Integrative Approaches to the Systematics and Conservation of the Reptiles of the Cape Verde Islands

Raquel Campos Soares de Vasconcelos

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Raquel Campos Soares de Vasconcelos

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Ilhas afortunadas

Que voz vem no som das ondas
Que não é a voz do mar?
E a voz de alguém que nos fala,
Mas que, se escutarmos, cala,
Por ter havido escutar.

E só se, meio dormindo,
Sem saber de ouvir ouvimos
Que ela nos diz a esperança
A que, como uma criança
Dormente, a dormir sorrimos.

São ilhas afortunadas
São terras sem ter lugar,
Onde o Rei mora esperando.
Mas, se vamos despertando
Cala a voz, e há só o mar.

Fernando Pessoa
Lisboa, 1934

À mãe Faty

NOTA PRÉVIA

Nos termos do nº 2 do artigo 8º do Decreto-Lei nº 388/70, foram incluídos em alguns capítulos desta dissertação os resultados de trabalhos já publicados ou em publicação. Em todos estes trabalhos, a candidata participou na obtenção, análise e discussão dos resultados, bem como na elaboração da publicação, embora sejam resultado de colaborações.

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SUMÁRIO

Dois dos maiores constrangimentos da Biogeografia da Conservação são a falta de conhecimento taxonómico e corológico, designados por défice de Lineu e de Wallace, respectivamente, e geralmente mais acentuados em áreas remotas como ilhas oceânicas. Esta tese contribuiu para diluir tais défices de uma dessas áreas, as ilhas de Cabo Verde, para um dos grupos menos estudados do país, os répteis.

Os objectivos específicos desta tese prenderam-se com a resposta a **que** diversidade ocorre nas ilhas, abordando factores biogeográficos explicativos do **porquê** essa diversidade estar distribuída de forma desigual. Posteriormente pretendeu-se responder a **onde** se encontra essa biodiversidade e, com base nos dados recolhidos, a **como** planear uma protecção optimizada dos diferentes níveis dessa biodiversidade.

Primeiramente, os padrões filogeográficos dos répteis terrestres foram estudados para identificar um agamídeo introduzido em Cabo Verde e taxa endémicos crípticos dos três géneros (*Hemidactylus*, *Tarentola* e *Chioninia*) e ainda para clarificar a sistemática dos mesmos. O novo taxon introduzido foi identificado como *Agama agama*. Algumas subespécies endémicas foram elevadas a espécies e três novas espécies (*Hemidactylus lopezjuradoi*, *Tarentola bocagei* e *T. fogoensis*) e subespécies (*Chioninia vaillanti xanthotis*, *C. spinalis boavistensis* e *C. s. santiagoensis*) crípticas foram descritas, combinando análises de caracteres morfológicos, genéticos e populacionais, empregando uma aproximação integrativa. Estes estudos enfatizaram a vantagem de recorrer nos campos da Taxonomia e Filogeografia a diferentes conjuntos de dados integrados e como estes podem melhorar a estimativa dos taxa existentes. Além do mais, a origem do *Agama* introduzido e os padrões de colonização dos taxa endémicos foram inferidos. Ainda, diversos factores históricos e ambientais, tais como as glaciações do Pleistoceno e a altitude, foram relacionados com a distribuição assimétrica da diversidade a nível intra-específico. A baixa divergência intra-específica entre linhagens de répteis da mesma ilha foi relacionada com a recente actividade vulcânica e com a elevada pressão ecológica que pode levar à extinção de populações, bem como com a baixa diversidade de habitats de algumas das ilhas que pode restringir as oportunidade para a diversificação alopátrica.

Em segundo lugar, dados de amostragens intensivas e de recolha bibliográfica foram compilados para produzir e actualizar um atlas de distribuição para todos os taxa, comentando registos erróneos e duvidosos, e ainda para desenvolver mapas preditivos de ocorrência para a maioria dos taxa endémicos recorrendo a modelos baseados no nicho ecológico. Estes dados facultaram também a detecção da ampla dispersão em Santiago e Boavista do *H. angulatus* introduzido e da colonização de duas novas ilhas pelo éxotico *H. mabouia*. Adicionalmente, permitiram a actualização dos estatutos de conservação dos taxa endémicos, evidenciando que cerca de metade destes estão ameaçados de extinção com base nos critérios da IUCN, sendo a restrita distribuição geográfica o critério com maior frequência nesta classificação. Os principais factores de ameaça identificados estão relacionados com desastres naturais, como secas e actividade vulcânica, factores intrínsecos, tais como distribuições restritas e a baixas densidades populacionais, e com a introdução de espécies exóticas.

Por último, este trabalho demonstrou ainda como os modelos baseados no nicho ecológico são úteis para inferir distribuições com elevada precisão em regiões sub-amostradas e remotas, e como estes podem ser aplicados à conservação, maximizando a eficiência do desenho de áreas protegidas. Os resultados demonstram que a designação de novas áreas protegidas em Santa Luzia, Branco, Raso, Sal, Boavista, Maio e Rombos para além das que serão implementadas não é prioritária, visto que os objectivos quantitativos de representação serão atingidos para todas as unidades evolucionárias significativas dessas ilhas e ilhéus. Por outro lado, novas áreas ou modificações das mesmas deverão ser implementadas nas restantes ilhas de forma a assegurar a protecção de todas as linhagens de répteis cabo-verdianos identificadas. Esta medida é especialmente importante no Fogo e Brava, onde nenhuma unidade de planeamento seleccionada pelos cenários de seriação de áreas prioritárias está incluída nos limites das áreas protegidas a implementar e onde nenhuma área protegida foi designada, respectivamente.

No conjunto, este trabalho exemplifica a utilidade da integração de diferentes disciplinas para um mais eficaz planeamento sistemático para a conservação da biodiversidade.

SUMMARY

Two of the main sensitivities of Conservation Biogeography are the inadequacies in taxonomic and chorological data, the so-called Linnean and Wallacean shortfalls, respectively. These shortfalls increase in the more remote areas such as oceanic islands. This thesis contributed to dilute those shortfalls in one of those remote areas, the Cape Verde Islands, for one of its least studied group, the reptiles.

The specific goals of this thesis were related to answering to **what** diversity occurs there and to address putative biogeographic factors that explain **why** diversity is unevenly distributed. Then, it is aimed to answer **where** this biodiversity can be found and, based on all the gathered data, to plan **how** to better protect it at different levels.

First, the phylogeographic patterns of terrestrial reptiles were studied to identify an introduced agamid and cryptic endemic taxa of the three genera (*Hemidactylus*, *Tarentola* and *Chioninia*) and to clarify their systematics. The new introduced taxon in Cape Verde was identified as *Agama agama*. Also, some endemic subspecies were upgraded to the specific status and three new cryptic species (*Hemidactylus lopezjuradoi*, *Tarentola bocagei* and *T. fogoensis*) and subspecies (*Chioninia vaillanti xanthotis*, *C. spinalis boavistensis* and *C. s. santiagoensis*) were described using an integrative approach combining morphological, genetic and population analyses. These studies highlighted the usefulness of integrative datasets in the fields of Taxonomy and Phylogeography and how they can improve the performance of taxa estimations. In addition, the origin of the introduced *Agama* and the colonisation patterns of the endemic taxa were inferred and several historical and environmental factors, such as the Pleistocene sea-level falls and altitude, were related with the uneven distribution of diversity at intraspecific level. Low intraspecific divergence between reptile lineages of the same island has been explained by the recent volcanic activity and high ecological stress that could lead to population extinctions, and the low habitat diversity within some islands that could restrain opportunities for allopatric diversification.

Secondly, extensive sampling and bibliographic chorological data were compiled to produce and updated distribution atlas for all taxa addressing doubtful or erroneous records and to develop predictive maps of occurrence based on ecological niche-based models for most of the endemic taxa. This data also allowed the detection of the wide-spreading of the introduced *H. angulatus* in Santiago and Boavista and the colonisation of two new islands by the exotic *H. mabouia*. In addition, it allowed updating the conservation status for the endemic taxa showing that around half of them are threatened under the IUCN criteria and that the most frequent classifying criterion was related to restricted geographic range. The most pervasive threats identified are related to natural disasters, as droughts and volcanic activity, intrinsic factors, such as low population densities and restricted range, and introduced species.

Finally, this work also demonstrated how ecological niche-based models are useful tools to infer ranges on relatively under-sampled and remote areas with high accuracies and how they can be applied to conservation, maximizing efficiency of reserve designs. Results depicted that in Santa Luzia, Branco, Raso, Sal, Boavista, Maio and Rombos designation of new protected areas is not a priority since the ones that are going to be implemented will reach the

conservation targets for all identified evolutionary significant units of those islands and islets. On the other hand, new or modified reserves should be implemented on the remaining islands to cover all identified lineages of Cape Verdean reptiles. This measure is especially important in Fogo and Brava, where no planning unit selected by the area prioritisation scenarios is within the protected areas limits and no protected area is planned, respectively.

Altogether, this work exemplifies the usefulness of integrating different disciplines to more effectively allowing systematic conservation planning of biodiversity.

RESUMÉ

Deux des plus grandes contraintes de la Biogéographie de la Conservation sont le manque de connaissance taxonomique et chorologique, désignés respectivement par déficit de Linné et de Wallace, et en règle générale plus accentués dans des secteurs éloignés comme des îles océaniques. Cette thèse contribue à minimiser ces déficits dans certains de ces secteurs, qui sont dans les îles du Cap-Vert, sur un des groupes moins étudiés du pays qui est celui des reptiles.

Les objectifs spécifiques de cette thèse sont liés à la réponse de certaines questions : **quelle** est la diversité qui se trouve dans les îles, en abordant des facteurs biogéographiques explicatifs, le **pourquoi** cette diversité est distribuée de façon inégale. Ensuite, en prétendant de répondre **où** se trouve cette diversité, en se basant sur des données rassemblées, et en fin **comment** planifier une protection optimisée des différents niveaux de cette biodiversité.

Premièrement, les patrons philogéographiques des reptiles terrestres ont été étudiés identifier une agamidé introduite au Cap-Vert et taxa endémiques cryptiques des trois genres (*Hemidactylus*, *Tarentola* et *Chioninia*) et puis pour clarifier la systématique de ceux-ci. Le nouveau taxon introduit a été identifié comme *Agama agama*. Quelques sous-espèces endémiques ont été élevées à un niveau d'espèce et trois nouvelles espèces (*Hemidactylus lopezjuradoi*, *Tarentola bocagei* et *T. fogoensis*) et sous-espèces (*Chioninia vaillanti xanthotis*, *C. spinalis boavistensis* et *C. s. santiagoensis*) cryptiques ont été décrites, en combinant des analyses de caractères morphologiques, génétiques et populationnelles, tout en employant une approche intégratif. Ces études ont souligné l'avantage d'utiliser dans les matières de Taxonomie et de Phylogéographie des différents ensembles de données intégrées et comme ceux-ci peuvent améliorer la performance d'estimation du taxa. Aussi, l'origine de l'*Agama* introduit et des voies de colonisation des taxa endémiques ont été inférées. Puis, divers facteurs historiques et environnementaux, tels que les glaciations du Pléistocène et l'altitude, ont été rapportés avec la distribution asymétrique de la diversité à un niveau intra-spécifique. La basse divergence intra-spécifique entre des lignées de reptiles de la même île a été rapportée avec la récente activité volcanique, puis avec l'élevée de la pression écologique qui peut entrainer à l'extinction des populations, et aussi avec la basse diversité des habitats de certaines îles qui peuvent restreindre l'occasion pour la diversification allopatrique.

Deuxièmement, les données d'échantillonnages intensifs et de collecte bibliographique ont été compilées pour produire et mettre à jour un atlas de distribution de tous les taxa, en commentant registres erronés et douteux, et encore pour développer des cartes prédictives de présence pour la majorité des taxa endémiques, pour en développer des modèles basés sur le niche écologique. Ces données ont facilité aussi la détection de la grande dispersion à Santiago et Boavista du *H. angulatus* qui est une espèce introduite et de la colonisation de deux nouvelles îles par l'espèce exotique *H. mabouia*. Supplémentairement, ils ont permis la mise à jour des statuts de conservation des taxas endémiques, en prouvant qu'environ la moitié de ceux-ci est menacée d'extinction sur des base de critères de l'IUCN, en étant la restreinte distribution géographique le critère plus fréquent dans ce classement. Les principaux facteurs de menace identifiés sont rapportés avec des désastres naturels, comme les sécheresses, l'activité

volcanique et facteurs intrinsèques, tels que les distributions restreintes et de basses densités populationnelles, et avec l'introduction des espèces exotiques.

Finalement, ce travail a démontré encore que les modèles basés sur le niche écologique sont utiles pour inférer des distributions avec une précision élevée dans des régions sus-échantillonnés et éloignées, et qu'ils peuvent être appliqués à la conservation, en maximisant l'efficacité du dessin des aires protégés. Les résultats démontrent que la désignation de nouvelles aires protégées outre lesquels ils seront mis en œuvre à Santa Luzia, Branco, Raso, Sal, Boavista, Maio et Rombos n'est pas prioritaire, vu que les objectifs quantitatifs de représentation seront atteints pour toutes les unités évolutionnaires significatives de ces îles et d'îlots. D'autre part, de nouveaux aires ou modifications de ces derniers devront être mis en œuvre dans les restantes îles de manière à assurer la protection de toutes les lignées de reptiles Cap-Verdiens identifiées. Ce mesure est spécialement important dans Fogo et Brava, où aucune unité de planification sélectionnée par les scénarios d'optimisation des aires prioritaires n'est incluse dans les limites des aires protégés mis en œuvre et dans aucun des aire protégés désigné pour être mis en œuvre plu tard, respectivement.

Dans l'ensemble, ce travail exemplifie l'utilité de l'intégration des différentes disciplines pour une plus efficace planification systématique de conservation de la biodiversité.

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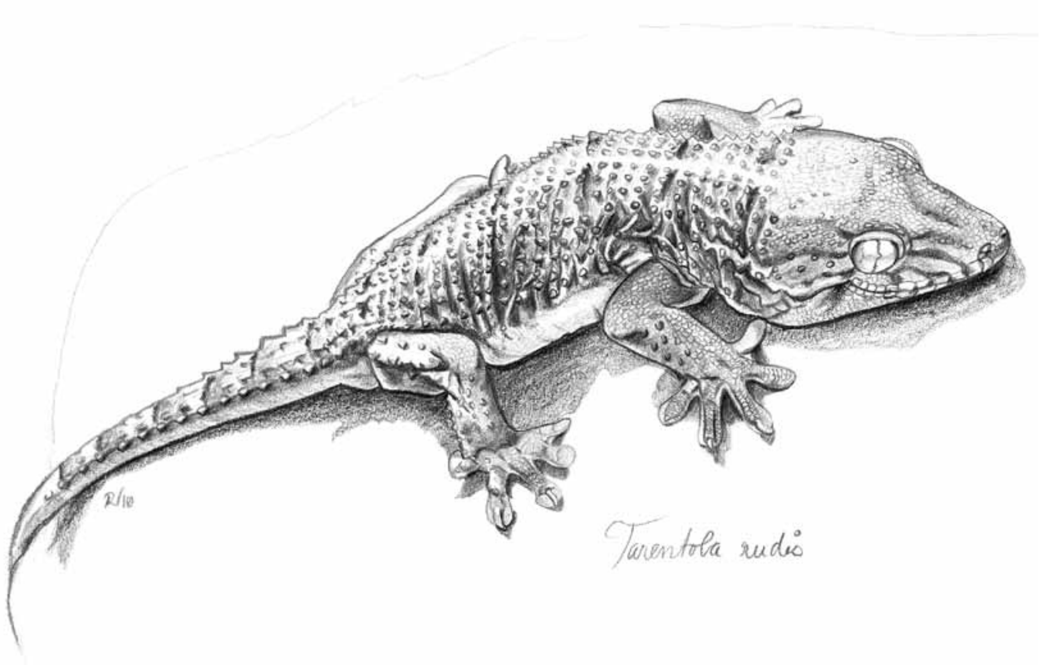
“An island may demonstrate certain biological phenomena
almost with the clarity of a test-tube experiment.”

Mayr 1967

CHAPTER 1

General Introduction



SECTION 1.1. BIOLOGICAL DIVERSITY

Biological diversity broadly defined refers to the variability of life on Earth from all sources (terrestrial, marine and aquatic ecosystems) and the ecological complexes of which they are part. It includes diversity within species, usually measured in terms of genetic differences between individuals or populations of a given species; between species, measured as a combination of the number and evenness of abundance of species; and of ecosystems, measured as the number of different species assemblages (Pullin 2002).

The term biodiversity is a contraction of biological diversity, and may have been coined during the National Forum on Biological Diversity held in Washington. It first appeared in the publication of the proceedings of that meeting by Wilson in 1986. After that, this term achieved widespread use among scientists and common citizens as the expansion of concern over biodiversity loss increased. The year 2010 has been declared as the **International Year of Biodiversity** in recognition of the international target to significantly reduce the rate of biodiversity loss at global scale.

Section 1.1.1. Biodiversity crisis

Extinctions are natural events. Rapid environmental modifications typically cause extinctions (Drummond & Strimmer 2001). Of all species that have existed on Earth, 99.9% are now extinct (Begon *et al.* 2006). Since life began on Earth, five major mass extinctions, evident in the geological record, have led to large-scale and sudden losses in biodiversity. However, humans have increased extinction rate, currently 100 times higher than in the fossil record (Millennium Ecosystem Assessment 2005), and the list of its causes. Overexploitation by hunting was probably the first cause of human driven extinctions, but more recently, new factors are threatening biodiversity as major habitat destruction, pollution and introduction of exotic species (Begon *et al.* 2006). Thus, some authors consider that a sixth mass extinction is ongoing, the Holocene extinction, primarily caused by human-made driving factors and climate change (e.g. Triantis *et al.* 2010).

Identification of **biodiversity hotspots** was considered one of the first and most important steps to prevent biodiversity loss (Myers 2003). This concept, put forward by Myers (1988), combines a measure of the concentration of biodiversity with an index of threat. Biodiversity hotspots are defined as areas featuring exceptional concentrations of endemic species and experiencing exceptional loss of habitats (Myers *et al.* 2000). The 2000 hotspot list of Conservation International (CI) identified 25 terrestrial areas of the world for priority conservation. These hotspots met two criteria: the area should possess at least 0.5% (1500) of the world-wide endemic plant species, and should have lost 70% or more of its primary vegetation (Myers *et al.* 2000). Recently that list was updated to 34 areas (Mittermeier *et al.* 2004) and islands feature prominently among that list (Fig. 1.1.1.). Hotspot areas altogether contain now 50% of all described vascular plant species world-wide and 42% of vertebrate species (fishes not included) though occupy only 2.3% of the global land surface (CI 2005). Thus, if the conservation community can effectively use the biodiversity hotspots approach, prioritizing efforts on those areas, there is a chance to protect over half of the species of the world (Brooks *et al.* 2002).

Nearly half of all plant species and one third of terrestrial vertebrates were considered endemic to hotspots and also more than half of all threatened plants and of all threatened terrestrial vertebrates (Brooks *et al.* 2002). It is expected that many of those hotspot endemics will either become extinct or threatened with extinction (Brooks *et al.* 2002). The relevance of this biodiversity crisis is becoming a major international issue, as scientific evidence is gathered on the global implications of biodiversity loss. Biodiversity provides ecological services and economical income and also benefits humanity with spiritual and aesthetic values (Costanza *et al.* 1997). The growing concern about biodiversity loss is hand to hand with the growing number of scientific studies on biodiversity. Two of the main sensitivities of conservation studies are the inadequacies in taxonomic and distributional data,

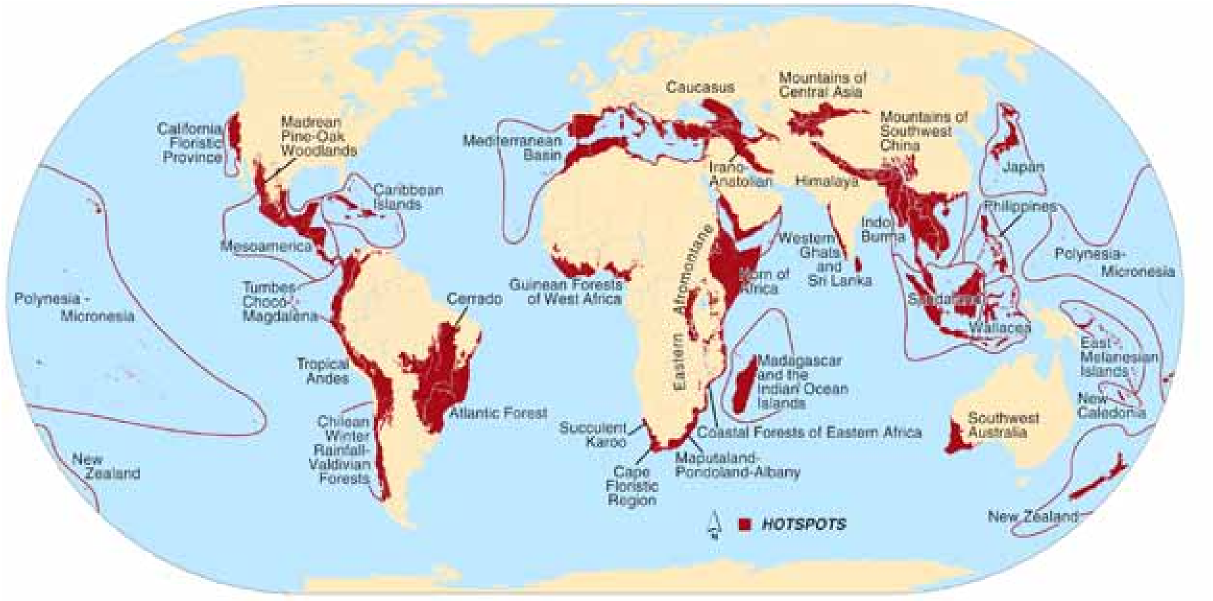


Figure 1.1.1 The 34 hotspots identified by Conservation International in 2005 (adapted from Mittermeier *et al.* 2004).

the so-called **Linnean and Wallacean shortfalls**, respectively (Whittaker *et al.* 2005). To shorten the referred shortfalls it is essential to first define and select the units of study of biodiversity, which can range from genes to landscapes.

Section 1.1.2. Units of the study of biodiversity

Species are a natural taxonomic rank to form the basis for both conservation assessments and management (Mace 2004). For instance, IUCN (World Conservation Union) produces a regular list of species most at risk of extinction in the short term, the Red List. Further, delineating species boundaries is crucial because it is the first step towards discussing broader questions on biogeography, ecology, conservation or evolution. However, the definition of species might be one of the most intensively debated subjects in biology; hence many definitions exist. All of them fail in some point because they are static concepts trying to capture a spatial and temporal dynamic process that is speciation (Fig. 1.1.2.). Some of the most commonly used are the following:

Biological species concept, BSC, (Dobzhansky 1935; Mayr 1942, 1963) is largely used. According to it, a species represents a group of interbreeding (or potentially interbreeding) natural populations that are reproductively isolated from other such groups by intrinsic pre- and/or post-zygotic barriers due to shared specific mate recognition or fertilisation systems. It allows the designation of subspecies (Futuyma 1998).

Evolutionary species concept, EvSC, (Simpson 1961; Wiley 1978) defines a species as an entity composed of organisms that maintains its identity from other such lineages and has its own independent evolutionary tendencies and historical fate. Considering species as temporal segments of separately evolving lineages allowed considering any kind of evidence (not just reproductive incompatibility or morphological differentiation) to propose an initial hypothesis of a species (Padial *et al.* 2009).

Ecologic species concept, EcSC, equates species based on the EvSc concept, considering that species are lineages evolving separately from all lineages outside its range, but emphasizing that lineages must occupy the same niche or adaptive zone, minimally different from that of any other lineage in its range (Van Valen 1976; Andersson 1990).

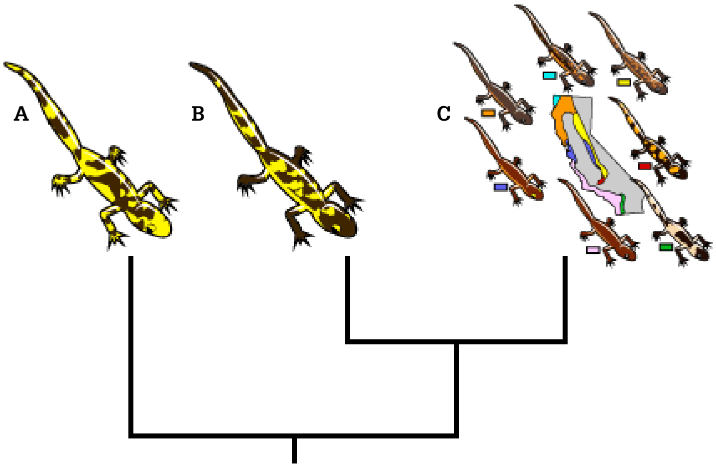


Figure 1.1.2 Representation of the different species concepts (figure adapted from UCMP 2010). Lineages A and B and some C population are separate species following the BSC if reproductively isolated; only A, B and C as a whole may be species following the EvSC because they evolve as single units and also according to the PSC because these are the only lineages with a common and unique ancestor; A, B and some C populations are species following the CSC because they show phenotypic cohesion. According to the GCS, A, B and C lineages or A and (B+C) may be different species, or A+B+C may be only one species depending on the isolation time considered and diagnostic characters used, thus several lines of evidence should be studied.

