verde archipelago are introduced predators such as cats (particularly in the nature reserve on Sta. Luzia) and rats, and browsing and grazing ungulates. The numerous goats on some islands are especially damaging, as they decimate the little remaining natural vegetation, which may be necessary for the survival of some

endemic lizards. For example, most specimens of *H. b. nicolauensis* encountered on S. Nicolau were found under bushes of the endemic *Euphorbia tuqueiana*. Clearly, studies are urgently required to assess the abundance of *H. lopezjuradoi* sp. n and its conservation needs. The same is true for the populations assigned to *H. bouvieri* which, as the present work makes it clear, comprise at least two genetically different geographical units which may have different conservation requirements. Careful GIS modelling to derive probability of occurrence/habitat suitability for each unit will be needed to decide the most appropriate areas to protect.

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