Cohesion species concept (Templeton 1989), CSC, emerged and defined species as the most inclusive population of individuals having the potential for phenotypic cohesion through intrinsic cohesion mechanisms.

Phylogenetic species concept (Cracraft 1983), PSC, defines species as the smallest diagnosable cluster of individual organisms with which there is a parental pattern of ancestry and descent. It derived focusing on monophyly (commonly inferred from possession of shared derived character states), exclusive coalescence of alleles (all alleles of a given gene descend from a common ancestral allele not shared with those of other species) and diagnosability of qualitative, fixed differences according to different authors (de Queiroz 1998).

According to de Queiroz (2007) one of the main problems related to the species recognition is that species delimitation has long been confused with that of species conceptualisation, leading to controversy concerning both the definition of the species categories and methods for inferring their boundaries and numbers. Recent progress in the field has been made through the general lineage species concept (de Queiroz 1998), GSC. It is now widely understood that almost all species concepts agree in defining species as population-level evolutionary lineages, and that the various species concepts refer to diagnostic characters of these lineages that become recognisable in a variable order and after different intervals of time. Hence, the best inferences about lineage separation will be based on lines of evidence described by several different species criteria but the only property necessary for delimiting species would be detecting a segment of a metapopulation lineage evolving separately (de Queiroz 1998). Other properties, such as pre- and post-zygotic reproductive isolation, reciprocal monophyly, phenetic distinguishability or occupation of a distinct niche or adaptive zone are no longer seen as part of the species concept but serve as important lines of evidence relevant to assessing the separation of lineages and therefore to species delimitation (de Queiroz 2007).

Species conservation is necessary, though certainly not sufficient for wider conservation policy and practice (Mace 2004). **Subspecies** have been defined as geographically defined aggregates of local populations which differ taxonomically from other subdivisions of the species (Mayr 1940). Afterwards, it was added that the evidence for BSC subspecies designation should come from the concordant distribution of multiple, independent, genetically based traits (Avise & Ball 1990; O´Brien & Mayr 1991).

Units for conservation action will almost always be populations or even individuals, thus the concept of **evolutionarily significant units** (ESUs) was put forward. Originally, it was intended to distinguish between populations that represented significant adaptive variation, and the identification of ESUs was to be based on concordance between sets of data (genetic, ecological, behavioural) derived by different techniques (Ryder 1986). Waples (1991) redefined ESUs to be populations that are reproductively separate from other populations and that have unique or different adaptations. Later, Moritz (1994) defined it as populations that are reciprocally monophyletic for mitochondrial DNA alleles, and that show significant divergence of allele frequencies at nuclear loci. Crandall *et al.* (2000) propose that ESU concepts be abandoned altogether and replaced with a more holistic concept of species, consisting of populations with varying levels of gene flow evolving through drift and selection that should be tested in the form of null hypotheses. Fraser & Bernatchez (2001) recovered the concept and defined ESUs as lineages demonstrating highly restricted gene flow from other such lineages within the higher organisational level of species. This is an integrative framework that unifies the strengths of various proposed criteria for imputing conservation units based on the notion that situational circumstances will demand different integrative approaches that may encompass a wide array of justifiable biological criteria in general (Fraser & Bernatchez 2001).

Despite different definitions, all authors agree that ESUs should be chosen to maximise the potential for evolutionary success and therefore to preserve adaptive diversity across the range of the taxon (Mace 2004).

Section 1.1.3. Study of biodiversity – the Linnean shortfall

Estimating the extent of the biodiversity crisis is a hard task since only a very small fraction of the estimated total number of species has been recorded (Whittaker & Fernández-Palacios 2007). One of the most fundamental biological sciences that deals with the Linnean shortfall is **Systematic Biology** (hereafter Systematics), the study of the relationships between groups of organisms and diversification of life though time. Systematics tries to infer the evolutionary history of the taxa and use this information to produce a biologically meaningful system of classification.

Phylogenetics is the field of Systematics that investigates the evolutionary history of the groups of organisms identified using morphological and molecular data. Phylogenetic trees may not perfectly reproduce evolutionary trees but are commonly used to infer the group interspecific relationships through branching order and the amount of evolution through branch length. The outputs of those trees allow the inference of demographic history, divergence times, migration rates, historical hybridisation events, hybrid zones, introgression occurrence or refugia prediction (Hickerson *et al.* 2010). These tree-based methods are of crucial importance to systematics to search for monophyletic groups that could represent species (Sites & Marchal 2004).

The current method of choice to infer phylogenetic trees and the most commonly-used methods to infer phylogenies are parsimony, maximum likelihood, and Markov Chain Monte Carlo-based Bayesian inference. Nevertheless, network approaches are considered to be more effective than classical phylogenetic ones for representing intraspecific evolution (Posada & Crandall, 2001). Recent analyses of specific taxa show that the 95% parsimony connection limit among networks can provide an additional and simple quantitative standard for phylogenetic species (Monaghan *et al.* 2006). The parsimony connection limit appears to have a higher true-positive rate for discovering new cryptic species from sequence data when applied to mtDNA loci (Hart & Sunday 2007), because they are assumed to be non-recombining and with rapid lineage sorting, in contrast to nuclear alleles that frequently recombine and are slow-evolving (Avise 1994). Recombination of nDNA may limit the rate at which ancestral polymorphisms shared between recently diverged species are lost from one (or both) of them by lineage sorting and thus reduce the rate at which haplotype differences between sister species approach the parsimony connection limit (Hart & Sunday 2007). Thus the choice of the type of molecular markers to use in phylogenetic inferences (mitochondrial or nuclear; neutral or under selection) has to be made with care, taking into account its mutation rate and the use of coding or non-coding regions according to aims of the study. Mutillocus approaches are advisable to avoid misleading interpretations result of introgression, hybridisation or incomplete lineage sorting (Shaw 2002).

The other branch of Systematics is Taxonomy, the discipline which classifies organisms. Its main goals are assigning scientific names to organisms (nomenclature), describing and organizing them in a hierarchical structure, preserving collections and developing identification keys. Collar (1997) summed up the importance of Taxonomy for conservation: 'Taxonomy precedes conservation. Without the formal structure of names and an agreed system of usage, there can be no understanding of what exists to be conserved.'

Species were clearly over-aggregated in earlier times, when systematics was based only on morphological characters. Study of the fossil record and comparative morphology are now less common than molecular studies (Williams & Ebach 2008). New studies and the application of new techniques (based on DNA sequencing) have led to the recognition of many new species, especially among 'cryptic' taxa (Mace 2004). Species taxonomy is currently confronted with the challenge to incorporate new theories, methods and data from disciplines that study the origin, limits and evolution of species, to produce the inventory of life in a reasonable time (Padial *et al.* 2010). The communication gap among different disciplines currently involved in delimiting species is an important and overlooked problem. To solve it, Dayrat (2005) suggested that Taxonomy should become integrative.

Integrative Taxonomy is defined as the science that aims to delimit the units of biotic diversity from multiple and complementary disciplines (Dayrat 2005). Those disciplines are, among others, Phylogenetics, Comparative Morphology and Population Genetics. Hence, morphological characters and molecular markers (mostly sequences of mitochondrial or chloroplast DNA and, increasingly, of nuclear genes), studied at species and population level, should be used as different complementary approaches to reliably identify species. However, disagreements concerning the degree of congruence that different characters must show to consider a population or a group of populations as a separate species split integrative taxonomists. The two main approaches are 'integration by cumulation' and 'integration by congruence' (Padial *et al.* 2010):

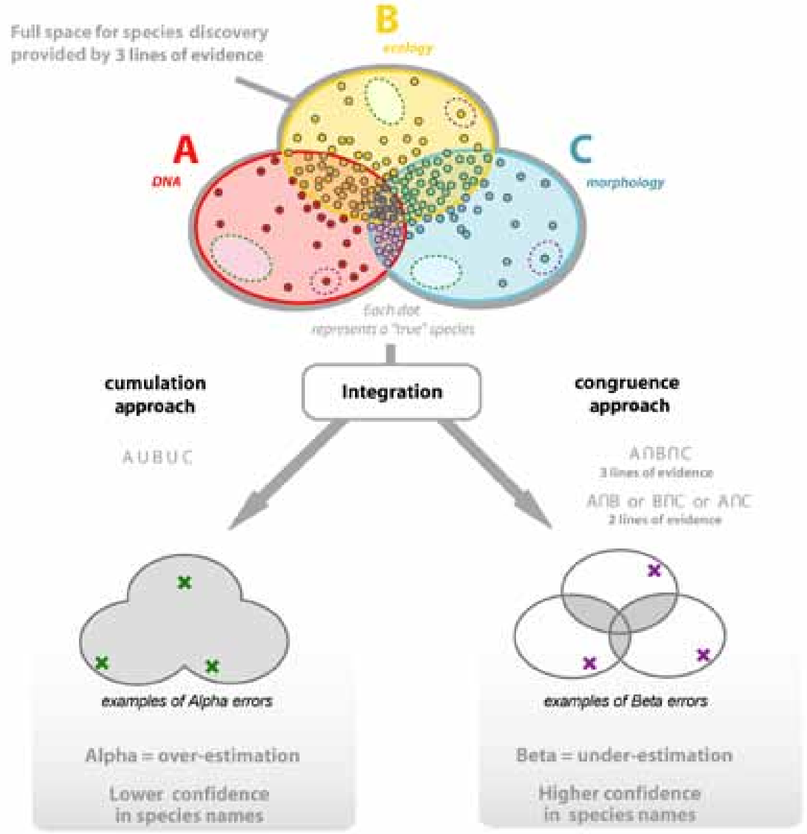


Figure 1.1.3.A Schematic representation of the two approaches of integrative taxonomy (adapted from Padial *et al.* 2010). Background yellow, red, and blue colours represent the spectrum of character variation, each dot being an independent evolutionary linage that requires identification and delimitation as separate species. Integration by cumulation identifies species limits with divergence in one or more not necessarily overlapping taxonomic characters, whereas the integration by congruence identifies species limits with the intersection of two or more independent lines of evidence.

The **cumulation** approach (Fig. 1.1.3.) assumes that divergences in any of the organism attributes that constitute taxonomic characters can provide evidence for the existence of a species if these characters are considered good indicators of lineage divergence. Congruence is desired but not mandatory. The character sets are assembled cumulatively, concordances and discordances are explained from the evolutionary perspective of the populations under study, and a decision is made based on the available information. This approach is probably most suitable to uncover recently diverged species as in adaptive radiations. Its main limitation is that it can lead to the overestimation of species numbers (alfa error) by identifying distinct species where there is intraspecific character variation only.

The **congruence** approach (Fig. 1.1.3.A) examines lineage divergence hypotheses and follows the phylogenetic species recognition concept (see above). This concept states that congruent identification of a population-level monophyletic lineage by several unlinked genetic loci indicates that it is genetically isolated from other such lineages, and thus qualifies as a species, because only in such isolated lineages will the coalescent histories of the different markers agree. It analogously assumes that concordant patterns of divergence among several taxonomic characters indicate full lineage separation. The major advantage of this approach is higher taxonomical stability and the disadvantage is the risk of underestimating species numbers (beta error) because the relative rates of character change during lineage divergence are heterogeneous. Thus, recent radiations and cryptic species may often be overlooked by a strict consensus approach.

Section 1.1.4. Study of biodiversity – the Wallacean shortfall

In so far as the knowledge of the number of species is poor, there is also inadequate knowledge for many taxa of their global, regional, and even local distributions, a problem labelled as the Wallacean shortfall (Lomolino 2004). The science which deals, among other problems, with the Wallacean shortfall is **Biogeography**, defined as the study at all possible scales of analysis of the distribution of biological variation across space, and how it has changed through time (Whittaker *et al.* 2005).

Early spatial analyses were purely spatial in nature (latitude, longitude and elevation). However, the urgency to achieve a significant reduction in the rate of biodiversity loss by 2010 and the availability of software designed specifically to perform spatial analyses transformed this (Fortin & Dale 2005). It is now possible to explore with Geographical Information Systems (GIS) and **species distributions models** (SDMs) the underlying causes of spatial heterogeneity of biological variation using assets of ecogeographical variables (EGVs) and chorological or eco-physiological data. These recent methods, can not only better represent distribution maps and make inferences regarding spatial relationships and the causes of spatial heterogeneity, but also create predictive maps of patterns of biological variation (Thomassen *et al.* 2010). There are two approaches to perform SDMs using mechanistic or correlative models (Fig. 1.1.3.B):

Mechanistic models base predictions of ecosystem processes on real cause-effect relationships. These models use resource gradients which address matter and energy consumed by species (e.g. water) and direct ecological gradients (e.g. temperature) as predictive parameters. For instance, a thermal performance curve represents a fitness component (e.g. survival, growth, reproduction) as a function of body temperature. The principles of biophysical ecology can then be used to translate multivariate environmental space into a set of ranges of variables as a function of key traits (e.g. size, solar reflectivity and metabolic rate), and the performance curve can be invoked to describe the climate space within which the performance curve constrains survival and reproduction. This mechanistic representation of a species fundamental niche (the function of all physiological conditions and ecosystem constraints related to the survival of the species) can subsequently be used to infer distribution limits. Such dynamic models are primarily tested based not on predicted precision, but rather on the theoretical cor-

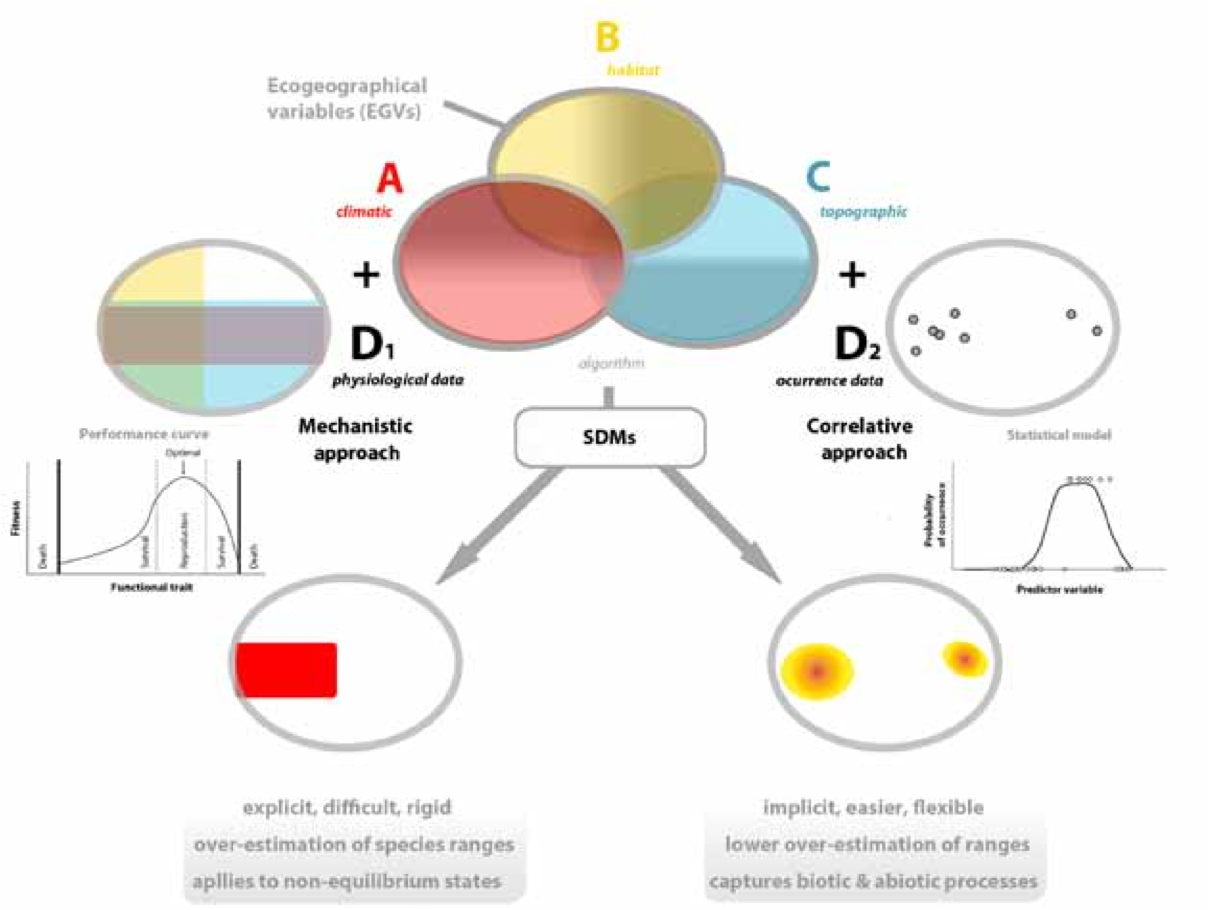


Figure 1.1.3.B Two main approaches used in developing species distribution models (SDMs) (adapted from Kearney & Porter 2009). In a mechanistic approach, SDMs can be derived through knowledge of physiological processes (D1). Functional trait data are linked to GIS data through a model that explicitly captures the key processes by which traits and habitat features interact to determine the species environment. The outcome of that environment for individual fitness (survival and reproduction) and ultimately population dynamics is then mapped to the landscape. In contrast, in a correlative approach, species occurrence data (D2) is modelled as a function of environmental data (A, B, C), ultimately describing a hyper-volume in multivariate space within which the organism has been observed. This niche is then mapped to the landscape to infer potential distributions.

rectness of the predicted response (Pickett *et al.*, 1994). The major advantage of this approach is that it provides deep understanding of the proximate constraints limiting distributions and abundances, so it can also be applied in non-equilibrium contexts such as invasions, translocations, climate change and evolutionary shifts (Kearney & Porter 2009). Its main limitation is that real cause-effect relationships are difficult and expensive to measure, hence only very few species have been studied in detail in terms of their dynamic responses to environmental variables (Guisan & Zimmermann 2000).

Correlative models based predictions on correlations between presence data of a taxon and environmental variables, most of them indirect gradients (with no direct physiological relevance for the species, as slope). Such static models are not expected to describe realistic ‘cause-effect’ relationships between model parameters and predicted response. Their main purpose is just to condense empirical facts (Wissel 1992). These are likely to predict the realized niche (the subset of the fundamental niche that the species actually occupies due to biotic interactions or geographic barriers that have hindered dispersal and colonisation). Often correlative distribution modelling remains the only available approach (Guisan & Zimmermann 2000). Its major advantage is that allows reducing sampling effort either in time and cost, since no detailed knowledge of the physiology and behaviour of the species involved is necessary (Guisan & Zimmermann 2000), contributing to reduce the Wallacean shortfall in a more effective way. It is considered most prudent when the main purpose is interpolative prediction (Dormann 2007). Because of this, it has been widely used in conservation applications to project patterns of diversity across unsampled areas of the landscape in remote areas (e.g. Brito *et al.* 2009) where chorological data most lacks. It can also be useful in the identification of suitable areas for rare species, in the assessment of conservation status of poorly known species (e.g. Papes & Gaubert 2007) and the design of reserves (e.g. Carvalho *et al.* 2010). In addition, there are many modelling techniques available for this approach that may differ in their ability to summarise useful relationships between response and predictor variables (Segurado & Araújo 2004). Differences rely mostly on the type of algorithm used to make the predictions, the type of occurrence data needed, which can be based on presence/absence data or presence-only data, and the type of output prediction. However, this approach has some drawbacks. A hardly realistic state of equilibrium between the environment and observed species patterns is a necessary assumption, at least for the purpose of large-scale distribution modelling. Furthermore, it does not take into account the influence of historical factors on the present day distribution of organisms, and therefore might predict a high likelihood of presence on a site were the species is absent due to past geological or climatic events, such as sea-level fluctuations, or physical barriers, such as high mountains (Guisan & Zimmermann 2000).

SECTION 1.2. ISLANDS AS MODELS FOR THE STUDY OF BIODIVERSITY

Emerson (2002) highlighted some of the reasons why island systems are so remarkable for approaching questions on evolution and conservation. Islands being discrete, internally quantifiable, numerous, and varied entities, can be used as model systems to study evolution and phylogeography, and in this context are often referred to as '**natural laboratories**' (Losos & Ricklefs 2009). As gene flow between islands is practically non-existent for terrestrial species, allowing fixation of genetic variation, differentiation of populations can occur through geographic isolation. If island ages are known, usually the phylogeography of taxa in archipelagos can be analysed within a known timeframe (Emerson 2002). Additionally, their often small geographical size makes the cataloguing of flora and fauna easier than in continental systems. Despite their size, they can contain a substantial diversity of habitats and are often geologically dynamic. Volcanic islands emerge above the ocean surface as blank slates for evolutionary diversification, offering a unique opportunity for observing the entire development of ecological and evolutionary system (Losos & Ricklefs 2009). Furthermore, the investigation and protection of remote islands is particularly important as they usually are not well-studied and possess large numbers of endemics, typically with a relatively higher risk of extinction (Frankham 1997). They can also harbour paleoendemisms, ancient lineages that have become extinct everywhere else and thus can be considered as 'evolutionary museums' (Brandley *et al.* 2010).

Oceanic islands are volcanic islands that have been formed over oceanic plates and have never been connected to continental landmasses. They are typically short-lived and may only exist for a few million years before subsiding and eroding back into the ocean. Remote island biotas differ from those of continents in a number of ways, being generally species-poor, disharmonic and peculiar in taxonomic composition, yet rich in endemic species. On islands, speciation is faster and morphological variation increased (Yoder *et al.* 2010). Also, particularly large and remote islands contribute disproportionately to global biodiversity (e.g. Moody 2000; Wilson *et al.* 2009) and are considered biodiversity hotspots for conservation.

Section 1.2.1. Evolution on islands

Current biodiversity observed on islands is the product of past evolution, which may result from any or all of the following factors: (1) adaptive radiation; (2) multiple successful colonisations from neighbouring islands or continental landmasses; (3) the diversification of a founding population into a number of species caused by vicariant events and; (4) increased speciation through bottleneck and founder flush events (Templeton 1980; Carson & Templeton 1984). Emerson & Kolm (2005) further suggested that species diversity itself could drive speciation by leading to greater community structural complexity. A brief explanation of these evolutionary processes follows.

1. **Adaptive radiation** can be defined as the diversification of a founding population into an array of differentiated forms within the same lineage differentially adapted to diverse environmental niches (Simpson 1953). A classic example of an adaptive radiation are the Galápagos finches, thought to be the result of a single colonisation from the South American continent (Grant & Grant 2008). Another well-studied case is the *Anolis* lizards from the Greater Antilles (Losos *et al.* 1998). According to Yoder *et al.* (2010), adaptive radiation is the result of ecological release (increased population size, broader habitat use and increased trait variation) possibly via relaxation of natural selection due to ecological opportunities (colonisation of new habitats, evolution of key innovations, extinction of antagonists or a combination of these events). Adaptive radiation can result in strong character displacement. This is the process by which initially allopatric similar species evolve in different directions in some character due to competition upon attaining sympatry (Diamond *et al.* 1989). Islands provide unique opportunities to study character displacement because pairs of species often occur in sympatry on some islands and alone on others (Losos & Ricklefs 2009). Extreme phenotypes, such as the largest species within lizard families and bird genera, are detected on islands more often than expected (Meiri *et al.* 2010), although this might also be explained just by ecological release. Molecular phylogenetic analyses of island organisms suggested that size displacement may account for sympatric species of different size as in the regular-sized '*Mabuya'* and the giant *Macroscincus* (=*Chioninia*) *coctei* skinks on the Cape Verde Islands (Carranza *et al.* 2001).

2. A given species group can be the result of a single colonisation event, or on the other hand, can be result of **multiple colonisations** from adjacent landmasses. In the first case, the species group within the archipelago will be monophyletic, while in the presence of multiple colonisations, it will be paraphyletic/ polyphyletic. These assumptions can only be effectively tested by the inclusion of all closely related species from continental areas and neighbouring archipelagos in a phylogenetic context. Molecular phylogenetic studies have revealed, for instance, multiple colonisations events for the *Tarentola* geckos in Macaronesia (Carranza *et al.* 2000, 2002).

3. **Vicariant events** within insular systems can be produced by a diverse array of factors, such as the formation of new volcanoes or lava flows, earthquakes, prolonged droughts or heavy storms, hurricanes, glacially mediated fluctuation in sea levels, among others. These events cause the isolation of small populations, and consequently their differentiation, sometimes until speciation is achieved. For instance, in the Canary Islands, reptiles exhibit phylogeographic patterns that are probably related to recent volcanic activities such as the joining of previously separated massifs in Tenerife, or promoting the isolation of populations, in Gran Canaria (Nogales *et al.* 1998; Brown *et al.* 2001; Juan *et al.* 2000).

4. **Founder-flush** speciation models propose that population bottlenecks can enhance evolutionary potential for rapid species formation (Carson & Templeton 1984; Coates 1992). In this model, a small founder population, highly affected by genetic drift, establishes itself in its new environment under relaxed ecological and selective conditions. Hence, the founding event is followed by a period of rapid population growth, the 'flush phase', in which an increase of genetic variation occurs due to recombination and altered pleiotropic balances. Moreover, because of the high levels of additive variation, the population is prepared to respond to selective forces by moving to alternative adaptive peaks, what might result in speciation (Carson and Templeton 1984). The best known studies implicating founder events in speciation have been conducted in the Hawaiian Islands for *Drosophila* where volcanic activity may have allowed multiple opportunities for isolation and founder events both within and between islands (Carson 1990) thereby promoting diversification of species.

The **general dynamic model** (GDM) of oceanic island biogeography (Whittaker *et al.* 2008) provides a general explanation of biodiversity patterns through describing the relationships between speciation, immigration and extinction through time and in relation to island ontogeny (Fig.1.2.1). It is based on the traditional dynamic equilibrium model of MacArthur & Wilson (1963, 1967) that recognised the number of species on an island as a function of its isolation and area, but adapted to oceanic island systems. On the more remote islands, the pace of immigration is so slow that increasing proportions of the biota mostly result from *in situ* evolutionary change, with cladogenesis most pronounced on larger islands towards the outer limits of the distributional reach of a taxon. Also oceanic islands typically have short life cycles. In the simplest scenario of GDM, an island builds relatively quickly to maximum area and altitudinal range in its youth, then becomes increasingly dissected as it erodes, resulting in loss of both elevational range and area, and then gradually subsides/erodes to disappear back into the sea or persist as a low-lying atoll (Whittaker *et al.* 2008). Considering this scenario, the maximum carrying capacity of an island, in terms of biomass and number of individuals across all species, will be reached roughly coincidently with maximum area and elevational range and with the maximum heterogeneity of environment, and thus maximum opportunity for within-island allopatry, occurring within the 'middle age' of the island. A general hump-shaped trend is expected in potential carrying capacity, species richness and in speciation rate. However, in reality most oceanic islands have rather more complicated scenarios, involving the junction of separated islands, catastrophic episodes like volcanism, slope failures and dramatic climate changes (Whittaker *et al.* 2008).

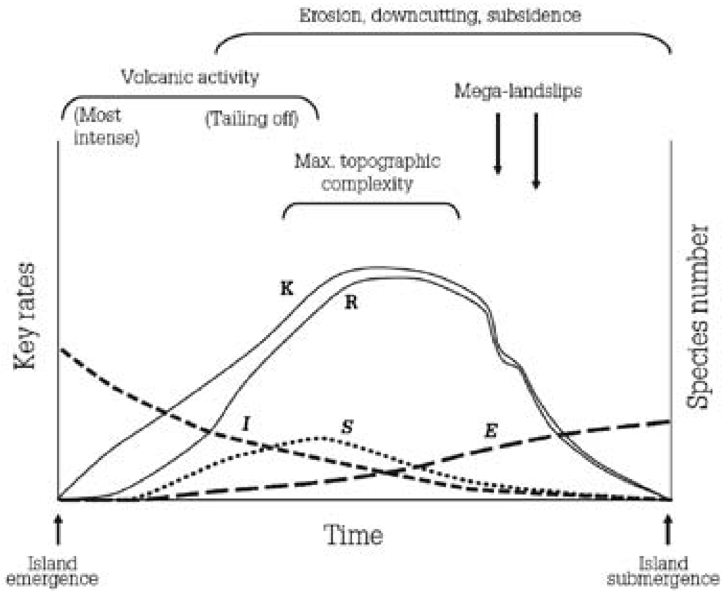


Figure 1.2.1 Graphical representation of the key rates and properties of the general dynamic model (GDM) of oceanic island biogeography, showing the postulated relationships between the biological characteristics and island ontogeny (adapted from Whittaker *et al.* 2008). I, immigration rate; S, speciation rate; E, extinction rate; K, potential carrying capacity for species number; R, realised species richness.

Section 1.2.2. Conservation on islands

The biodiversity crisis is nowhere more apparent and in need of urgent attention than on islands. In fact, islands not only represent disproportionate amounts of endemic diversity (Whittaker & Fernández-Palacios 2007), but they also account for a high proportion of recorded global extinctions over the last few hundred years (Fig. 1.2.2.A) and a high proportion of globally threatened species, especially small oceanic islands (Pullin 2002). A stress on islands is thus an appropriate part of any global conservation assessment based on the currency of species and indeed is common to schemes promoted by all the major international conservation non-governmental organisations (NGOs).

Following Pullin (2002), there are a number of probable reasons for oceanic island faunas being **prone to extinction** including small population sizes; lack of adaptation to large predators and competition and vulnerability to introduced species.

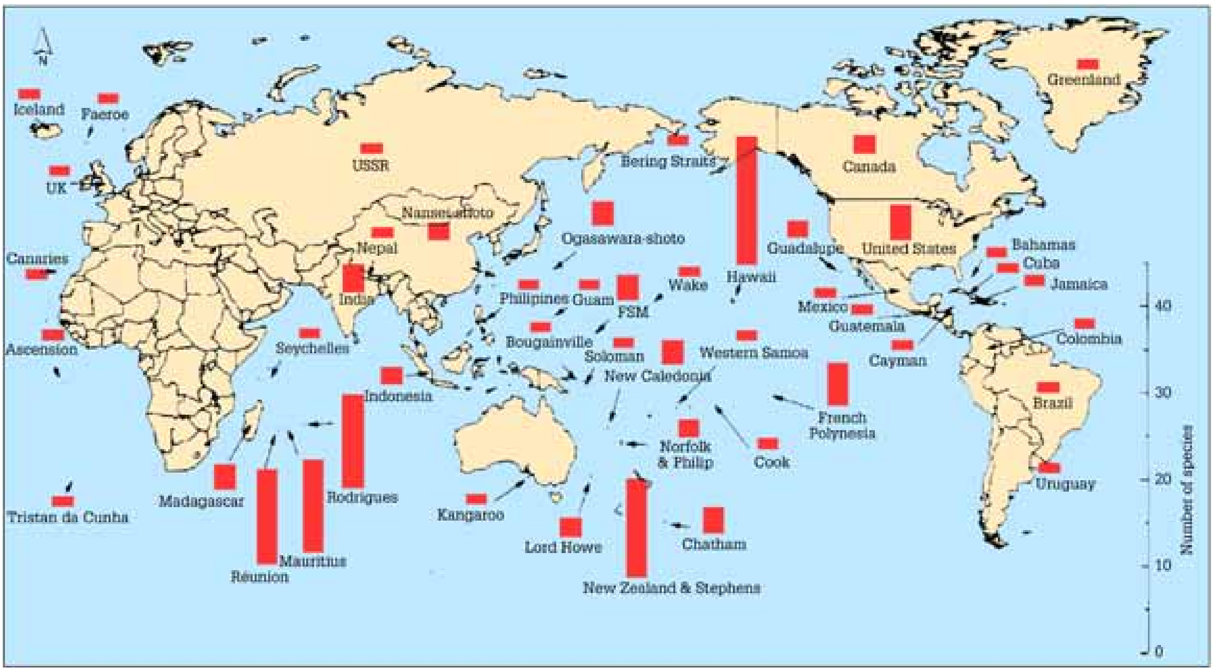


Figure 1.2.2.A Map of recorded bird extinctions since 1600 (adapted from Pullin 2002). Note the high extinction rates on oceanic islands (scale bar on the right side).

In small populations, such as most populations of species restricted to islands, more slightly deleterious mutations are expected to drift to fixation (Woolfit & Bromham 2005). In addition, since island populations experience relaxed selective constraints, few defence mechanisms evolve. The naivety of natives turns them into easy preys or potential habitat-displaced individuals; hence population sizes and distributions can be rapidly and dramatically reduced by new predators and competitors (Case & Bogler 1991). Introduced species can have serious negative impacts on native ones. These impacts include predation, competition for food and other resources, hybridisation, spread of diseases and parasites, and, in the case of reptiles and amphibians, poisoning through toxic skin glands or venomous bites. They may also alter the habitat of native species and disrupt ecosystem dynamics. Unfortunately, it is on islands that this phenomenon is occurring with terrestrial vertebrates more frequently and with a higher probability of successful establishment relative to mainland systems (Kraus 2003). The same also applies to oceanic island floras (Caujapé-Castells *et al.* 2010).

To prevent taxa from going extinct, the Convention on Biological Diversity encouraged governments to endorse *in situ* conservation by establishing a system of **Protected Areas** (PAs). A PA is ‘a clearly defined geographical space, recognised, dedicated and managed, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values’ (Dudley 2008). These areas are an important tool for controlling access to sensitive areas, regulating harvest of certain wildlife, and preventing introduction of plague or predator species and are one of the most effective tools available for long-term biodiversity conservation (Possingham *et al.* 2006). More than 35% of the hotspots total area is already protected in parks and reserves but all are in urgent need of stronger safeguards, especially unprotected areas (Myers *et al.* 2000). Designating PAs is a complex task because there are several competing land-use options and considerable socio-economic costs associated with PAs implementation, thus a prioritisation procedure is mandatory.

The theory of Island Biogeography of MacArthur & Wilson (1963, 1967) was extended to the **Reserve Design** on the assumption that a PA is destined to become an island itself in a sea of habitats modified by man (Wilson & Willis 1975). The goal of reserve design is to predict where the equilibrium between extinction and immigration might fall and how to design a reserve minimising species loss. These ideas were first explored by Wilson & Willis (1975), Terborgh (1974, 1975) and Diamond (1975) and from them a number of 'geometrical rules of design' of nature reserves arose (Fig. 1.2.2.B). One of the rules was that a single large reserve would be better at preserving species than a set of smaller, separate reserves covering the same area. This idea became controversial and therefore became known as the 'single large or several small' (SLOSS) debate. Although few conclusions derived from that debate, it became clear that the better shape, size and number of reserves varied according to the target species, being always preferable to be as large and as many as possible (Kingsland 2002).

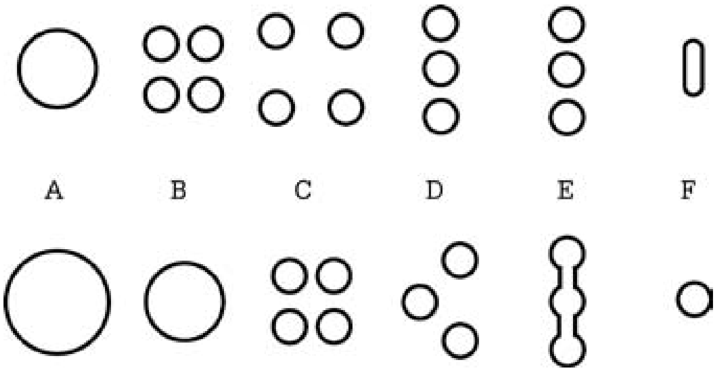


Figure 1.2.2.B Geometric design strategies, based on the equilibrium theory of island biogeography and the species-area relationship, proposed for the design of nature reserves (Diamond 1975). For each of the six designs, A to F, extinction rates are said to be lower and the number of species held at equilibrium are said to be higher for the design at the bottom than at the top.

The SLOSS debate also drew attention to important underlying assumptions concerning the evaluation of conservation efforts, such as representativeness and persistence, two milestones of the current studies on reserve design (Margules & Pressey 2000). To achieve **representativeness** it is required that all relevant features of biodiversity are covered within the selected protected areas with a desired target, while to assure biodiversity **persistence** it is necessary to cover and manage a variety of ecological and evolutionary processes to ensure the long-term maintenance of populations of native species and natural ecosystems.

Currently, new mathematical techniques and the development of computers, have allowed solving two major classes of conservation prioritisation in reserve design: the 'minimum set' and the 'maximal cover' problems (Kingsland 2002). In the '**minimum set**' problem, the objective is to minimise the total number of selected sites, total area, or cost such that each biodiversity unit is represented at or above a pre-determined target. In the '**maximal cover**' problem, the objective is to find a reserve system that contains the largest number of biodiversity units meeting their targets given a limit for the number of sites, cost or area of the selected planning units (see Cabeza & Moilanen 2001). These problems can presently be mathematically formalized and implemented in computational tools that objectively inform the decision-making process, such as multi-criteria optimisation methods (Moilanen *et al.* 2009).

An effective **conservation planning** needs to follow systematically the six-stage framework proposed by Margules & Pressey (2000). First, it is needed to map and measure biodiversity, or to choose the features to be used as surrogates for overall biodiversity in the planning process, and secondly to identify explicit conservation targets for the planning. Third, it is needed to recognise the extent to which conservation goals have been met in existing reserves. Then, explicit gap analyses methods are used and explicit criteria are applied for implementing conservation action on the ground (fourth and fifth stages, respectively). Gap analysis is a planning approach based on assessment of the comprehensiveness of existing protected area networks and identification of gaps in coverage (Scott *et al.* 1993). Once identified, gaps are filled through new reserve acquisitions or designations, or through changes in management practices. Finally, it is needed to adopt explicit objectives and mechanisms for maintaining the conditions within reserves that are required to foster the persistence of key natural features, together with monitoring of those features and adaptive management.

Conservation planning has focused more on achieving representativeness than persistence. Since conservation is not about protecting a static welfare, but a dynamic mechanism by which diversity of life is maintained and generated, evolutionary processes must be taken into account. **Genetic diversity** is the reservoir for future evolution; it is thus important to make sure that the widest possible range of existing diversity is protected (Petit *et al.* 1998). Intraspecific genetic diversity, as the primary motor of evolution, is thus central in this endeavour (Bonin *et al.* 2007). Nevertheless, maintaining species diversity has been the main objective of conservation policies so far, to the detriment of intra-specific genetic diversity (Margules & Pressey 2000). It is now regarded necessary to consider the conservation of intraspecific diversity together with the protection of species and habitats in an integrative approach of conservation biology (Bonin *et al.* 2007), incorporating technologies to speed up and increase the accuracy of conservation decision-making (DeSalle & Amato 2004). Detailed maps of genetic, phenotypic and demographic variation have recently been used to address a broad array of topics, such as the prioritisation of areas for conservation (Thomassen *et al.* 2010).

Moritz (2002) argued for separation of genetic diversity into two dimensions, one concerned with adaptive variation arising directly from adaptive evolution due to natural selection and the other one with neutral divergence caused by isolation, genetic drift, mutation or migration. Adaptive features may best be protected by maintaining the context for selection, heterogeneous landscapes, and viable populations, rather than protecting specific phenotypes (Moritz 2002). By contrast, conservation of species and specific areas should emphasise protection of historically isolated lineages or so-called evolutionarily significant units (ESUs) because these cannot be recovered (Moritz 2002; Höglund 2009). Given the difficulty in measuring adaptive variation for wild species, molecular markers are valuable surrogates and in some cases may be conservative estimates of the expectations of loss and recovery of quantitative genetic variation (Lynch *et al.* 1999). Furthermore, molecular methods are less time and effort consuming, so surveys of molecular variation have rapidly become a convenient shortcut to evaluate global genetic diversity (Petit *et al.* 1998, Garner *et al.* 2005).

Island populations have the potential to be genetically valuable, this is, to be differentiated from other populations, or to contain high levels of allelic diversity, especially on large or highly remote islands (Wilson *et al.* 2009). This turns island populations into obvious candidates for within-species conservation. Nevertheless, few reserve design studies have taken into consideration genetic variability among and within populations in islands systems. Smith *et al.* (2000) and Kahindo *et al.* (2007) studied the mitochondrial lineages of avian species in an island-like system, the mountain regions on Africa, and considered distinctive lineages worthy of conservation concern. Setiadi *et al.* (2009) tested whether the two disjunct blocks constituting a National Park of an Indonesian island adequately captured the full breadth of genetic diversity of endemic species of herpetofauna. These studies evidenced that the study of the distribution of genetic variation within species can provide useful information for biodiversity conservation, however its concrete application to reserve design at a national scale remains unexplored.

SECTION 1.3. STUDY AREA: THE CAPE VERDE ISLANDS

The Cape Verde Islands were included in the top 200 most biologically valuable terrestrial ecoregions identified by Olsen & Dinerstein (1998) and as part of one of the 25 and 34 hotspots by Conservation International (Myers 2000; Mittermeier 2004), within the European and Central Asian Mediterranean Basin. However, only 2.47% of the terrestrial territory of this country is protected, following the World Database on Protected Areas (IUCN & UNEP-WCMC 2010).

Section 1.3.1. Geography and climate

Biogeographically, Cape Verde belongs to the **Macaronesian region** (from the Greek *makaron= fortunate*), which is composed by the Madeira, Selvagens, Azores, Canaries and the Cape Verde archipelagos. Some authors include as well in this region an enclave on the African mainland, comprising southern Morocco and Western Sahara. This group of islands is the Atlantic equivalent of Hawaii and the Galápagos, providing a rich mix of geological, evolutionary and ecological insights on the one hand and biodiversity conservation problems on the other (Whittaker & Fernández-Palacios 2007).

The Cape Verde archipelago lies in the North Atlantic Ocean, 570 km from the West African Coast and 1500 km south of the Canary Islands in the West Mediterranean region, situated between 14º45'-17°10' N and 22º40'- 25°20' W (Fig. 1.3.1.A). It spreads over 58,000 Km^2 of ocean and has about 1050 km of coastline (Duarte & Romeiras 2009). The archipelago is composed by ten main islands and several islets. These islands are usually classified in two groups, the Windward (Santo Antão, S. Vicente, Santa Luzia, S. Nicolau, Sal and Boavista) and Leeward Islands (Maio, Santiago, Fogo and Brava). However, in the present work, they are topologically divided into north-western (Santo Antão, S. Vicente, Santa Luzia and S. Nicolau), eastern (Sal and Boavista) and southern (Maio, Santiago, Fogo and Brava) island groups (Fig. 1.3.1.A). Santiago is the largest island, where more than half of Cape Verdeans live (around 450,000 inhabitants as of the 2000 census), whereas the smallest island – Santa Luzia – is uninhabited. Several seamounts also come close to the sea surface (Noroeste, Nova Holanda, Bancona and João Valente) around these islands.

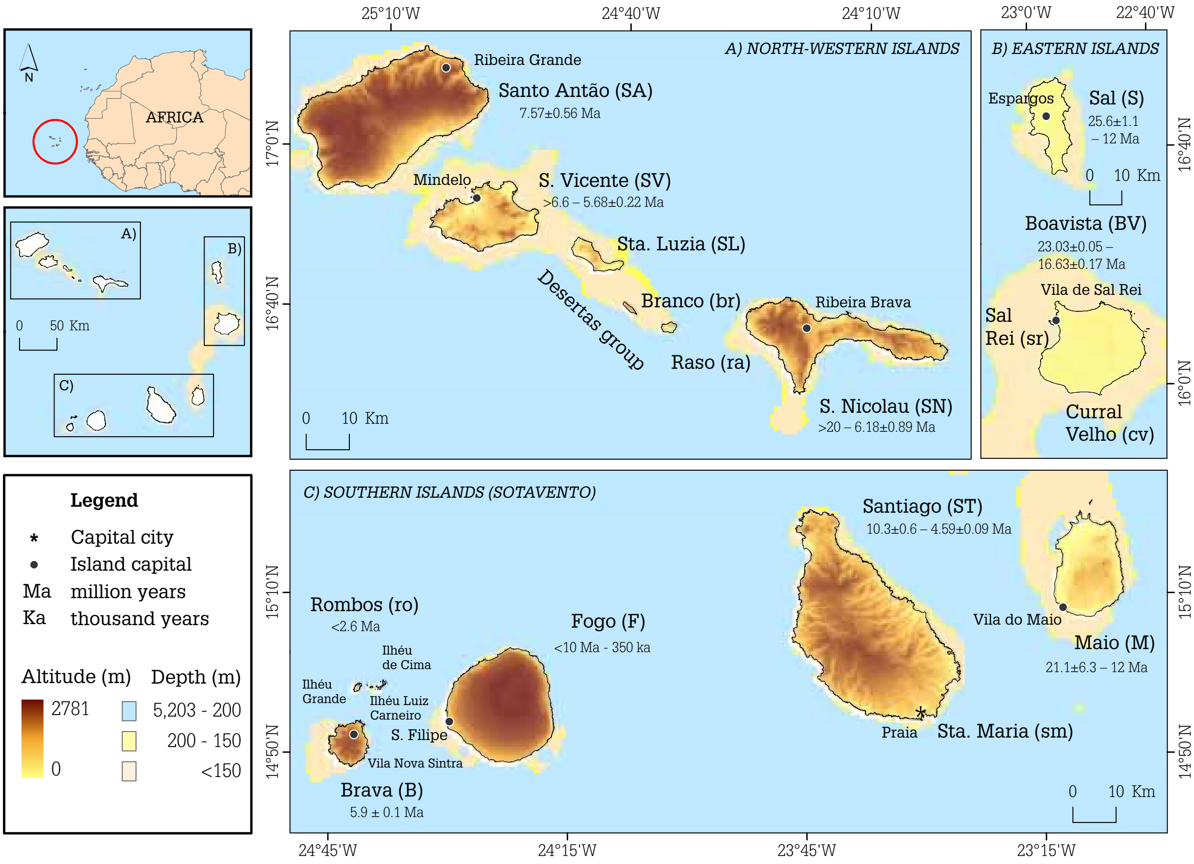


Figure 1.3.1.A Map of the Cape Verde Islands showing the geographic location, bathymetries and elevations of the three island groups (Geographic Coordinate System, Datum WGS84). Estimated age ranges of most islands and extent of the islands exposed by lower sea levels during the Pleistocene ice ages (in beige) are also indicated.

The landscape of the north-western and southern islands, in particular Santo Antão, São Nicolau, Santiago and Fogo is characterised by steep, high mountains and deep river valleys and offer a wide range of habitats (Fig. 1.3.1.B) in relatively small areas. Steep slopes suffer from active fluvial erosion (average of 7.8 tons/ ha/ year). Overgrazing and poor agricultural practices have further exacerbated the problem. Conversely, the eastern islands of Boavista and Sal, and the southern island of Maio, having experienced greater erosion, are more flat and less diverse in habitats, with peaks only few hundred meters in height and surrounded by relatively broad extents of plain arid land, where deposition is dominant (Fig. 1.3.1.B).

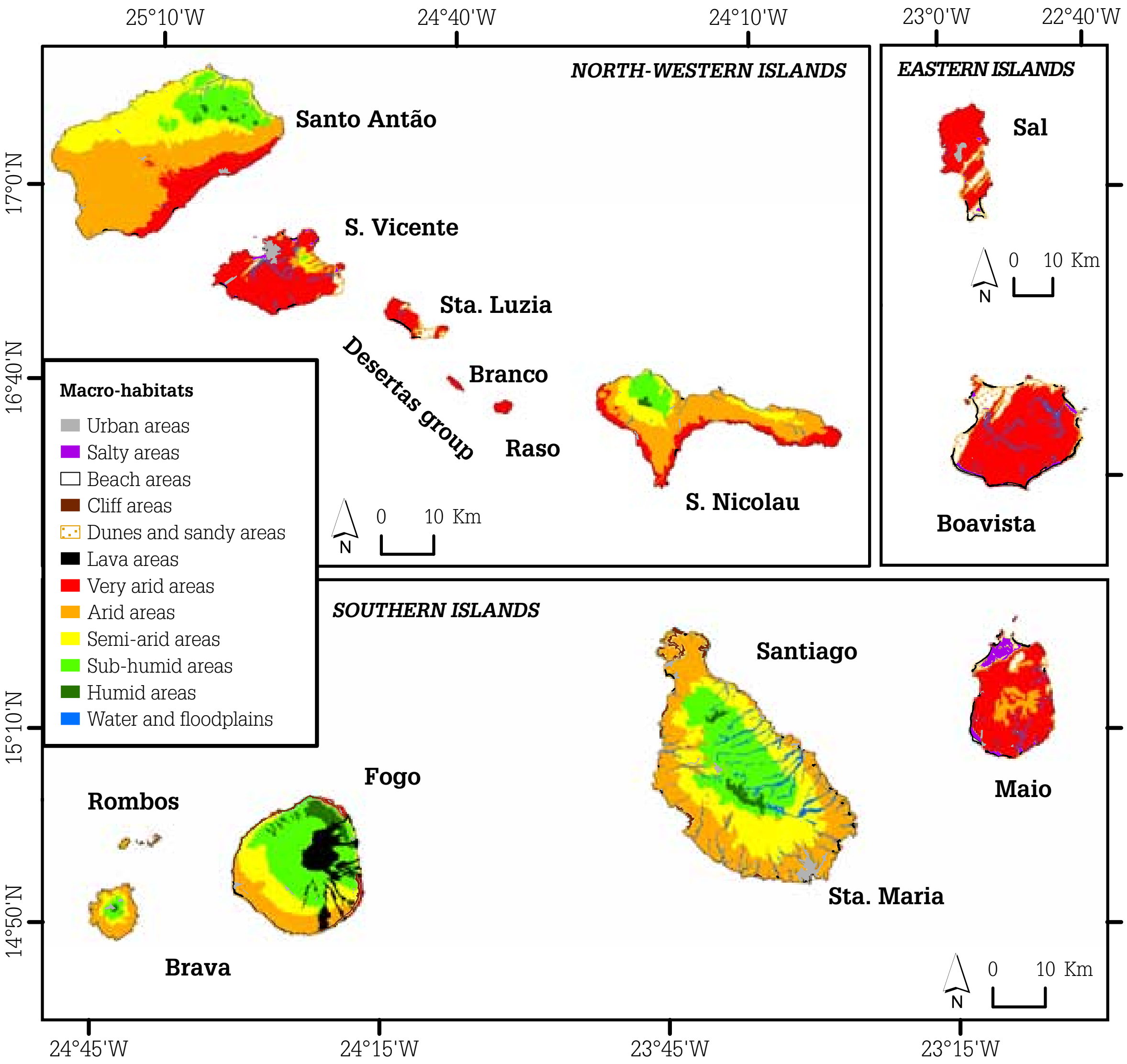


Figure 1.3.1.B Main habitat types in the Cape Verde Islands (Geographic Coordinate System, Datum WGS84; adapted from Diniz & Matos 1986, 1987, 1988 a, b, 1993, 1994, 1999 a, b, c).

Soils are mainly of volcanic origin. They originated from volcanic rocks like basalts, phonolites, trachytes, andesites, tuffs, scorias, and sedimentary rocks, mainly limestone (Duarte & Romeiras 2009). The variety of soils reflects its microclimatic and topographic diversity: on the north-eastern slopes of the higher mountains it possesses good physical and chemical properties; at lower altitudes soils are incipient with low organic matter and nitrogen contents; in the eastern islands and Maio, dunes display maximum development (Duarte & Romeiras 2009).

The archipelago is located at the border of the North African arid and semiarid climatic regions, with a **climate** defined as dry tropical Sahelian. It experiences climates ranging from tropical dry to semi-desert, which are governed by the Azores anti-cyclone, the Inter-tropical Convergence Zone (ITCZ) and the mid-Atlantic air mass movements induced by their seasonal changes of location (Duarte & Romeiras 2009).

Annual precipitation (Fig. 1.3.1.C) might be the primary limiting factor for distribution of biodiversity since it is between 40 to 604 mm (mean=235±135 mm), reaching 0 to 2 mm in the driest month and 23 to 213 mm in the wettest month (mean=97±48 mm) (Hijmans *et al.*, 2005). Rainfall is lower for the 65% percent of the territory that is located below 400 meters in elevation and is concentrated between July and October with potential evaporation exceeding precipitation throughout the year (Duarte & Romeiras 2009). Analysis of the hydrological balance shows that a total of 180 million cubic meters of water fall upon Cape Verde annually. However, due to a lack of intake and storage structures, 87% of this rain fall is lost to run-off and evaporation (MAAP-DGA 2004). North-eastern trade winds, representing 78% of all winds (Schleich & Schleich 1995), carry moderate humidity throughout the year. Another important wind mass is the Harmattan, a dust-laden, hot, dry wind that blows from the southern Sahara Desert, usually between November and May.

Temperature ranges are narrow as the climate is moderated by the surrounding ocean (Fig. 1.3.1.C). The annual mean temperature is between 9.4 and 26.7 °C (mean=22.1±2.8 °C), ranging only in 8.0 to 12.2 °C (mean=10.4±1.2 °C) throughout the year, with temperatures on the warmest month ranging from 15.0 to 31.2 (mean=27.3±2.9 °C) and on the coolest from 4.0 to 22.3 (mean=16.9±2.7 °C) (Hijmans *et al.* 2005).

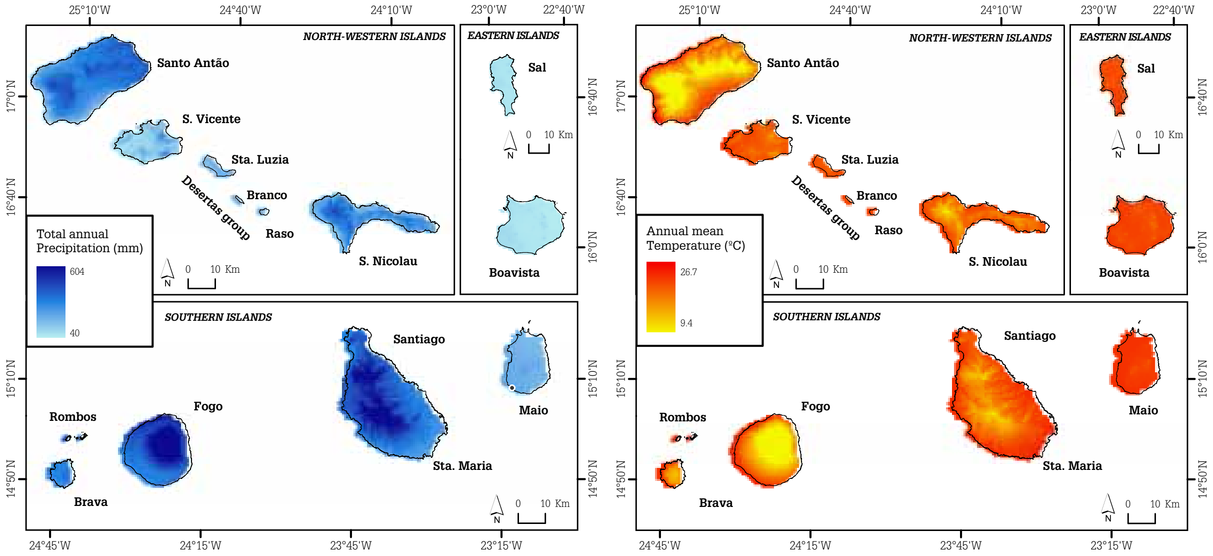


Figure 1.3.1.C Annual precipitation (mm) and annual mean temperature (°C) in the Cape Verde Islands (Geographic Coordinate System, Datum WGS84; adapted from Hijmans *et al.* 2005).

Section 1.3.2. Geology and oceanic currents

The Cape Verde Rise is one of the largest swells in the oceans, rising some 2.2 km above the expected depth of late Jurassic to early Cretaceous-aged sea floor within a pseudo-circular region circa 1200 km in diameter (Williams *et al.* 1990). The Cape Verde Rise and its associated **volcanism** were probably originated by hot-spot bathymetric swells, the surface expressions of plumes ascending from the deep mantle (Pim *et al.* 2008). This hot-spot is still active: recent volcanic activity was register on Fogo Island in 1951 and 1995, and appears to be moving southwest where it may form a new oceanic island in the future (Grevemeyer *et al.* 2010).

The archipelago is located in the southwest part of the Cape Verde Rise. The Cape Verde Islands appear to be composed of the oldest subaerial rocks in Macaronesia (Duarte & Romeiras 2009). The archipelago does not form a linear island chain, but a horseshoe-shaped clustered group of volcanic edifices with the concavity facing westwards (see Fig. 1.3.1.A). They show a weak age progression from east to west, which is thought to have been induced by the slow movement of the African tectonic plate, and so the youngest islands are the ones on the tips of the arch (Holm *et al.* 2006). The subaerial volcanism probably began during the Miocene or pre-Miocene. Quaternary igneous activity is concentrated at the western end of the archipelago. The age of the oldest rocks, found on Sal Island (see Fig. 1.3.1.A), is about 25.6±1.1 million years, My, old (Torres *et al.* 2002). Boavista is thought to be around the same age as Sal (Mitchell-Thomé 1976, 1985; Stillman *et al.* 1982), certainly >16.63±0.17 My old (Dyhr & Holm 2010). The islands of Santo Antão and Brava thus present the youngest subaerial Tertiary volcanism, which can be dated to 7.57±0.56 (Plesner *et al.* 2002, Knudsen *et al.* 2003, Holm *et al.* 2006) and 5.9±0.1 My old (Torres *et al.* 2002), respectively. Santiago Island dates from 10.3±0.6 to 4.59±0.09 My old and Maio Island 21.1±6.3 My old (Torres *et al.* 2002, Holm *et al.* 2008). The ages of S. Vicente and S. Nicolau Islands are estimated between >6.6 Ma and 5.68±0.22 My (Jørgensen & Holm 2002; Holm *et al.* 2008) and >20 My and >6.18±0.89 My old (see Duprat 2007), respectively.

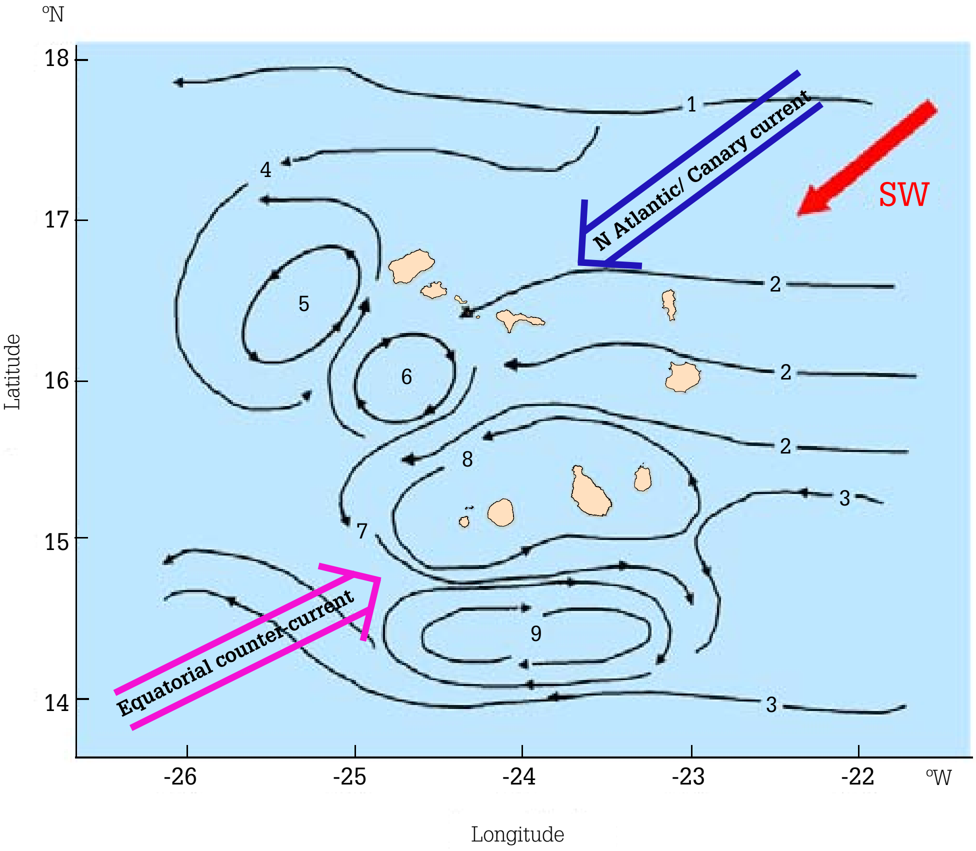


Figure 1.3.2 Large and small scale oceanic currents model in Cape Verde Islands, following Medina (2008). Small scale currents are numbered from 1 to 9. Main south-western trajectory of particles at surface is signalled by a red arrow. (1) Northern Canary current; (2) Middle Canary current; (3) Southern Canary current; (4) Cyclonic current; (5) Temporary cyclonic current (December & January); (6) Anti-cyclonic current; (7) North-South current; (8) Circum Leeward current; (9) Anti-cyclonic North-South current (dry season).

During sea-level fluctuations in the Pleistocene there were some islands of the north-western group (São Vicente, Santa Luzia, Branco and Raso islets) and possibly also Boavista and Maio (see Fig. 1.3.1.A) that were most likely linked (Mitchell *et al.* 1983), possibly allowing fauna migrations between them. However, in general the archipelago is highly fragmented and dispersed, with islands and group of islands physically iolated by depths often over 3000 m (Medina *et al.* 2007).

The islands are also under the strong influence of large-scale **oceanic currents**. These islands are in between the southern boundary of the cold northern anti-cyclonic current of the North Atlantic and Canaries and the northern limit of the warm equatorial counter-current (Fig. 1.3.2.). These two systems of oceanic currents present seasonal variations regulated by the Azores anti-cyclone (Medina *et al.* 2007). The small-scale oceanic currents identified by Medina (2008) are (Fig. 1.3.2.): 1) Northern Canary current, which passes through the North without strong effects on the circulation between islands; 2) Middle Canary currents, which cross the islands from East to West having a major impact on the circulation between islands; 3) Southern Canary current, which passes on the South without strong effects on the circulation between islands; 4) part of North-current that changes direction towards the South; 5) and 6) North-eastern asymmetric eddies circulation, originating from currents 4 and 2 after penetrating the islands; 7) North-South current, which transports significant amount of water from the North and is originated in currents 2, 4, 5 and 6; 8) Circum-Leeward current, originated from currents 2 and 7 and which encloses southern islands completely; 9) anti-cyclonic North-South circulation originated from currents 7, 8 and 3 which is unstable and degenerates in the southern current. This circulation pattern is driven by interactions between the climate seasonality, the large-scale oceanic circulation and the local small-scale effects of islands geomorphology.

The main trajectory of particles at surface (Fig. 1.3.2.) recovered during Lagrangian drift simulations is south-west (Medina 2008), coinciding with the direction of the trade winds (Duarte & Romeiras 2009). This information might be important to understand colonisation patterns of organisms that reached the islands by rafting. Nevertheless, it is unknown if oceanic currents suffered any changes since the Miocene until the present days.

Section 1.3.3. State of terrestrial biodiversity

Presently about 3251 terrestrial species are known in the Cape Verdes, of which 540 are endemics and 240 of those exclusive of only one island (Arechavaleta *et al.* 2005). This country encompasses 9% of the Macaronesian endemisms. However, the species are unequally distributed by taxonomic groups and islands. Around 60% are arthropods and only two percent are vertebrates (Fig. 1.3.3.A). Santiago presents the highest number of species and endemisms and Desertas group (Santa Luzia Island and Branco and Raso Islets) the lowest (Fig. 1.3.3.B). The present state of the different taxonomic groups is presented in the following paragraphs.

There are **fungus species** from seven different classes, although none is endemic, and most species are Urediniomycetes. There are at most 320 taxa of lichens and fungi associated with lichens, although endemics are rare (Mies 1993). A high percentage of the lichens are threatened or extinct in the archipelago (29%) mainly due to increased aridity (MAAP-DGA 2004).

Considering **plant species**, since no description of the original vegetation or studies about pollen records exists it is difficult to evaluate its lost. It has been deduced from the few available early records that, at the time of their discovery, the Cape Verde Islands probably supported a fairly continuous cover of perennial grasses and small shrubs (Bullock *et al.* 1996). It would also have supported dry monsoon forest, dominant only in the wetter interiors and valley bottoms of the mountainous islands (Bullock *et al.* 1996). However, the original vegetation cover has been destroyed over the centuries. Presently more than 50% of the flora is probably introduced (Brochmann *et al.* 1997). Forest fragments are now restricted to areas where cultivation is not possible, such as mountain peaks and steep slopes (WWF & McGinley 2008).

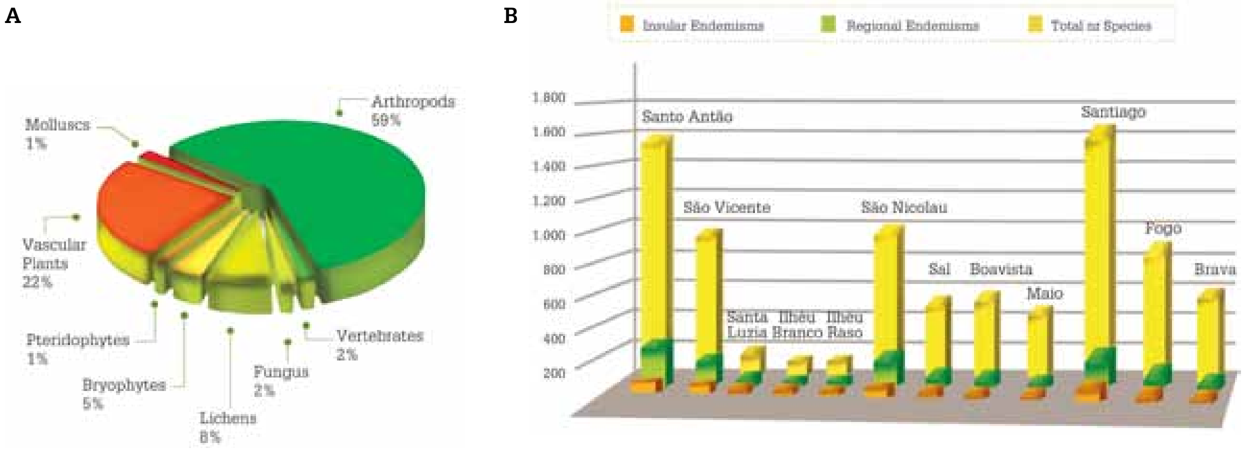


Figure 1.3.3.A) Terrestrial biodiversity in the Cape Verde Islands among taxonomic groups; **B)** Total number of insular and regional endemisms and of all terrestrial species among the Cape Verde Islands. Adapted from Gobierno de Canarias Consejería de Medio Ambiente y Ordenación Territorial (2008).

The native flora of the Cape Verde Islands consists of around 150 briophyte taxa (Frahm *et al.* 1996), circa 35 pteridophyte taxa (Lobin *et al.* 1998) and 240 angiosperm taxa, of which 85 are endemic species. All gymnosperms are introduced (Gomes *et al.* 1995, Brochmann *et al.* 1997). Most of the endemic species are woody perennials, mainly shrubs or sub-shrubs, with only few native tree species, such as the endemic date palm (*Phoenix atlantica*) and the Critically Endangered marmulan (*Sideroxylon marginata*) (Leyens & Lobin 1996; Arechavaleta *et al.* 2005). It is important to mention that more than a third of the bryophytes present on the archipelago are threatened and that two endemic pteridophyte species have already disappeared. Also many of the endemic angiosperm taxa are threatened, such as some ciperaceas, restricted to the northeast of Santo Antão, and *Echium* species (Leyens & Loban 1996; Romeiras *et al.* 2007).

The main threats to plants are the combined effects of poor agricultural techniques, the devastating effects of grazing herds and harvests for medicinal and traditional uses, such as fuel wood extraction (Duarte & Romeiras 2009). Another threat is the introduction of exotic plants for agriculture and pastures, especially *Furcraea sp.* and *Lantana camara*, and tree species for reforestation. The process of desertification of Cape Verde Islands also affects this group (MAAP-DGA 2004).

Considering the **invertebrates**, around 1915 arthropod species are known of which at most 435 are endemics (Arechavaleta *et al.* 2005). Insects are the most represented group with more than 1650 species. Endemic freshwater crustaceans, shrimps of *Atyidae* family were all recently extinct and around 30% of endemic arachnids are threatened. The molluscs are represented by extra-marine and terrestrial freshwater gastropods, the latter ones occurring at high altitude areas. More than half of these are threatened with extinction. The main threat to the invertebrate fauna is overexploitation of the water resources (MAAP-DGA 2004).

Concerning the **vertebrates**, birds are the most represented group, since no native amphibians and few mammals are found on the archipelago, as is usual on oceanic islands (Whittaker & Fernández-Palacios 2007). No references to fresh-water fish species are found, probably because the archipelago has almost no watercourses on the surface. Regarding amphibians, there is one supposedly introduced species of toad, the African common toad (*Amietophrynus regularis*), probably brought by the Portuguese from continental Africa to fight mosquitoes (see Vasconcelos *et al.* 2010 in Appendix A.I). There is also an old reference of an unknown species of frog, with non-confirmed presence, made by Serpa Pinto in 1896 in a letter to Bocage. Information concerning reptiles is detailed on the following section 1.4.

The current conservation status of avian species is of concern. There are 187 species of which 36 to 40 are terrestrial that reproduce on the interior of the islands and around 14 are endemic taxa (Naurois 1994; Hazevoet 1995). Around 47% of the birds of the Cape Verde Islands are threatened, including 17 species that reproduce solely on these islands (Leyens & Lobin 1996). Several endemic birds are also listed as Endangered, including the endemic Raso lark (*Alauda razae*), which only exists on a seven-squared-kilometre-islet, Raso (Clarke 2006), and the bird of prey Cape Verde buzzard [*Buteo (buteo) bannermani*]. Birds are threatened by direct persecution, pesticides, hybridisation with other species, increased aridity, deforestation and introduction of exotic predators, such as domestic cats.

Concerning the mammal fauna, there are several widespread introduced species, namely rats (*Rattus rattus*, *R. norvegicus*), domestic mouse (*Mus musculus*), cat (*Felix catus*), goat (*Capra hircus*), donkey (*Equus africanus asinus*), green-monkey (*Chlorocebus sabaeus*), presently only on Santiago and perhaps Fogo Islands (Masseti & Bruner 2009) and domestic rabbit (*Oryctolagus cuniculus*), introduced a few centuries ago (Masseti 2010) and now totally disappeared from the archipelago (Naurois 1994). There are also five species of bats (Naurois 1994) that might have colonised the islands by passive transport (Pucetti & Zava 1988). The species of bats were identified as *Taphozous nudiventris*, *Pipistrellus savii*, *Pipistrellus kuhli*, *Plecotus austriacus* and *Miniopterus schreibersi* (Pucetti & Zava 1988). All bat species were considered recent and rare on the archipelago (Tranier & Naurois 1985). However, all of these few records of this cryptic group are based on morphological characters only. Thus, it is also possible that they might be native and that the far distance to the African continent and adaptation to the arid Cape Verdean habitats could have led to speciation as has occurred in the Canary Islands (Juste *et al.* 2004). Additionally, in 1990, skeleton remains of the Mediterranean monk seal (*Monachus monachus*) were found on Sal and some live animals were reported by fisherman, raising the hypothesis of a small population still persisting there (Hazevoet 1995; Hazevoet & Wenzel 1997).

Since the discovery of the uninhabited archipelago by the Portuguese in 1462, terrestrial biodiversity is being lost fast. Slaves were brought from the West African coast to work on cotton, fruit-trees and sugar-cane plantations. Introduced mammals also accentuated soil erosion and biodiversity lost. Many terrestrial endemic and native species, some of which are economically valuable, are now at risk of extinction. Cape Verdean biodiversity is of enormous scientific value; therefore conserving it is a world concern.

Apart from the specific threats to biodiversity above mentioned, there are other threats to the ecosystems that lead to the decrease of water quality, soil erosion and consequentially to species extinctions. The unsustainable and inefficient management of abiotic natural resources, as extraction of rock, sand, and soil for construction and of water resources are such examples. Also habitat degradation and destruction, and dispersal of untreated human waste are preoccupying. Nevertheless, Cape Verde has undertaken since the 1970's strong **conservation actions** to restore the environmental equilibrium. Reforestation and construction of stonewalls and dikes programs were implemented to aid in combating the problem of erosion, which has an averaging rate of 7.8 tons/ha/year. Although the problem remains severe (MAAP-DGA 2004), reforestation significantly increased avifauna populations (MAAP-DGA 2004) for species such as of the endemic grey-headed kingfisher (*Halcyon leucocephala*) and the native common quail (*Coturnix coturnix*).

In 1982 at the world congress on national parks, the Macaronesian Islands were identified as priority area for PAs development because of the low percentage of representative habitats protected in this region (Harrison *et al.* 1982). Then, in 1988, the National Institute of Agrarian Development and Research (INIDA) took the first steps toward a wildlife conservation program by initiating a national PAs network project. As a consequence, the Desertas island group (Sta. Luzia and Raso, and Branco islets; see Fig. 1.3.1.A) were declared as Natural Reserves in 1990 (Anonymous 1990), helped by the pressure made by international researchers. Later, in 1995, the government ratified the Convention of Rio de Janeiro on Biodiversity which led to the publication of the First Red List of Cape Verde (Schleich 1996). This resulted in the promulgation of the law for the protection of plant and animal species

(Anonymous 2002) and for the creation of a PAs network (Anonymous 2003a). One marine reserve and 46 terrestrial PAs will outline the national PAs network. All islands and the islets of the archipelago except Brava are targeted in that program. Four PAs are legally established in Santiago, S. Nicolau, Fogo and Sta. Luzia and three of them already have management plans (Anonymous 2003b, 2007a, b, 2008).

Other international conventions were signed, namely the RAMSAR convention in 2005, on the protection on important wetlands, especially for birds, and the CITES agreement on the international trade of endangered wild species. Civilians also mobilised two NGOs directed to the environmental protection. Recently, the General Direction of Environment (DGA) together with the Ministry of Environment, Agriculture and Fisheries (MAAP) published several reports on the state of the environment and biodiversity (MAAP-DGA 2004). Also a database on biodiversity and a monitoring mechanism of the state of the biodiversity was created and a National Strategy and Action Plan on Biodiversity and for the Environment (PANA) were elaborated and are valid until 2013 (MAAP 2004).

The stage is set, yet chorological, ecological and genetic data are missing for most of the species, particularly in formats that policymakers and administrators can interpret (Miller 1993). Gathering the data needed to perform conservation management is thus a challenging task of higher importance.

SECTION 1.4. STUDY GROUP: THE CAPE VERDE REPTILES

Reptiles, because of their low metabolic rates and resistance to dryness and, in some groups, to salinity are the second most capable vertebrates of colonizing oceanic islands after birds (Carranza *et al.* 2000). Among reptiles, geckos and skinks are more prone to long-distance colonisation (Carranza & Arnold 2003). Geckos are especially favoured on transmarine dispersals by their adhesive toes, which increase the ability to maintain position on natural rafts (Carranza *et al.* 2000), and the capacity to lay calcareous eggs that can often resist exposure to salt water.

Reptiles in general, and in the Cape Verde Islands in particular, are good model species for taxonomic and phylogeographic studies because they are diverse, some cryptic but with alpha-taxonomy roughly known, most locally abundant, easy to manipulate and to collect non-invasive samples and poorly studied (Jesus 2005). They are also non-volant, thus good models from where to extract information on historical patterns and evolutionary processes that certainly affected most other terrestrial taxa. Furthermore, a considerable proportion of this taxonomic group are globally threatened (Gibbons *et al.* 2000). There have been dramatic losses of reptilian species, as a result of the vulnerability of isolated island endemics, with up to 90% of reptile extinctions being island endemics (WCMC 1992).

In Cape Verde, reptiles are present in every island, which present different sizes, habitats and altitudes and for which some of the ages are known; hence reptiles may provide valuable insights into colonisation patterns and adaptive radiation. Reptiles are the less studied vertebrate group in the archipelago; hence extensive studies targeted on them are more relevant for conservation purposes.

Section 1.4.1. Previous studies

From the 18th century until the beginning of the 20th century, European museums ordered various explorers and naturalists to bring reptile specimens of each species from the Cape Verde archipelago to their national collections. The Lisbon Museum received specimens from João Feijó (1780-1800's), Leygarde-Pimenta and Ferreira Borges (1860's), Serpa Pinto (1890's), Newton (1890-1900's), Hoppfer (1870-1900's) and others. Similarly, museums from Paris, Geneva and London received them from Chevalier (1930's), Fea (1890's) and Rev. Lowe (1900's), respectively.

The firsts studies on the taxonomy, systematic and morphology of the Cape Verdean herpetofauna were conducted by Bocage (1873, 1875, 1896, 1897, 1902), Boucourt (1870), Boulenger (1885, 1887, 1906), Duméril & Bibron (1839), Gray (1845), Orlandi (1894), O' Shaughnessy (1874), Peracca (1891) and Vaillant (1882), describing several new species to science. They were particularly interested in the giant saurian (Fig.1.4.1) of the Desertas group (see Fig. 1.3.1.A). Later Angel (1935, 1937), Brygoo (1985, 1990), Dekeyser & Villiers (1951), Greer (1976), Mertens (1955) and Loveridge (1947) also addressed morphological studies on the Cape Verdean endemic reptiles. In the late XX century, Schleich visited the Islands during the 1980's and published several articles on distribution, taxonomy and systematic of these reptiles (Schleich 1980, 1982, 1984), describing new taxa (Gruber & Schleich 1982), and reviewing their distributions essentially at an inter-island scale (Schleich 1987). Later, Joger (1984a, 1993) described two more new reptile taxa for the Cape Verdes; Mateo and colleagues (1997, 2005) and Lopéz-Jurado and colleagues (1999, 2005) focused specially on the Desertas group (see Fig. 1.3.1.A) and the giant skink, and listed all reptiles species and Andreone (2000) revised the collections made by Fea.

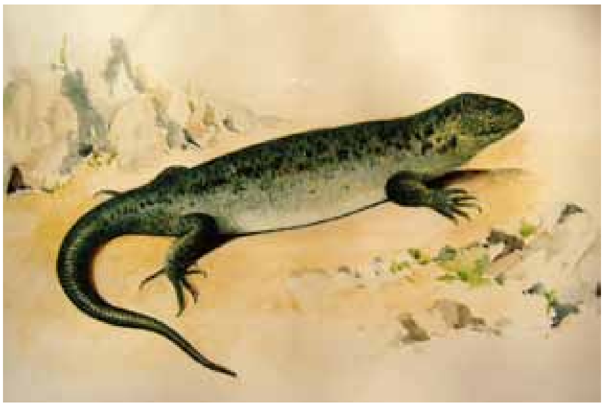


Figure 1.4.1 Giant skink, *Chioninia* (=*Macroscincus*) *coctei*, of the Desertas island group (from painting by Silva Lino).

More recently, genetic studies were conducted by Brehm *et al.* (2001), Brown *et al.* (2001), Carranza *et al.* (2000, 2001, 2002), Carranza & Arnold (2003, 2006), Jesus *et al.* (2001, 2002) and Mausfeld-Lafdgiya (2002) for phylogeographic purposes, although using few individuals per island. All these latter studies pointed out the need of a complete systematic and taxonomic revision of the Cape Verdean reptiles. The molecular relationship estimates also indicated possible cryptic species and paraphyly/ polyphyly of some species (Brehm 2001; Brown *et al.* 2001; Carranza *et al.* 2000, 2001, 2002; Jesus *et al.* 2002). Moreover, not all the islands of the archipelago were sampled in those studies and therefore not all taxa were included. Therefore additional lineages might be uncovered. In addition, intraspecific variation was not assessed.

Section 1.4.2. Diversity and origins

Presently, there are 12 native reptile species with 26 recognised taxa in the Cape Verdes (Schleich 1996), which can be divided into three genera (Fig. 1.4.2), the *Hemidactylus* and *Tarentola* geckos (Families Gekkonidae and Phyllodactylidae, respectively) and the *Chioninia* skinks (Family Scincidae). Cape Verde has the highest number of endemic reptile taxa for the Macaronesia (Schleich 1987; Pleguezuelos *et al.* 2002; López-Jurado *et al.* 2005; Oliveira *et al.* 2005). There are also exotic reptile species with recent confirmed presence on the archipelago, namely two geckonids, *Hemidactylus angulatus* and *H. mabouia* (Jesus *et al.* 2001).

The **Gekkonidae** family has cosmopolitan species occurring in all the tropical and subtropical regions of the world. *Hemidactylus* Oken, 1817 is a genus with more than 85 gecko species inhabiting all warm continental land masses and hundreds of intervening continental and oceanic islands, and is one of the most species-rich and

Figure 1.4.2 Examples of endemic reptiles from the Cape Verde Islands.

widely distributed of all reptile genera (Carranza & Arnold 2006). These house geckos, very frequently associated to humanized habitats, are found in all the tropical regions of the world, extending into the subtropical parts of Africa and Europe, reaching the Mediterranean region and South America. They are mainly nocturnal climbers which can be distinguished by the presence of slender distal clawed joints on every finger or toe that bears underneath two rows of lamellae (Arnold & Ovenden 2004). As referred above, three species of *Hemidactylus* can be found on the Cape Verdes, the exotics *H. angulatus* and *H. mabouia* and the endemic *H. bouvieri* (López-Jurado *et al.* 2005).

The two exotics are world widespread species often commensal with man (Jesus *et al.* 2005). Both were considered invasive on the archipelago (López-Jurado *et al.* 2005). As already noted by Jesus *et al.* (2001), the haplotype of *H. angulatus* specimens from Sal in the Cape Verde archipelago shows a genetic divergence of about 5% from those animals on other islands (S. Nicolau, Boavista, Santiago, and Santo Antão), which exhibit little differentiation between themselves (Carranza & Arnold 2006). Specimens from Sal also present morphological differences when compared with specimens from the remaining islands (Rösler & Glaw 2010). However, both sets of Cape Verdean haplotypes of *H. angulatus* are similar or identical to ones found in coastal Mauritania and Guinea, about 460-600 km to the east (Carranza & Arnold 2006). One probable explanation is that all these geckos have been moved between islands anthropogenically along the extensive trade routes that exist in this region. If this is the case, *H. angulatus* had to reach the islands independently twice (Carranza & Arnold 2006). Concerning *H. mabouia*, specimens found on S. Vicente (Jesus *et al.* 2001) are thought to be a very recent anthropogenic introduction too (Jesus *et al.* 2005) from an uncertain tropical African source (Carranza & Arnold 2006). The precise area of occupancy and extent of occurrence of both introduced geckos is unknown.

The endemic *H. bouvieri* clusters within the African-Atlantic clade (Carranza & Arnold 2006). The pattern of water circulation in the Atlantic (see Fig. 1.3.2) suggests that the ancestor of *H. bouvieri* reached the Cape Verdes from extreme West Africa on the south-west-running Canary current between 6 to 16 million years ago (Mya) (Carranza & Arnold 2006). In addition, these authors suggested that this taxon showed considerable mtDNA variation among the Cape Verde Islands.

The **Phylodactylidae** is a trans-Atlantic gecko clade composed by eight genera based on a single synapomorphy of three base pairs deletion in phosducin gene (Gamble *et al.* 2008). *Tarentola* Gray, 1825 is a phyllodactylid group of geckos currently comprised of 21 species commonly called wall geckos. All of them present robust bodies, non-divided subdigital lamellas and well-developed claws only on the third and fourth digits (Arnold & Ovenden 2004) and have a conservative morphology (Harris *et al.* 2004). These climbing geckos are mostly active by night and typically inhabit dry, open and rocky areas and also artificial habitats, as houses and drystone walls. This genus is found across southern Europe, Mediterranean islands, North Africa and on many islands of the Macaronesian region (Arnold & Ovenden 2004). On the other side of the Atlantic Ocean, *T. americana* (Gray, 1831), the recently described *T. crombiei* Díaz & Hedges, 2008 and the probably extinct *T. albertschwartzi* Sprackland & Swinney, 1998 occur in the West Indies (Cuba, Bahamas and Jamaica, respectively). *Tarentola* members were divided into five different subgenera based on anatomical, biochemical, immunological and phylogenetic data (Joger 1984b;

Carranza *et al.* 2000). These are: *Sahelogecko* and *Saharogecko* in North Africa, *Tarentola* sensu stricto in North Africa, southern Europe and the eastern Canary Islands, *Neotarentola* which includes *T. americana*, *T. crombiei* and *T. albertschwartzi* and *Makariogecko* in Macaronesian Islands (Carranza *et al.* 2000; Weiss & Hedges 2007).

The subgenus *Makariogecko* presents a synapomorphy: the supraciliar scales are bigger than the remaining interorbital scales and are divided (Joger 1984b). Nevertheless, recent molecular phylogenies including *Tarentola chazaliae* (previously *Geckonia chazaliae*) do not seem to support the monophyly of this subgenus (Carranza *et al.* 2002). *Tarentola* from Cape Verde are part of Makariogecko and have a very interesting origin from a single colonisation event by propagules that rafted southwards from the western Canaries around 7 Mya by way of the Canary current (Carranza *et al.* 2000). Occupation of this archipelago first occurred on the north-western group, perhaps São Nicolau, with subsequent spread to its close neighbours. The eastern and southern islands were later colonised, at least two invasions widely separated in time being involved. The single invader of the Cape Verde Islands radiated into four species, *T. darwini*, *T. caboverdiana*, *T. gigas* and *T. rudis*, most of the islands being inhabited by two species. A minimum of 16 journeys took place in the Cape Verde Islands (Carranza *et al.* 2000). The molecular studies referred above unravelled some paraphyletic/ polyphyletic taxa and lack to sample some lineages.

The **Scincidae** family currently contains more than 1300 species grouped into over 85 genera (Bauer 1992) distributed in the inter-tropical regions in all continents but Antarctica (Zug 1993). Most skinks are mainly diurnal and medium-sized with a length from the snout to the vent of up to 12 cm. This family differs from Lacertidae by most species lacking pronounced neck and femoral pores and by supporting relatively small limbs, with several genera having no limbs at all (Arnold & Ovenden 2002). Within this family, the Lygosomine is the most diverse and widespread subfamily. About 100 species were grouped in the lygosomine genus *Mabuya* (sensu Greer, 1977), which is the only lizard genus with a circum-tropical distribution. It seems that this group was originated in tropical Asia and colonised Africa at a later stage, giving rise to an extensive African radiation (Mausfeld *et al.* 2002), and then America (Carranza & Arnold 2003; Miralles & Carranza 2009).

During the last decade, several phylogenetic analyses (Honda *et al.* 2000; Mausfeld *et al.* 2002; Carranza & Arnold 2003) identified distinct geographic monophyletic lineages within *Mabuya* supporting its breakup into four genera. As a consequence, *Mabuya* sensu stricto is now a term restricted to the Neotropics, whereas *Eutropis* Fitzinger, 1843 is applied to the Asian clade, *Trachylepis* Fitzinger, 1843 (see Bauer 2003) to the Afromalagasy clade (including *T. atlantica*, from Fernando de Noronha and *T. tschudii*, described from the Peruvian Amazonia; see Miralles *et al.* 2009) and *Chioninia* Gray, 1845 exclusive to the Cape Verdean clade (Mausfeld *et al.* 2002; although see criticisms in Jesus *et al.* 2005 and Whiting *et al.* 2006).

Chioninia skinks morphologically show an intermediate position between the Asian and the South American groups and are characterised by the following combination of characters: palatine bones in contact in the median; palatal notch separating the pterygoids, extending forwards to between the centres of the eyes; pterygoid teeth absent or present; 26-27 presacral vertebrae; reproduction either viviparous or ovoviviparous; the most posterior supraocular contacted by the frontal is always the third (Mausfeld *et al.* 2002).

Chioninia skins were studied with genetic markers to infer its geographical origin. The first studies indicated that the *Chioninia* species form a monophyletic unit, indicating a single colonisation of the Cape Verde Islands, probably from West Africa (Brehm *et al.* 2001). This was also supported by other study, which estimated that the colonisation event took place possibly in the Late Miocene or Early Pliocene period (Carranza *et al.* 2001). The ancestor of the endemic Cape Verdean skinks made at least 17 inter-island journeys within the archipelago (Carranza *et al.* 2001). The older eastern islands were probably occupied first and then the southern ones (Brown *et al.* 2001; Carranza *et al.* 2001). Following the latter authors, colonisation of the north-western islands was slow perhaps because colonisation cut across the north-east trade winds (see Fig. 1.3.2). Conversely, the southern islands appear to have been recently colonised with rapid expansions, perhaps because earlier inhabitants were exterminated by climatic events or volcanic activity (Carranza *et al.* 2001). Speciation and dispersal has resulted in many islands having more than one species, three on some southern ones, probably resulting from multiple colonisations (Carranza *et al.* 2001).

Seven species are considered endemic of these islands, *C. vaillanti*, *C. delalandii*, *C. fogoensis*, *C. geisthardti*, *C. stangeri*, *C. spinalis* and *C. coctei* (Schleich 1996). However, molecular studies referred above revealed that some taxa were paraphyletic/ polyphyletic and that hence further studies should be performed.

Section 1.4.3. Conservation state

In recognition of the importance to levels of global biodiversity, endemic island taxa are increasingly being recognised as of high conservation priority (Myers *et al.* 2000; Brooks *et al.*2006; Caujapé-Castells *et al.*2010). Reptiles are particularly important to study in the Cape Verdes since all native reptiles are endemics and were not considered during the selection of the future protected areas in the country due to lack of data. Moreover, 28% of reptile taxa from this archipelago were considered threatened or extinct (Schleich 1996), as the giant skink *Chioninia* (=*Macroscincus*) *coctei* which was victim of massive collection for scientific purposes on the XIX century (Bocage 1896; see Appendix II) and introduced predators (Mateo *et al.* 2005; see Appendix III). Some of these reptiles are already protected by national laws, such as the endemic *Hemidactylus* (Anonymous 2002).

The major threats to the endemic reptiles are intrinsic factors, such as reduced range, increased aridity and the introduction of mammal predators and exotic reptiles. Another threat to this group is the lack of knowledge on the ecology and behaviour of the species, essential for implementing conservation measures, such as precise chorological data to infer their distributions and revaluate their conservation status.

SECTION 1.5. OBJECTIVES AND THEMATIC ORGANISATION OF THE THESIS

This thesis intends to integrate ecological modelling, phylogeography, morphology taxonomic revisions and reserve design, combining GIS and molecular tools for unveiling phylogenetic relationships, cataloguing the diversity (at both genetic and specific level) and promoting the conservation of Cape Verdean reptiles. Hence, this work aimed to contribute to a better understanding of the biogeographic and phylogeographic patterns of Cape Verde reptiles, and to use this knowledge to clarify the systematics of the three endemic genera, to update its conservation status and optimise the reserve design of the protected areas (PAs) for this group. Several main question and objectives were defined for this work:

a) **What is there?** Which reptile species exist on the Cape Verde Islands?
Objectives:
To sample the ten islands of the archipelago extensively;
To identify new introduced species;
To unravel the phylogenetic relationships among taxa of each genus;
To clarify the taxonomy of the three endemic genera, *Hemidactylus*, *Tarentola* and *Chioninia*.

b) **Why?** Which factors explain taxonomical and genetic diversity and distribution of the Cape Verde reptiles?
Objectives:
To infer origins of introduced taxa;
To infer colonisation patterns of the three endemic genera;
To relate recent and past historical events and environmental factors with reptiles diversity and distribution.

c) **Where are they?** Which are their distributions at island and intra-island level?
Objectives:
To produce a precise distribution atlas for introduced and endemic taxa based on new chorological and bibliographic data;
To clarify uncertain and doubtful occurrences;
To predict potential maps of occurrence using ecological niche-based models.

d) **How to conserve them?** Which is the conservation status of the endemics and which are the priority areas for their conservation?
Objectives:
To re-evaluate the conservation status of the endemics with updated worldwide criteria based on the bibliographic record and new distribution data;
To access the main threats for each taxa;
To identify the gaps of the proposed network of protected areas at taxon and island level;
To locate the optimised areas for conservation of its taxonomic and genetic diversity;
To compare an ideal and realistic model of cost;
To propose new areas important for the conservation of the genetic diversity of the endemic reptiles.

This thesis is organised in four chapters and contains seven articles, included in two chapters. **Chapter 1** is the present chapter and includes a general introduction containing basic information on the study of biodiversity, explaining why islands are such good models for evolution and conservation studies, focusing on the Cape Verde archipelago by presenting relevant information regarding them, more specifically on its reptile species, the organisms used as models.

Chapter 2 concerns the assessment of diversity of reptile taxa across the archipelago. It provides identification of a new introduced reptile species on the archipelago and clarification of the systematics and taxonomy of the three endemic genera, by inferring phylogenetic relationships among taxa of each genus and by analysing morphological characters. It also intends to estimate times of divergence and colonisation patterns within each genus and to relate taxonomic and genetic diversity with the ages and ecologic and geological features of the islands. This chapter is organised in five scientific papers, four of them published in journals indexed in the Science Citation Index (SCI):

Article I is entitled 'First report of introduced African rainbow lizard *Agama agama* (Linnaeus, 1758) in the Cape Verde Islands' and has been published in *Herpetozoa*. The main objectives of this short-note were to report the introduction of an agamid in the Cape Verde archipelago, highlighting the problematic of introduced species on islands, including the study area, and to identify the species based on phylogenetic analyses.

Article II is entitled '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 sequence' and has been published in *Zoologica Scripta*. In this article, the systematic of the endemic *Hemidactylus* geckos was revised, with the description of a new species from Fogo Island and reassignment of species status to Sal and Boavista populations, based on morphological and genetic analyses extended to eight islands. Additionally, a highly divergent mitochondrial lineage was identified in S. Nicolau. Asymmetrical abundances of taxa further support that the conservation requirements of the group should be reassessed. Concerning the colonisation pattern, analyses suggested that the ancestor of this group reached independently the archipelago from extreme West Africa about 10 Mya. It supposedly first arrived on Sal, then spreading to Fogo and slowly to the north-western islands, from east to west.

Article III focuses on the systematics and intraspecific genetic diversity of the endemic *Tarentola* geckos, relating the latter with the ages and ecological and geological features of the islands. In this paper, 'Insight into an island radiation: the *Tarentola* geckos of the Cape Verde archipelago', published in the *Journal of Biogeography*, the phylogenetic relationships between all known forms of this genus were estimated for the first time using mitochondrial markers, unveiling cryptic diversity and paraphyletic species. It was also confirmed that genetic variability was positively correlated with size, elevation and habitat diversity of the islands, but was not linearly related to the age of the islands. Despite the large sample size, low intraspecific diversity was found compared to the Canary Islands reptiles. Recent volcanic activity, high ecological stress and poor habitat diversity might explain this result. Concerning the colonisation pattern, it was inferred that *Tarentola* arrived to the archipelago from the western Canary Islands approximately 8 Mya. It first reached S. Nicolau and then spread into two directions, southeast and west, radiating in several taxa. Since this study concluded that more studies were needed to align taxonomy with phylogenetic relationships, in the following article this was accomplished.

In **Article IV**, 'Integrative taxonomic revision of the *Tarentola* geckos (Squamata, Phyllodactylidae) of the Cape Verde Islands', which is currently submitted to *Zoological Journal of the Linnean Society*, apart from previously published mitochondrial data, three nuclear markers and about 20 morphological characters were used to fully revise the taxonomy of this group. With an integrative approach, two new species are described and seven subspecies elevated to species rank. The results show that there is a remarkable degree of concordance between the units defined based on mtDNA data and those observed by morphological analyses and multilocus nuclear data. However, nuclear genealogies do not support conclusively all the partitions observed in mtDNA possibly due to incomplete lineage sorting of ancestral polymorphism.

Article V, the last article of this chapter, is entitled 'An integrative taxonomic revision of the Cape Verdean skinks (Squamata, Scincidae)' and it has been published in *Zoologica Scripta*. In this paper, a comprehensive taxonomic revision of the third endemic genus, *Chioninia*, is proposed based on mtDNA, nDNA and morphological data of live and museum specimens. Using an integrative approach, three new subspecies of skinks are described, two more are elevated to species rank and the complex taxonomic status of *C. fogoensis fogoensis* resolved. The molecular results of this work point to low haplotypic diversity of the group and that first speciation event may have been earlier than previously suggested and around 6 Mya. Colonisation probably first occurred on S. Nicolau and from there to the southern island, where a very recent expansion was confirmed for some taxa, and also to the north-western group, following a stepping-stone model. This pattern might again be related to extinction of some lineages by volcanic activity.

With this set of articles the major evolutionarily significant units (ESUs) of native reptiles from the Cape Verde Islands were identified by assessing intraspecific genetic variation in mitochondrial genes, their taxonomies updated based on morphological and molecular characters and phylogenetic relationships clarified. Due to the taxonomical and systematic reassessment in all three genera and to the increase of knowledge regarding within-island distributions, the conservation status of some taxa needed to be updated. Thus, in Chapter 3 this was accomplished.

Chapter 3 is devoted to the study of the distributions of the introduced and endemic reptiles at island and intra-island level and its implications to conservation status and optimisation of priority areas for conservation.

In **Article VI**, 'Review of the distribution and conservation status of the reptiles of the Cape Verde Islands', submitted to Oryx, a distribution atlas of all terrestrial reptiles taxa occurring in this Macaronesian archipelago is presented, based on extensive fieldwork and bibliographic references. In addition, a bibliographic revision was accomplished to deal with uncertainties and clarify reptile distributions. The evaluation of conservation status was considered following IUCN Red List criteria and using RAMAS software and the main threats for each taxon were identified. The most striking result of this article is revealing that more than a third of taxa presented small areas of occupancy and extent of occurrence, geckos more than skinks due to high habitat specialisation. Moreover, more than half of taxa occur in only one island or islet and about half were considered threatened, mainly due to natural disasters, intrinsic factors and introduced species. In this work, several conservation measures are proposed, including optimised design of PAs. This was the focus of the following article.

In **Article VII**, 'Priority areas for island endemics using genetic diversity – the case of the reptiles of the Cape Verde Islands', which is still in preparation, the main goals are to locate the optimised areas for conservation of endemic reptiles from the Cape Verdes. It is aimed to identify the gaps of the proposed network of PAs, using an ideal and realistic model of costs, and to propose new PAs to conserve the taxonomic and genetic diversity of these reptiles, based on ecological niche-based models. The main results depicted that the present implemented PAs only guarantees cover of one taxon and that even the future network would be incapable of targeting all taxa and ESUs. Hence, new PAs would be needed on all except four islands. Surprisingly, it was also found that the realistic and ideal model were equally efficient in the reserve design.

Finally, **Chapter 4** consists of a general discussion that summarises and contextualises the major findings that can be drawn from the work presented in the former chapters and provides question to be addressed and directions for future work, and of concluding remarks.

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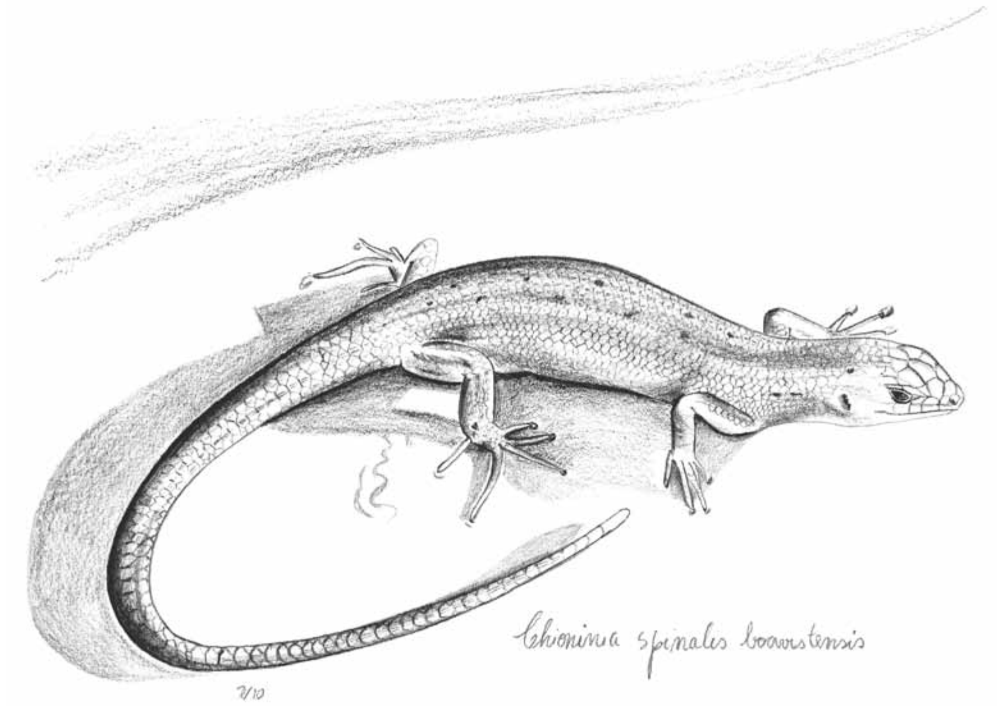
“In the end we will conserve only what we love.
We will love only what we understand.
We will understand only what we are taught”

Baba Dioum

CHAPTER 2

Reducing the Linnean shortfall
What is there? Why?

Systematics and insights into the diversity of the reptiles of Cape Verde



SECTION 2.1

The introduced species

Article I. First report of introduced African rainbow lizard *Agama agama* (Linnaeus, 1758) in the Cape Verde Islands

R. Vasconcelos, S. Rocha, J.C. Brito, S. Carranza & D.J. Harris (2009)

Herpetozoa, 21, 183-186.

ARTICLE I

First report of introduced African rainbow lizard *Agama agama* (Linnaeus, 1758) in the Cape Verde Islands

R. Vasconcelos [1,2,3], S. Rocha [1,2,4], J.C. Brito [1,2], S. Carranza[3] & D.J. Harris [1,2]

[1] CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos,
Campus Agrário de Vairão, R. Padre Armando Quintas, 4485-661 Vairão, Portugal.

[2] Departamento de Zoologia – Antropologia, Faculdade de Ciências da Universidade do Porto,
Pr. Gomes Teixeira, 4099-002 Porto, Portugal.

[3] Departament de Biologia Animal, Universitat de Barcelona,
Av. Diagonal 645, E-08028 Barcelona, Spain.

[4] Departamento de Bioquímica, Genética e Inmunología,
Facultad de Biología, Universidad de Vigo, Vigo 36310, Spain.

KEY WORDS

Reptilia: Squamata: Agamidae, *Agama agama*, Cape Verde Islands, introduction, mitochondrial DNA, 16S rRNA

INTRODUCTION

Introduced reptile species can have various negative impacts on native ones, including predation, competition for food, basking sites and other resources, hybridization and other genetic effects, spread of diseases and parasites, and poisoning through toxic skin glands or venomous bites. They may also alter the habitat of native species and disrupt ecosystem dynamics. These processes are especially dangerous if they happen on islands (Butterfield *et al.* 1997), where the number of endemic species is higher (Whittaker 1998) and ecosystems more vulnerable to introductions (Shine *et al.* 2000). Unfortunately, it is on islands that this phenomenon is occurring 110 times more frequently and with a higher probability of successful establishment relative to mainland systems (Kraus 2003).

Case & Bolger (1991a, 1991b) examined introduction success rates for exotic reptiles (primarily lizards) on Pacific islands and found that communities with a rich reptile fauna were more resistant to invasion by exotic reptiles than communities with fewer reptile species. They also presented evidence supporting the hypothesis that predation and competition set important constraints on the distribution, colonization and abundance of lizards, predominantly on islands. Other authors confirm this theory through various case studies on islands around the globe. For example, in the West Indies, where introduced Cuban Green Anole *Anolis porcatus* Gray, 1840 occurred, its ecological analogue, the native Hispaniolan Green Anole *Anolis chlorocyanus* Duméril & Bibron, 1837 was uncommon or absent and vice-versa, suggesting competition occurs between the two species (Powell *et al.* 1990).

Similarly the anthropogenically introduced Common House Gecko *Hemidactylus frenatus* Schlegel, 1936 has displaced on the Christmas Island the endemic Christmas Island Gecko *Lepidodactylus listeri* (Boulenger, 1889) (Cogger *et al.* 1983). The same happened to the Polynesian gecko *Hemidactylus garnotii* Duméril & Bibron, 1836 (Case *et al.* 1994) and to the native common smooth-scaled gecko *Lepidodactylus lugubris* (Duméril & Bibron, 1836) throughout the Pacific (Petren & Case 1996) and to the endemic night gecko *Nactus* populations in the Mascarene Islands (Cole *et al.* 2005) that suffered catastrophic decline and extinction by competition. In the Aeolian Islands, on the Mediterranean, the Italian Wall Lizard *Podarcis sicula* (Rafinesque, 1810) has reduced the range and eradicated many populations of the native *Podarcis raffonei* (Mertens, 1952) partly through competitive exclusion and hybridization (Capula 1993). In the Madeira Island, in Macaronesia, the Moorish Gecko *Tarentola mauritanica* Linnaeus, 1758 and House Gecko *Hemidactylus mabouia* (Moreau de Jonnès, 1818) were introduced a few decades ago and are spreading (Baéz & Biscoito 1993; Jesus *et al.* 2002a); in the Azores, Madeiran Lizard *Lacerta dugesii* Milne-Edwards, 1829 was also introduced recently.

The Cape Verde Islands are relatively poor in reptile species diversity but very rich in endemisms (Schleich 1987; Carranza *et al.* 2001; Jesus *et al.* 2002b; Arnold *et al.* in press). The introduction of alien house gecko species, *Hemidactylus angulatus* Hallowell, 1852 (Fea 1899) and *H. mabouia* (Jesus *et al.* 2001), is probably already causing problems in the endemic Cape Verde Leaf-toed Gecko *Hemidactylus bouvieri* Bocourt, 1870 (Arnold *et al.* in press). Given that some endemic forms such as *H. bouvieri razoensis* Gruber & Schleich, 1982 and *Tarentola gigas* (Bocage, 1875) are in a delicate situation (critically endangered and endangered, respectively, Schleich 1996) (Mateo *et al.* 1997), knowledge regarding additional introductions is vital. This note details the collection of an introduced reptile, *Agama agama* (Linnaeus, 1758) in the Cape Verde Islands.

MATERIALS AND METHODS

The specimen was collected dead on the 22 of June of 2006 nearby Porto Novo (Lagedos, N 17,0184 W 25,0561 – WGS 84) in Santo Antão Island. The voucher is deposited in the collection of Centro de Investigação em Biodiversidade e Recursos Genéticos, Vairão, Portugal (CIBIO). Genomic DNA was extracted following a standard high-salt protocol. Part of the 16S rRNA gene (483 base pairs) was amplified by Polymerase Chain Reaction using the universal primers 16S A-L (light chain) and 16S B-H (heavy chain) (Palumbi *et al.* 1991) and conditions described in Harris *et al.* (2007). The amplified products were sequenced on an automated sequencer (ABI 310® by Amersham Biosciences®) and then aligned with other agamas from GenBank and others collected in continental Africa (Fig. I.1) as part of a separate phylogeographic study of these species (unpubl. data). These new sequences were deposited on GenBank under the accession numbers: FJ159558 to FJ159562.

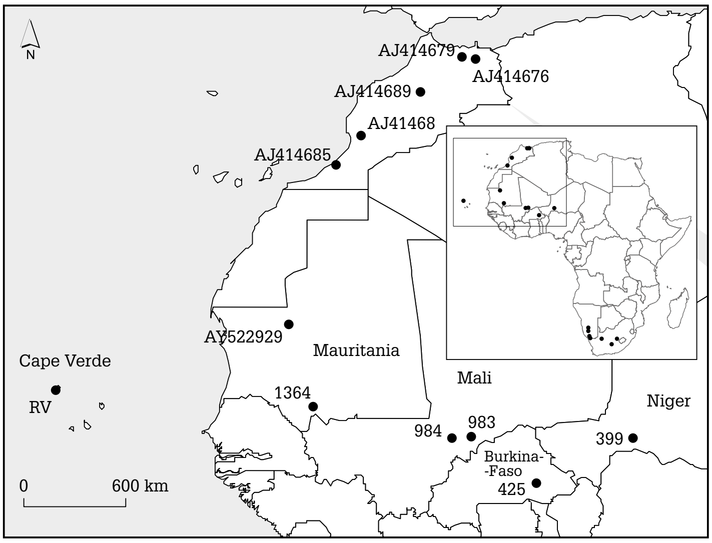


Figure I.1 Sampling localities (from this study, Brown *et al.* 2002 and Matthee & Flemming 2002).

RESULTS

Morphological analysis of the voucher found in Santo Antão Island clearly indicates that it is an agamid. However due to the bad conservation status of the animal, some characters such as coloration and scale count can not be taken into account to allow identification to the species level. The results of the phylogenetic analyses indicate that it is an *Agama agama* since it is nested within this species (Fig. I.2). The phylogenetic position of the sample from Cape Verde suggests it might have originated in Mali but further sampling would be needed to confirm this.

DISCUSSION

Porto Novo is a port, so it is easy to imagine an accidental introduction of this animal by cargo boats from western continental Africa, from countries situated in front of the Cape Verde islands. In fact, more introductions in the Macaronesian Islands have occurred in the last 20 years than in the entire history of the islands. Indeed the greatest danger for many endemic species results from recent introductions (Pleguezuelos 2002). Reduction of entrance events of exotic species by biological control is the only way to minimize impacts since it is known that after becoming widespread, eradication becomes extremely expensive if not impossible.

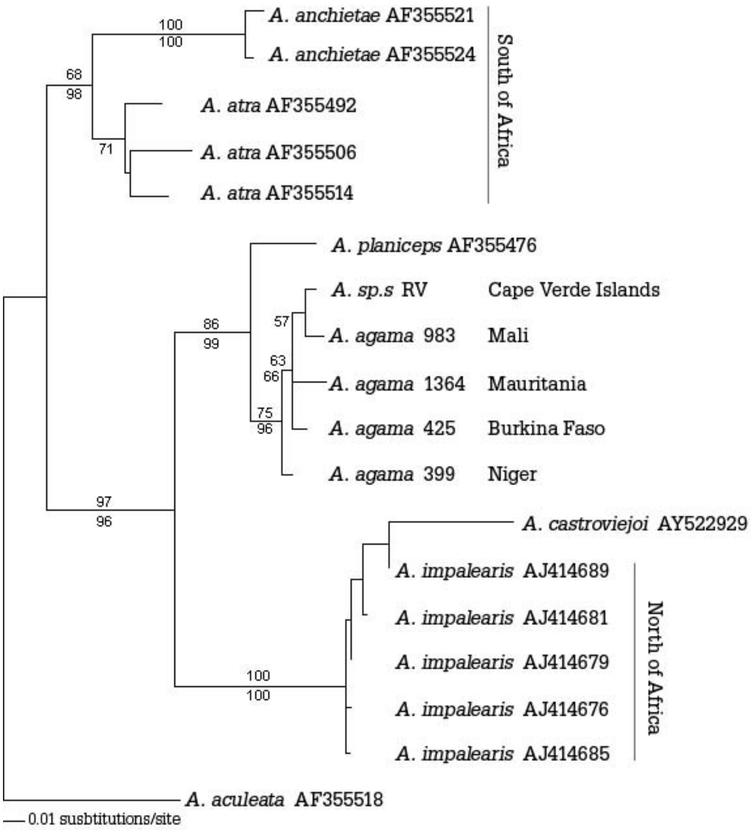


Figure I.2 Maximum Likelihood (ML) tree for the 16S sequences using GTR + γ model, following methodology of Harris *et al.* (2007). A strict consensus of 10 Maximum Parsimony (MP) trees (197 steps) differed only in being less well resolved and in that *Agama castroviejoi* was sister taxon to a monophyletic *Agama impalearis*. ML and MP bootstraps (1000 replicates) are given above and below nodes, respectively.

The Agamidae is one of the top-ten most successful introduced families in the world, with a successful establishment rate around 70% in North America (Bomford *et al.* 2005). It has been introduced in many islands systems such as in Malta (Schembri & Lanfranco 1996) and in the Comoros (Carretero *et al.* 2005) possibly also as a result of accidental importation with cargo. In Florida, the introduced *A. agama* population is spreading (Enge *et al.* 2004). After intensive sampling throughout the island in 71 sites (conducted between 5 to 27 of June of 2006) with at least 2 observers, no other agamids were found. However, locals suggested at least two specimens had been seen together in the wild. It is therefore essential both to inform local authorities of the presence of exotic species and to take actions against these introductions as quickly as possible.

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SECTION 2.2

The Endemic Species

Article II. 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 (2008)
Zoologica Scripta, 37, 619–636.

Article III. Insight into an island radiation: the *Tarentola* geckos of the Cape Verde archipelago.
R. Vasconcelos, S. Carranza & D.J. Harris (2010)
Journal of Biogeography, 37, 1047–1060.

Article IV. An integrative taxonomic revision of the *Tarentola* geckos (Squamata, Phyllodactylidae) of the Cape Verde Islands.
R. Vasconcelos, P. Geniéz, A. Perera, S. Carranza & D.J. Harris (2010)
Zoological Journal of the Linnean Society, submitted.

Article V. An integrative taxonomic revision of the Cape Verdean skinks (Squamata, Scincidae).
A. Miralles*, R. Vasconcelos*, D.J. Harris, A. Perera & S. Carranza (2010)
Zoologica Scripta, 40, 16–44.
* These authors contributed equally to this work

ARTICLE II

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 [1], R. Vasconcelos [2,3,4], D.J. Harris [2], J.A. Mateo[5] & S. Carranza [4]

[1] Department of Zoology, The Natural History Museum, SW7 5BD, London.

[2] CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos,
Campus Agrário de Vairão, R. Padre Armando Quintas, 4485-661 Vairão, Portugal.

[3] Departamento de Zoologia – Antropologia, Faculdade de Ciências da Universidade do Porto,
Pr. Gomes Teixeira, 4099-002 Porto, Portugal.

[4] Departament de Biologia Animal, Universitat de Barcelona,
Av. Diagonal 645, E-08028 Barcelona, Spain.

[5] Centro de Recuperación del Lagarto Gigante de La Gomera;
Antoncojo, E-38870 Valle Gran Rey, Canary Islands, Spain.

ABSTRACT

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 use d 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. bouvieri* for the present. *Hemidactylus b. razoensis* from Raso is genetically similar to *H. b. bouvieri* 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. bouvieri* 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.

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. II.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 bouvieri* (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. *Hemidactlylus bouvieri* has three currently recognized subspecies (Schleich 1987). *Hemidactylus bouvieri bouvieri* (Bocourt, 1870) described originally from S. Vicente is also recorded as occurring on Sto. Antão, Santiago, Fogo and Brava; *Hemidactlylus bouvieri boavistensis* (Boulenger, 1906) described from Boavista is also found on Sal; and *Hemidactlylus bouvieri razoensis* (Gruber & Schleich, 1982) is reported only from Raso and Sta. Luzia (Mateo *et al.* 1997). *Hemidactylus b. bouvieri* grows to less than 40 mm from snout to vent and has 3 – 4 scansors and enlarged scales under the first toe and 4 – 5 under the fourth; *H. b. boavistensis* reaches around 50 mm and has higher digital scansor counts of 5 – 6 and 6 – 8, respectively; *H. b. razoensis* is very small, not exceeding 29 mm and has similar scansor counts to *H. b. bouvieri*. 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. bouvieri* has been reported from S. Nicolau (López-Jurado

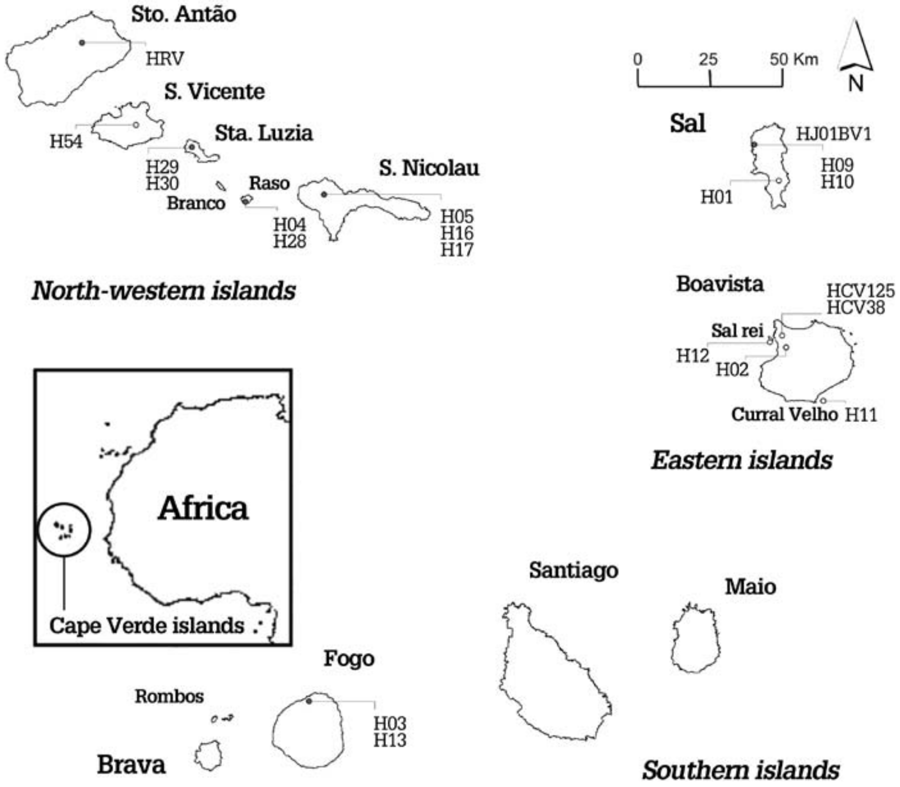

Figure II.1 Map of the Cape Verde islands showing the origins of the *Hemidactylus* samples included in the analyses. Unfilled circles indicate samples used by Jesus *et al.* (2001) and Carranza & Arnold (2006); filled circles are additional specimens used in the present study.

et al. 2005; Köhler *et al.* 2007; J. A. Mateo and P. 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.

MATERIALS AND METHODS

Samples, DNA extraction, amplification and sequencing

Identifications, localities and GenBank accession numbers of the samples used are listed in Table II.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 *b* 1, cyt *b* 2 (Kocher *et al.* 1989), the forward primer of cyt *b* 2 (cyt *b* 2F) 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 Verde *Hemidactylus* and to estimate dates of divergence. It consisted of 689 bp of mtDNA (303 bp of cyt *b* — the cyt *b*1 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 *b*1 and 363 bp of the cyt *b*2 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 *b*2 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.

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

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 $1.5{\times}10^6$ 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 relationships for the same set of taxa were both supported with bootstrap values ≥ 70% or posterior probability values ≥ 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; 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 (Sanderson & 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 confirmed 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. II.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. II.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,

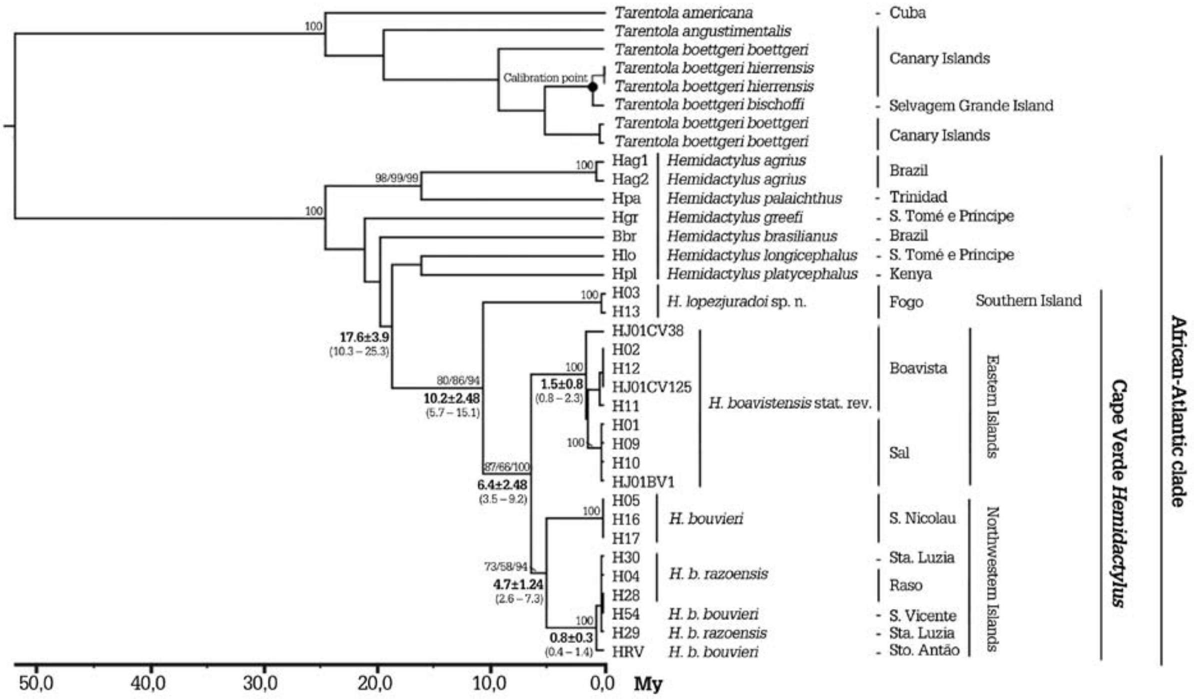

Figure II.2 Relationships and estimated times of divergence in endemic Cape Verde *Hemidactylus* and their relatives based on an analysis of 689 bp (303 bp cyt *b* and 386 bp of 12S rRNA). Output tree from r8sb program is shown, which includes other members of the African-Atlantic clade of *Hemidactylus* (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 II.1.

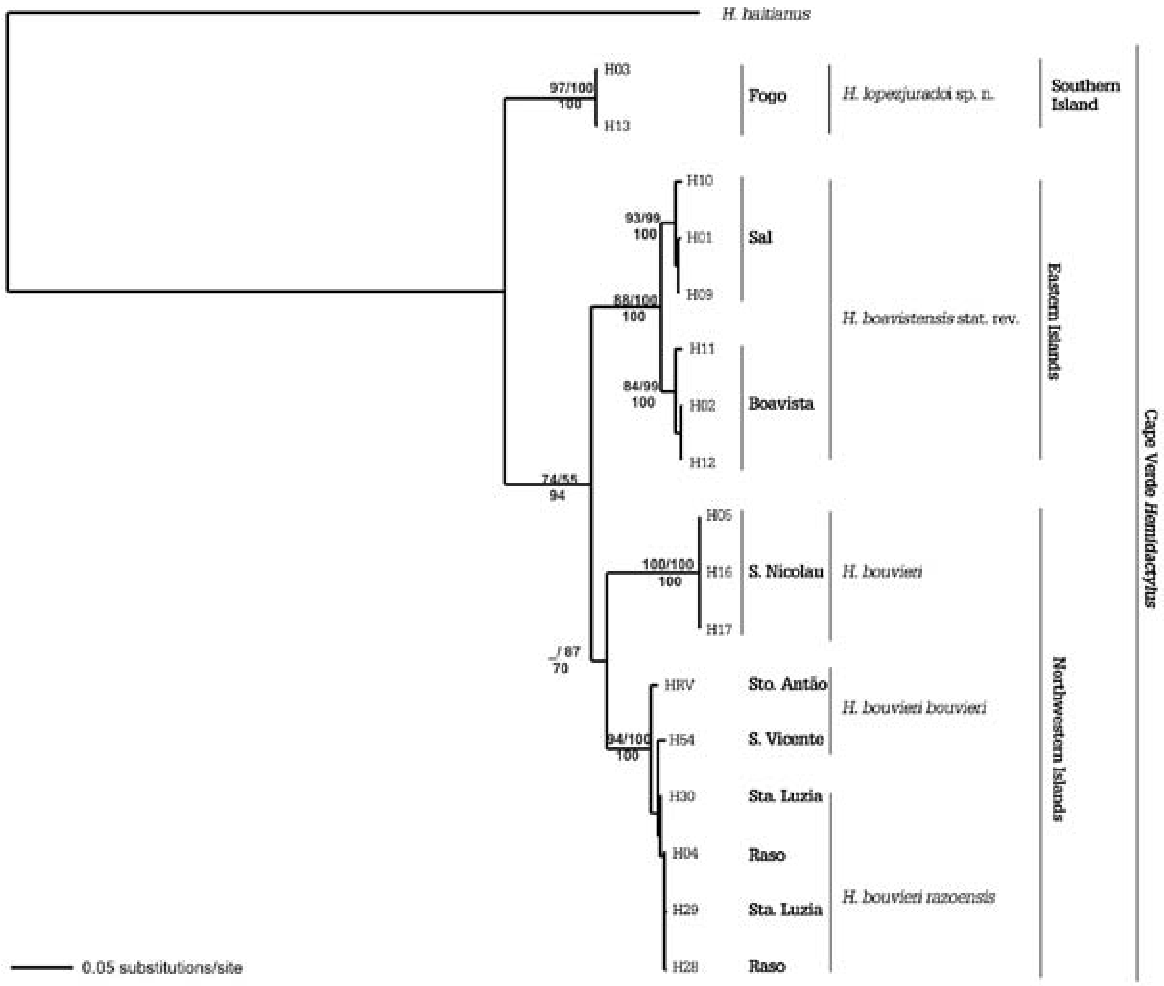

Figure II.3 Relationships within Cape Verde endemic *Hemidactylus*. ML tree based on an analysis of 1050 bp of mtDNA (669 bp cyt *b* and 381 bp of 12S rRNA), rooted using *H. haitianus* as outgroup. Topologies from ML and MP analyses were very similar. Figures above nodes indicate bootstrap support in 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 II.1.

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 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. II.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 additional 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.

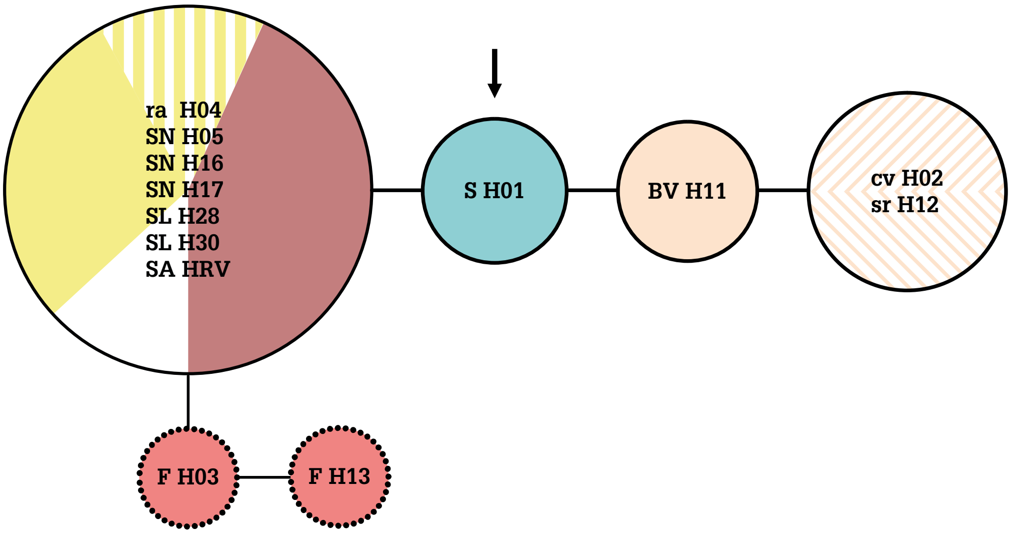

Figure II.4 Network showing RAG2 sequence variation. Lines represent mutational steps and circles represent haplotypes. The area of the circles is proportional to the number of individuals. The arrow indicates where the network is rooted to the two outgroups used (*Hemidactylus platycephalus* and *H. 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 II.1.

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, 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 northwestern 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. II.5. A, 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 midback; 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 scansors 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 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 scansors and enlarged scales under first hind toe, six to seven under third,

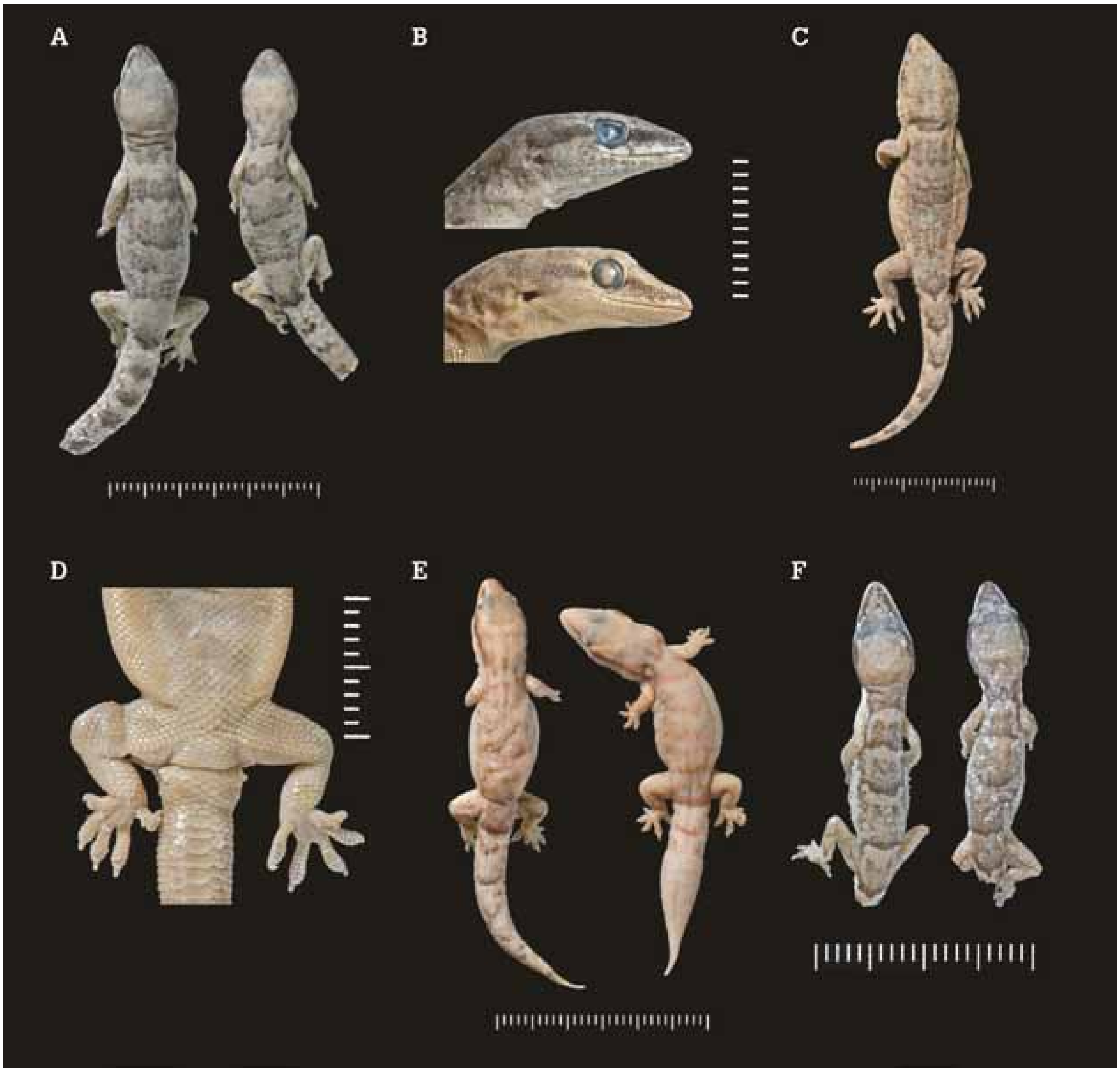

Figure II.5 **A** – **F** Endemic *Hemidactylus* from the Cape Verde Islands. **A**) *Hemidactylus lopezjuradoi* sp. n. Holotype (left) and one of the paratypes (BMNH 2005.1633–1634), both males, from between Ribeira Ilhéu and Atalaia, northern Fogo; **B**) *H. lopezjuradoi* sp. n. (holotype) and *H. 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.

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 scansors 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. II.5.B – 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 scansors 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. II.5.E, 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 scansors 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. Vincente, 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. II.5.E)
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. Vincente (Boucourt 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. II.5.F)

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 P. 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. II.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).

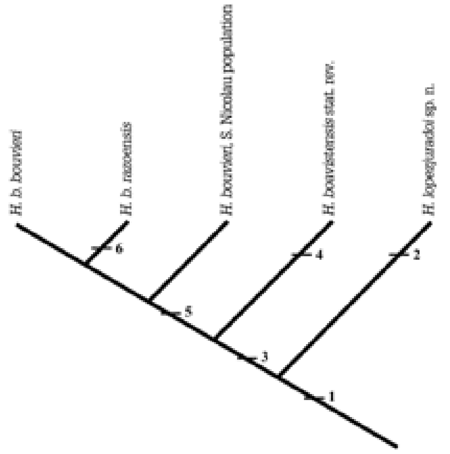

Figure II.6 Some morphological changes in the history of endemic Cape Verde *Hemidactylus* geckos. Where parsimony does not indicate direction of change, as for example with size, size of ventral scales and scansors under toes, values are given for more than one taxon. (1) Small size (only up to about 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).

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. II.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 northern-western 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 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 P. 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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ARTICLE III

Insight into an island radiation: the *Tarentola* geckos of the Cape Verde archipelago

R. Vasconcelos[1,2,3], S. Carranza[3] & D.J. Harris[1,2]

[1] CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos,
Campus Agrário de Vairão, R. Padre Armando Quintas, 4485-661 Vairão, Portugal.

[2] Departamento de Biologia, Faculdade de Ciências da Universidade do Porto,
Rua Campo Alegre s/n, 4169-007 Porto, Portugal.

[3] Institute of Evolutionary Biology (CSIC-UPF),
Passeig Marítim de la Barceloneta, 37-49, E-08003 Barcelona, Spain.

ABSTRACT

Aim To reassess the relationships between *Tarentola* geckos from the Cape Verde Islands by including specimens from all islands in the range. To determine the variation within forms by sequencing over 400 specimens, thereby allowing the discovery of cryptic forms and resolving some of the issues raised previously. This extensive sampling was also used to shed light on distributions and to explain genetic diversity by comparing the ages and ecological and geological features of the islands (size, elevation and habitat diversity).

Location The Cape Verde Islands: an oceanic archipelago belonging to the Macaronesian biogeographic region, located around 500 km off Senegal.

Methods A total of 405 new specimens of *Tarentola* geckos were collected from nine islands with very different geological histories, topography, climate and habitats. Mitochondrial cytochrome *b* (cyt *b*) gene and 12S rRNA partial sequences were obtained and analysed using phylogenetic methods and networks to determine molecular diversity, demographic features and phylogeographic patterns.

Results The phylogenetic relationships between all known forms of Cape Verdean *Tarentola* specimens were estimated for the first time, the relationships between new forms were assessed and previously hypothesized relationships were re-examined. Despite the large sample size, low intraspecific diversity was found using a 303-bp cyt *b* fragment. Star-like haplotype networks and statistical tests suggest the past occurrence of a rapid demographic and geographical expansion over most of the islands. Genetic variability is positively correlated with size, elevation and habitat diversity of the islands, but is not linearly related to the age of the islands. Biogeographical patterns have, in general, high concordance with phylogenetic breaks and with the three eco-geographical island groups. Volcanism and habitat diversity, both tightly linked with island ontogeny, as postulated by the general dynamic model of oceanic island biogeography, as well as present and historical size of the islands appear to be the main factors explaining the genetic diversity of this group.

Main conclusions The *Tarentola* radiation was clarified and is clearly associated with the geological and ecological features of the islands. Two factors may account for the low intraspecific variation: (1) recent volcanic activity and high ecological stress, and (2) poor habitat diversity within some islands. More studies are needed to align taxonomy with phylogenetic relationships, whereas GIS modelling may help to predict precise species distributions.

KEY WORDS
12S, biogeography, Cape Verde Islands, cyt *b*, geckos, island radiation, Macaronesia, phylogeny, *Tarentola*.

INTRODUCTION

Islands can be used as model systems to study evolution and phylogeography, and in this context are often referred to as ‘natural laboratories’. In particular, oceanic archipelagos, such as the Galapagos, Hawaii, Madeira and the Canary Islands, allow the testing of various evolutionary hypotheses. As gene flow between islands is practically non-existent, allowing fixation of genetic variation, differentiation of populations can occur through geographical isolation. If the ages of the islands are known, the phylogeography of taxa in archipelagos can be analysed within a known timeframe. Additionally, the investigation and protection of endemic island species is particularly important as they typically have a relatively higher risk of extinction (Frankham 1997) and remote islands possess large numbers of endemics (Whittaker 1998).

Many factors, including area, island shape, habitat diversity, distance to the mainland and to other islands, geological events, taxon biology and human influence are known to affect biodiversity on islands (Fattorini 2009). Recently, Whittaker *et al.* (2008) published a development of the classic dynamic equilibrium theory of island biogeography introduced by MacArthur & Wilson (1963, 1967), known as the general dynamic model (GDM) of oceanic island biogeography, which combines the former relationships with island ontogeny. This model is more applicable to remote hotspot oceanic archipelagos, where immigration rates are very low, and postulates that ‘middle-aged’ islands have maximum realized species richness and potential carrying capacity.

The Cape Verde Islands are an oceanic archipelago located approximately 500 km off the West African coast. The archipelago was formed by a volcanic hotspot (Plesner *et al.* 2002) and has never been connected to the mainland (Mitchell-Thomé 1976). It has ten main islands, plus several islets, which are topologically divided into north-western, eastern and southern islands (Fig. III.1). They are arranged in a horse-shoe shape with the concavity facing westwards. The islands are between 6 and 26 million years (My) old and the youngest ones are on the westernmost tips of the arc (see Stillman *et al.* 1982; Mitchell *et al.* 1983; Plesner *et al.* 2002; Torres *et al.* 2002). Some of the islands of the north-western group (São Vicente, Santa Luzia, Branco and Raso islets), and possibly also Boavista and Maio, were most likely to have been linked during sea-level fluctuations in the Pleistocene. Elsewhere, the water channels are very deep, so it is highly improbable that the other islands were ever connected by land (Morris 1989). Their sizes and topographies vary dramatically: Santiago is the largest (around 1000 km^2) and Raso islet (<6 km^2) among the smallest; Fogo is the highest (approximately 2800 m a.s.l.) and Santa Maria islet the flattest.

Although Darwin, during his voyage on the Beagle, considered the Cape Verde Islands to be ‘utterly sterile’ (Darwin 1845), he made note of the lizards in the more humid valleys. There are approximately 27 currently

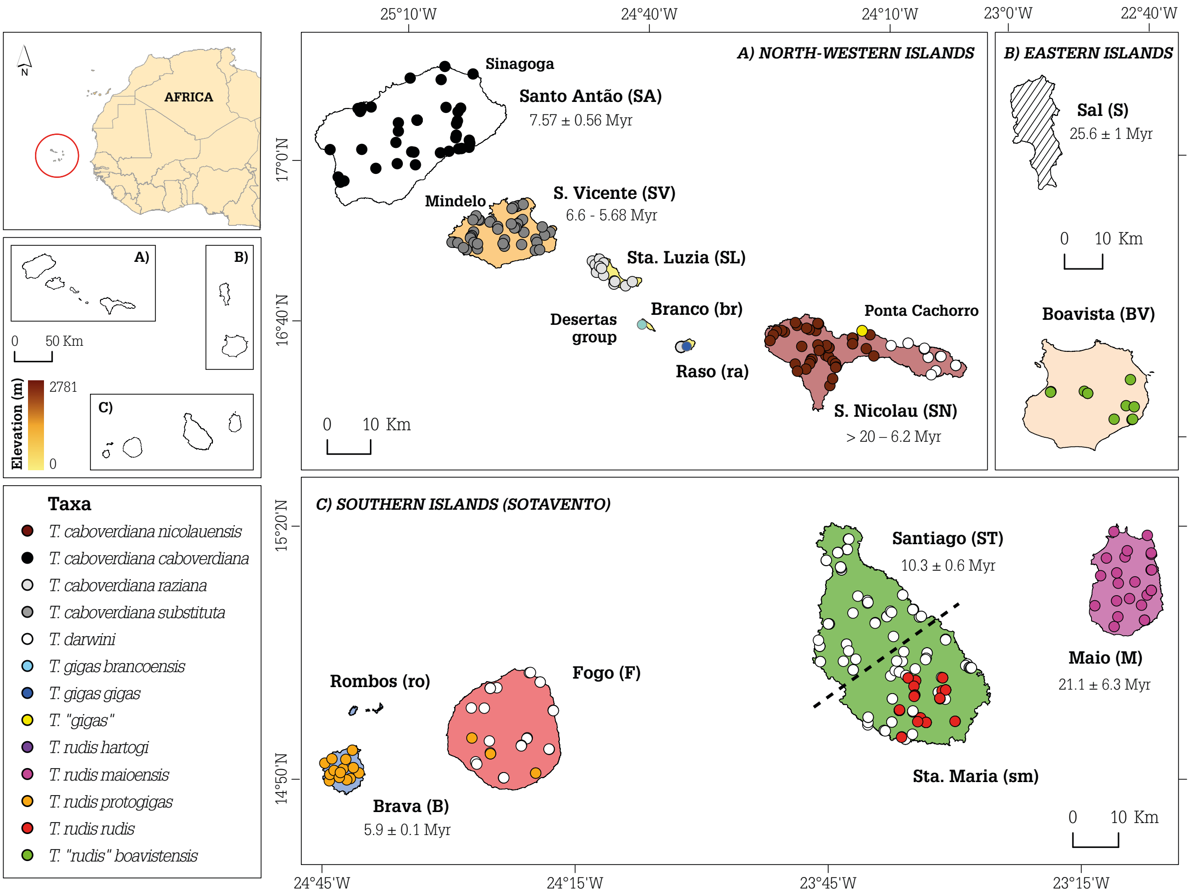


Figure III.1 Map of the Cape Verde Islands showing the geographic location and elevations of the islands and the origins of the *Tarentola* samples included in the analyses (Geographic Coordinate System, Datum WGS 84). No specimens were found on Sal Island. The dashed line divides the *Tarentola darwini* southern and northern haplotypes from Santiago.

recognized native lizard taxa, all of which are endemic to the Cape Verdes and can be divided into three genera: the *Chioninia* skinks and the *Tarentola* and *Hemidactylus* geckos. The genus *Tarentola* is biogeographically interesting because it arrived on the Cape Verde Islands approximately 7 million years ago (Mya) from a propagule that dispersed from the western Canary Islands situated 1500 km to the north (Carranza *et al.* 2000). The endemic *Tarentola* species have been studied phylogenetically (Carranza *et al.* 2000; 2002; Jesus *et al.* 2002) and relationship estimates indicated possible cryptic species and paraphyly of some species. However, not all the islands of the archipelago were sampled in these previous studies and therefore not all taxa were included. Moreover, those studies were based on a small number of samples per taxon and per island, so intraspecific variation was not assessed. Such information is valuable as the genus *Tarentola* on the Canary Islands shows considerable intraspecific variation, possibly associated with island sizes, volcanic activity, ecological niche availability, or a combination of these factors (Gübitz *et al.* 2005). The study of intraspecific variation may uncover additional cryptic lineages and therefore prove highly relevant for any conservation assessment (Schwartz *et al.* 2006).

The aim of the present study was to reassess the relationships between *Tarentola* geckos (Reptilia: Gekkonidae) from the Cape Verde Islands by including specimens from all islands where they are found, including distinct subspecies that have never previously been analysed. Likewise, sequencing over 400 new specimens would allow variations within forms to be determined. The expectation was that this more complete sampling would resolve some of the issues raised in earlier phylogenetic works whilst decreasing the possibility that any cryptic forms have been overlooked. Extensive intra-island sampling would also shed light on possible barriers to gene flow within species and would allow genetic diversity to be compared in terms of the age and geological and ecological features of the islands (size, elevation and habitat diversity).

MATERIALS AND METHODS

Sampling and gathering of the molecular data set

The ten islands of the Cape Verde archipelago were prospected between 2006 and 2008 (mid-May to mid-July). The sampling stations were chosen randomly and stratified according to the different habitats existing on each island, based on agro-ecological and vegetation zoning maps (see Appendix III.1 in Supporting Information) and the number of sites per habitat, according to its area. This allowed most of the variability between and within each habitat – elevation, vegetation, climate and geographic position – to be covered by the different sampling stations. The sampled area (440 stations of 1 x 1 km^2) corresponds to around 11% of the area of the country. Each station was sampled along transects for an average of 35 min, depending on the difficulty of the terrain, by two observers walking parallel to each other (total sampling time 263 h).

A total of 405 new specimens of *Tarentola* were included in the genetic analyses. Specimens were identified in the field using diagnostic characters published by Joger (1984, 1993) and Schleich (1987), digital photographs were taken and a piece of tail was removed and stored in 96% ethanol. Sampled animals were released afterwards. The identification codes, localities and GenBank accession numbers of the new samples used are listed in Appendix III.2.

Total genomic DNA was extracted from small pieces of tail using standard methods (Harris *et al.* 1998). The cytochrome *b* (cyt *b*) and 12S rRNA mitochondrial (mtDNA) genes were amplified. The polymerase chain reaction (PCR) primers used in amplification and sequencing were 12Sa and 12Sb for the 12S rRNA, and cyt *b*1 and cyt *b*2 (Kocher *et al.* 1989; Palumbi 1996) for the first fragment and cyt *b* 2F and CB3-3' (Palumbi 1996) for the second fragment of the cyt *b* gene. Thermocycling was performed following Carranza *et al.* (2000). Amplified mtDNA fragments were sequenced from both strands.

The first fragment of the cyt *b* gene [cyt *b*1 and cyt *b*2 primers, 303 base pairs (bp)] from 459 individuals was used to identify all lineages by network analysis and to assess intraspecific variation. These 459 sequences comprised 405 new sequences and 54 GenBank sequences from 276 sites on nine islands and four islets across the Cape Verde archipelago (no specimens of *Tarentola* were found on Sal Island). The first and second fragments of the cyt *b* gene (684 bp) plus the 12S rRNA (403 bp), in total 1087 bp, from 70 individuals were used for the phylogenetic analyses, including all previously published sequences and 13 new ones in order to include representatives from all taxa and lineages.

Data analyses

Phylogenetic analyses

DNA sequences were aligned using ClustalX (Thompson *et al.* 1997) with default parameters. All the 70 cyt *b* sequences had the same length, therefore no gaps were postulated. Although some gaps were postulated in order to resolve length differences in the 12S rRNA gene fragment, all positions could be unambiguously aligned and were therefore included in the analyses.

Two methods of phylogenetic analysis, namely maximum likelihood (ML) and Bayesian analysis (BI), were employed for the two independent partitions (cyt *b* and 12S) and the combined data set, respectively, and their results were compared. jModeltest v.0.1.1 (Posada 2008) was used to select the most appropriate model of sequence evolution for the ML and BI of the independent partitions and the combined data sets, under the Akaike information criterion. The models selected were: GTR+I+G for the cyt *b* partition and combined data set and GTR+G for the 12S rRNA partition.

Bayesian analyses were performed using MrBayes v.3.0b4 (Huelsenbeck & Ronquist 2001). The analyses were run for 2×10^6 generations, with sampling intervals of 100 generations, to produce 20,000 trees. After verifying that stationarity had been reached by plotting -ln *L* against generation time, the first 4000 trees in the cyt *b* + 12S data set were discarded and independent majority rule consensus trees generated from the remaining (post-'burn-in') trees.

Maximum likelihood analyses were performed using phyml (Guindon & Gascuel 2003), with model parameters fitted to the data by likelihood maximization. The reliability of the ML trees was assessed by bootstrap analysis (Felsenstein 1985), with 1000 replications.

Any topological incongruence between partitions was tested using the incongruence length difference (ILD) test (Michkevich & Farris 1981; Farris *et al.* 1994), with 10,000 heuristic searches performed after removing all invariable characters (Cunningham 1997). A reciprocal 70% bootstrap proportion (Mason-Gamer & Kellogg 1996) or a 95% posterior probability (PP) threshold was also used to test for incongruence between data sets. Topological constraints to test alternative topologies were constructed using MacClade v.4.0 (Maddison & Maddison 1992) and compared with optimal topologies using the Shimodaira–Hasegawa (SH) test (Shimodaira & Hasegawa 1999) implemented in PAUP* 4.0b10 (Swofford 1998).

Population genetics, demographic analyses and correlations

Network approaches are more effective than classical phylogenetic ones for representing intraspecific evolution (Posada & Crandall 2001). Therefore, the genealogical relationships between groups were assessed with haplotype networks constructed using statistical parsimony (Templeton *et al.* 1992), implemented in the program TCS v.1.21 (Clement *et al.* 2000), with a connection limit of 95%. Genetic differentiation between populations belonging to the same network was calculated using the *Snn* statistic (Hudson 2000) implemented in the program DnaSP v.5 (Rozas *et al.* 2003) (Appendix III.3). Independent networks and those island populations which were part of a network but presented significant *Snn* values were considered distinct evolutionarily significant units (ESUs), following Fraser & Bernatchez (2001).

Haplotype (*Hd*) and nucleotide diversity (π) values, number of haplotypes (*h*) and segregating sites (*S*) were also calculated using DnaSP v.5 (Table III.1). A series of analyses were carried out to test for the hypothesis of a rapid expansion and to estimate the time since expansion. Fu's F_S statistic (Fu 1997) was calculated to test for deviations from the neutral Wright–Fisher model consistent with a population expansion under the neutrality hypothesis, using coalescent simulations in DnaSP (based on the segregating sites and assuming no recombination, with 10,000 replicates and 0.95 as confidence interval).

To characterize the expansion pattern further, Arlequin v.3.1 (Excoffier *et al.* 2005) was used to determine the historical demography of the population using mismatch distributions and the models of Rogers & Harpending (1992) and Rogers (1995). Recent growth is expected to generate a unimodal distribution of pairwise differences between sequences (Rogers & Harpending 1992). The distribution is compared with that expected under a model of population expansion (Rogers 1995), calculating the estimator expansion time (τ) and the initial and final θ (θ_0 and θ_1, respectively), according to Schneider & Excoffier (1999). Monte Carlo simulations of 1000 random samples assessed the fit of the mismatch distribution to the theoretical distribution under an expansion scenario. The sum

Table III.1 Mitochondrial cytochrome *b* diversity, neutrality tests and demographic parameters in the 15 evolutionarily significant units (ESUs) of the four phylogenetic groups (A to D) of *Tarentola* taxa from the Cape Verde Islands.

Group	ESUs	n	π	h	Hd	S	F_s	SSD	τ	θ_0	θ_1	t (years)
A	1 – *T. “rudis” boavistensis* BV	17	0.00451	3	0.654	4	0.53603	0.03746	2.461	0.00200	2.750	
	2 – *T. darwini* SN	16	0.00289	6	0.542	7	-3.10275**	0.00347	1.537	0.00000	1.487	66 973
	3 – *T. darwini* F	39	0.00373	12	0.750	12	-8.36432**	0.01009	1.256	0.00352	99999	54 729
	4 North – *T. darwini* ST	66	0.00574	11	0.717	11	-2.86202	0.01050	2.908	0.00000	3.322	
	4 South – *T. darwini* ST	72	0.00867	18	0.815	17	-6.62733**	0.02075	3.383	0.00000	7.461	147 412
B	1 – *T. caboverdiana substituta* SV	52	0.00342	12	0.632	11	-7.96204**	0.00325	1.367	0.00000	3.470	59 566
	2 – *T. caboverdiana raziana* SL+br+ra	24	0.00377	8	0.764	7	-3.92264*	0.01285	1.316	0.00000	99999	57 343
	3 – *T. caboverdiana caboverdiana* SA	44	0.01241	23	0.942	25	-13.00275**	0.10558**	1.309	0.00000	99999	
C	*T. caboverdiana nicolauensis* SN	49	0.00576	12	0.844	10	-3.53715*	0.00142	1.850	0.00000	99999	80 612
D	1 – *T. gigas* br+ra	6	0.00198	2	0.600	1	0.79518	0.05428	0.947	0.00000	99999	
	2 – *T. rudis rudis* ST	23	0.00172	3	0.379	2	-0.03308	0.00421	0.887	0.00000	0.900	
	3 and 4 – *T. rudis protogigas* B+F	22	0.06683	6	0.702	9	-0.00650	0.04318	0.125	1.30400	99999	
	4 and 5 – *T. rudis protogigas* and *T. rudis hartogi* B+ro	23	0.00269	5	0.628	4	-1.47199	0.01347	0.932	0.00200	99999	
	6 – *T. rudis maioensis* M	25	0.00341	6	0.577	6	-1.80635	0.00850	0.242	0.84199	99999	

BV, Boavista; SN, São Nicolau; F, Fogo; ST, Santiago; SV, São Vicente; SL, Santa Luzia; br, Branco; ra, Raso; SA, Santo Antão; B, Brava; ro, Rombos; M, Maio.

n, sample size; π, nucleotide diversity; h, number of haplotypes; Hd, haplotype diversity; S, segregating sites; F_S, Fu’s statistic; SSD, sum of squared deviation statistics; τ, tau; θ_0, initial theta; θ_1, final theta; t, expansion time for the six populations for which the tests suggested expansion.

*$P < 0.05$; **$P < 0.01$.

of squared deviations between observed and expected mismatch distributions was used as a test statistic, with the P-value representing the probability of obtaining a simulated sum of squared deviations (SSD) larger than or equal to the observed one (Table III.1). The τ parameter is an estimate of time after expansion (t) in mutational units. Thus, if the divergence rate per nucleotide per year ($\tau = 2\mu$, where μ is the substitution rate per lineage) and the number of nucleotides of the fragment analysed (l) are known, it is possible to calculate the age when the expansion occurred using the expression $\tau = 2 \mu l t$ (modified from Harpending *et al.* 1993).

Spearman’s rank correlations (Table III.2) were calculated to establish comparisons between the number of sequences (n), haplotype diversity (Hd), number of ESUs and geographical and ecological characteristics of the islands (Appendix III.4) – size (area, perimeter), elevation (maximum, medium and median), location (latitude and longitude of the centroid of the island) and habitat diversity (number of habitats). Longitude is an estimate of the age of the islands for this archipelago. Haplotype diversity was considered rather than haplotype number, as the former is independent of sample size. Correlations between these variables were considered if the Spearman rank correlation coefficient (ρ) was ≥0.60 and $P < 0.05$ and calculated using the jmp package (SAS Institute, Cary, NC, USA). The geographical variables were obtained using the geographic information system (GIS) ArcMap 9.0 (ESRI 2004) with elevations being derived from a digital elevation model (Jarvis *et al.* 2006) and habitat diversity by adapting the information available in the agro-ecological and vegetation zoning maps presented in Appendix III.1.

Estimation of divergence times and mutation rate (μ)

The computer program r8s v.1.6.4 was used to estimate divergence times between lineages (Sanderson 2002). The outgroup sequence of *Tarentola americana* (Gray, 1831) was eliminated from the tree prior to the analysis. Smoothing of rate variation along the tree was performed with the Langley & Fitch (1974) and penalized likelihood (Sanderson 2002) methods. Sixteen smoothing factors with log10 from -2 to 5.5 were used for the penalized likelihood method. The lowest χ^2 cross-validation score, as calculated by r8s, was used to select the best method.

Table III.2 Spearman's correlation q values between genetic variability parameters of endemic Cape Verde *Tarentola* geckos and geographical and ecological characteristics of the islands.

	Size		**Elevation**			**Location**		**Habitat diversity**
	Area	Perimeter	Maximum	Mean	Median	Longitude	Latitude	No. habitats
n	0.7802**	0.6967**	0.8022**	0.7503**	0.8471**	-0.2220	0.0681	0.8912**
Hd	0.7734**	0.6267*	0.6645**	0.6385*	0.7275**	-0.1600	0.2578	0.7348**
No. ESUs	0.1949	0.1283	0.2591	0.2952	0.3298	-0.0469	-0.1826	0.2957
No. habitats	0.8578**	0.8667**	0.9289**	0.8577**	0.9111**	-0.0867	0.1245	

n, sample size; *Hd*, haplotype diversity; ESUs, evolutionarily significant units; location (latitude and longitude of the centroid of the island). *$P < 0.05$; **$P < 0.01$.

A parametric bootstrap analysis, in which 1000 Monte Carlo simulations of alignments with the same length as the complete data sets were generated with Seq-Gen (Rambaut & Grassly 1997), using the phylogenetic tree and model parameters previously obtained, was performed to account for the error involved in the calibration of the *Tarentola* phylogeny. This allowed the stochastic errors of date estimates associated with sampling a finite number of base pairs to be evaluated (Sanderson & Doyle 2001; Lalueza-Fox *et al.* 2005).

Two calibration points were used to estimate absolute rates. The first of these was based on the assumption that divergence between *Tarentola boettgeri hierrensis* Joger & Bischoff, 1983 and *Tarentola boettgeri bischoffi* Joger, 1984 began approximately 1 Mya (see Carranza *et al.* 2000). The second calibration point was based on the assumption that *Tarentola delalandii* (Duméril & Bibron, 1836) from north Tenerife colonized the island of La Palma 2 Mya (Ancochea *et al.* 1994; Gübitz *et al.* 2000). The ML phylogenetic tree from Fig. III.2 was also used with the same calibration points as stated above, but using the Langley–Fitch algorithm, to infer the average mutation rate (μ) for the genus *Tarentola*.

RESULTS

Phylogenetic analyses

Independent ML and BI analyses of the two genes (cyt *b* and 12S) produced trees that differed in some minor arrangements of taxa or individual samples. These differences had low bootstrap and posterior probability support in all cases (<70% and 95%, respectively). It was therefore considered that there were no major topological conflicts between the two gene partitions (Mason-Gamer & Kellogg 1996). The ILD test ($P > 0.60$) similarly showed that the two independent data sets were not incongruent. In total, the combined data set included 1087 bp (684 bp from cyt *b* and 403 bp from 12S rRNA), of which 674 positions were variable and 637 parsimony-informative (522 and 515 for cyt *b* and 152 and 122 for 12S rRNA, respectively).

The results of the ML and BI phylogenetic analyses of the combined cyt *b* + 12S rRNA data sets are shown in Fig. III.2 and support the hypothesis that *Tarentola* from the Cape Verde archipelago is a clade that originated as a result of a single transoceanic dispersal event from the Canary Islands.

The combined tree of the ML and BI analyses shows four major groups (see Fig. III.2): (A) the *Tarentola darwini* Joger, 1984 – *Tarentola 'rudis' boavistensis* Joger, 1993 group, not well supported; (B) the *Tarentola caboverdiana* Schleich, 1984 group, with subspecies from São Vicente (*T. caboverdiana sustituta* Joger, 1984), Santa Luzia and Raso islet (*T. caboverdiana raziana* Schleich, 1984) and Santo Antão (*T. caboverdiana*

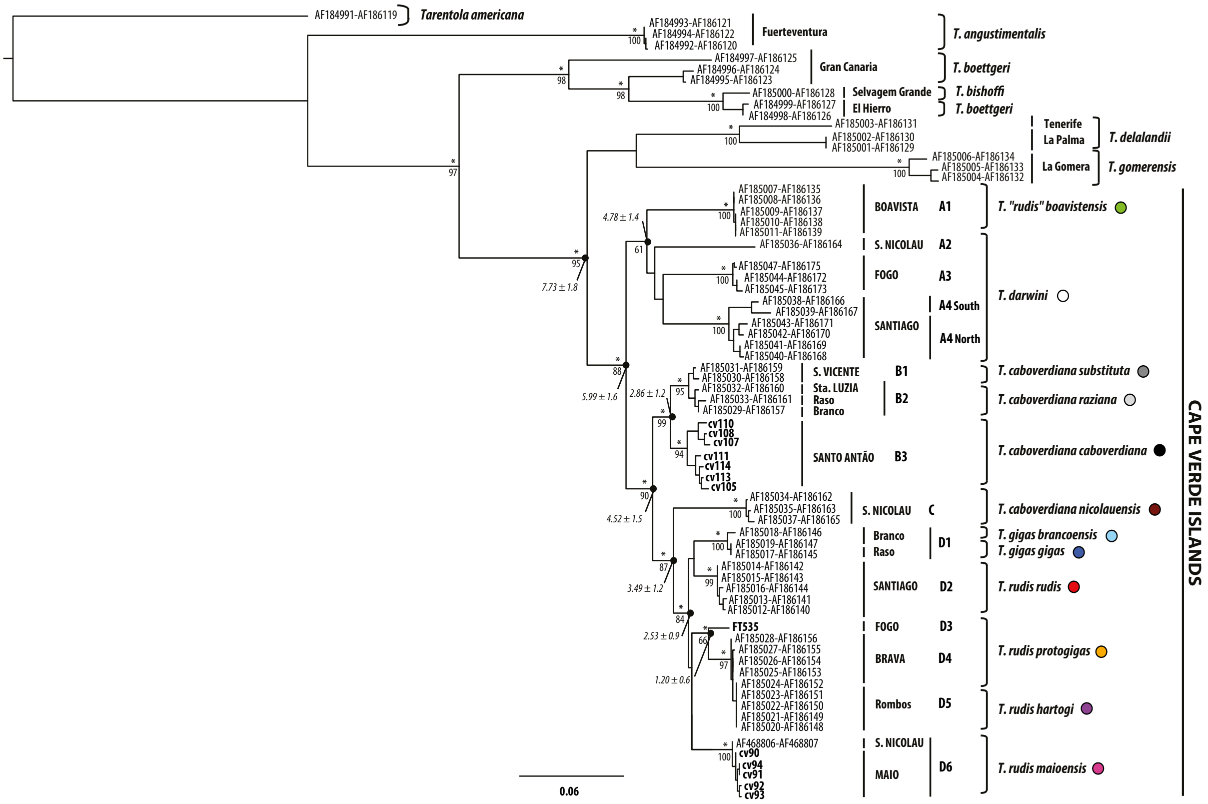


Figure III.2 Maximum likelihood (ML) tree inferred using the GTR+I+G model of sequence evolution (log likelihood = -6468.896) showing relationships and estimated times of divergence of endemic Cape Verde *Tarentola* taxa and their relatives from the Canary Islands. The tree is rooted using *Tarentola americana*. Bootstrap support values above 60% for the ML analysis are shown below nodes. Posterior probability (PP) values higher than 95% for the Bayesian analysis are represented by an asterisk (*) and are shown above nodes. Italic numbers in some selected nodes (highlighted with a filled circle) indicate the estimated age of the speciation event of that node in millions of years ago, followed by the standard deviation obtained with parametric bootstrap using the original topology (see Materials and Methods). Sequences downloaded from GenBank are shown in the figure with their respective GenBank accession numbers for the cytochrome *b* and 12S rRNA genes separated by a dash. For locality data and GenBank accession numbers (ranging from GQ380699 to GQ381129) of the new sequences see Appendix III.2. Letters immediately to the right of island names correspond to the 15 evolutionarily significant units (ESUs) recognized in the present work and shown in Fig. III.3. Coloured dots correspond to taxa shown in Fig. III.1.

caboverdiana Schleich, 1984); (C) the *T. caboverdiana nicolauensis* Schleich, 1984 group; and (D) the *Tarentola gigas* (Bocage, 1896) – *Tarentola rudis* Boulenger, 1906 group; the latter three are very well supported.

The phylogeny indicates that *T. rudis* is polyphyletic, with *T. 'rudis' boavistensis*, which is endemic to the island of Boavista, being more closely related to *T. darwini* from São Nicolau, Fogo and Santiago than to the remaining species of *T. rudis*. To test this result further, the log likelihood of the ML tree presented in Fig. III.2 (-6468.9) was compared with the log likelihood of a ML tree constrained so that *T. rudis* was monophyletic (-6501.7). The results of the SH test showed that the constrained tree had a significantly worse log likelihood value than the unconstrained solution (Diff -ln L = 32.8; $P < 0.005$), hence the tree from Fig. III.2, where *T. rudis* is polyphyletic, is preferred.

Tarentola caboverdiana, *T. gigas* and *T. rudis* form a very well-supported clade, which is sister to group 'A' formed by *T. darwini* and *T. 'rudis' boavistensis*. The phylogenetic analyses show that *T. caboverdiana* is paraphyletic, with the subspecies from São Nicolau (*T. caboverdiana nicolauensis* – group 'C') being more closely related to *T. rudis* and *T. gigas* (group 'D') than to the remaining subspecies of *T. caboverdiana* (*T. c. caboverdiana*, *T. c. raziana* and *T. c. substituta* – group 'B'). However, the results of the SH test showed that the log likelihood of the constrained tree in which *T. caboverdiana* was forced to be monophyletic (-6474.3) was not significantly worse than the 'best' tree presented in Fig. III.2 (Diff -ln $L = 5.4$; $P > 0.40$).

The three lineages of *T. darwini* within group 'A', are very divergent, thus indicating that populations from Fogo, São Nicolau and Santiago have been evolving in isolation for several million years. The bootstrap and PP values that support the monophyletic status of *T. darwini* are very low (Fig. III.2).

The three subspecies of *T. caboverdiana* from group 'B' form a robust monophyletic assemblage that is further subdivided into the population from Santo Antão (*T. c. caboverdiana*) and the populations from São Vicente (T. c. substituta) and the Desertas group, Santa Luzia, Raso and Branco (*T. c. raziana*).

Within group 'D', *T. gigas* and *T. rudis* from the southern islands form a very well-supported clade. *Tarentola gigas* appears in the phylogeny as a sister taxon to *T. r. rudis* from Santiago, although support for this assemblage is low. A constraint analysis in which *T. rudis* from the southern islands was forced to be monophyletic produced a tree with a log likelihood almost identical to the log likelihood of the unconstrained tree presented in Fig. III.2 (Diff -ln $L = 0.314$; $P > 0.79$), thus indicating that the apparent paraphyletic status of *T. rudis* recovered in Fig. III.2 is not well supported by our data. It is also shown that populations of *T. rudis protogigas* Joger, 1984 and *T. rudis hartogi* Joger, 1993 from the southern islands of Fogo, Brava and Rombos islets form a clade apart from *T. rudis maioensis* Schleich, 1984 from Maio.

Population genetics and demographic analyses

A 303-bp fragment of the cyt *b* gene was analysed for 459 sequences of *Tarentola*, corresponding to 276 localities from the nine islands and four islets across the Cape Verde archipelago where the genus is extant (no specimens were found on Sal). Over the whole data set, 105 polymorphic sites and 120 haplotypes were identified. Eight independent networks could be inferred based on the connection limit of 95%. The phylogenetic lineages leading to these independent networks are highlighted in Fig. III.2 and the networks themselves are shown in Fig. III.3. The significant *Snn* comparison tests (Appendix III.3) indicate that northern and southern populations from Santiago (A4North, A4South), the three island populations of *T. caboverdiana* from network 'B' (B1, B2 and B3), and five populations from network 'D' (D1, D2, D3, D4 and D5) are genetically differentiated and should be considered as independent units in the demographic analyses (see below). The mtDNA analyses therefore highlighted the existence of 15 independent ESUs in *Tarentola* from the Cape Verde archipelago. The number of individuals sampled (*n*), number of haplotypes (*h*), nucleotide diversity (π), haplotype diversity (*Hd*), segregating sites (*S*) and other relevant data for each of these ESUs are listed in Table III.1.

As expected from the star-like topologies of some of the networks, seven cases (A2, A3, A4South, B1, B2, B3 and C) were detected from the 15 ESUs identified in Fig. III.3 in which Fu's F_S test was significantly negative, thus indicating that these populations could have experienced a demographic expansion event. To characterize the expansion pattern further, a model of sudden demographic growth was fitted to the pairwise sequence mismatch distribution of the seven populations. In six of these cases, the mismatch distributions were not significantly different from the sudden expansion model of Rogers & Harpending (1992). The results of Fu's F_S test, the squared deviation statistic (SSD) and other relevant demographic parameters are listed in Table III.1. The mutation rate inferred from the ML tree using r8s (see Materials and Methods) was 3.7×10^{-8} per site, per year, therefore the approximate onset of expansion for the six populations was estimated (Table III.1) assuming a generation time of 1 year for Cape Verdean *Tarentola* (R. Vasconcelos pers. obs.).

Correlations between the genetic variability parameters and the geographical characteristics of the islands showed that the haplotype diversity and the habitat diversity present in each island are strongly and positively correlated to the area and elevations but not to the latitudinal or longitudinal location of the island, and therefore are not linearly related to the age of the islands (Table III.2). Also the number of habitats was positively and significantly correlated with the haplotype diversity present in the islands, whereas the number of ESUs per island was not correlated with any of these geographical or ecological characteristics.

DISCUSSION

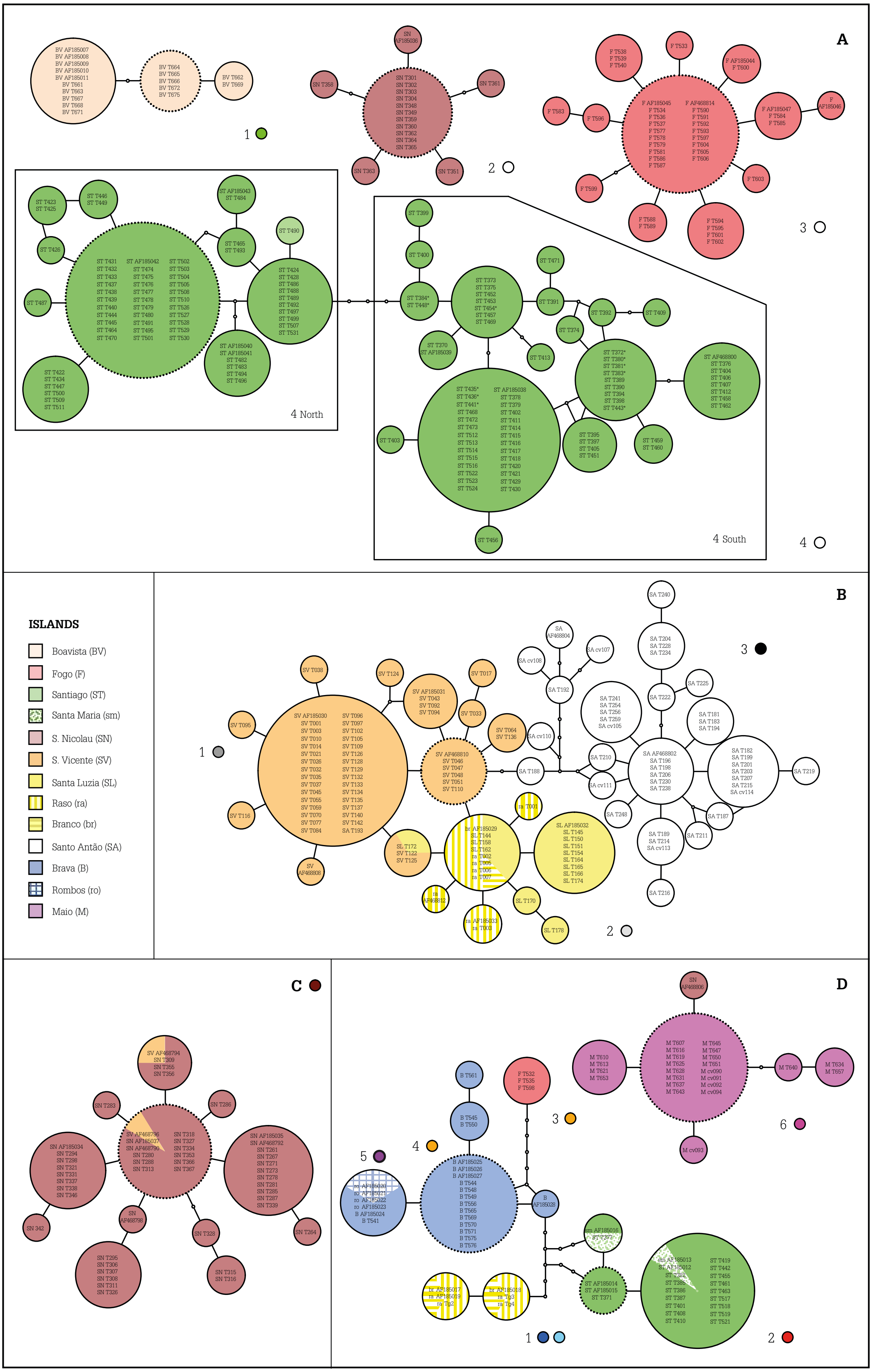
Phylogeography of *Tarentola* from the Cape Verdes

More than one species of Cape Verdean *Tarentola*, a well-supported clade, is found on some of the islands, and some species are paraphyletic (Carranza *et al.* 2000). To clarify the distribution and phylogeographic patterns, three new forms were included in this study: two new taxa, *T. rudis maioensis* and *T. caboverdiana caboverdiana* (endemic subspecies from Maio and Santo Antão, respectively), and *T. rudis protogigas*, which also occurs on Brava, from a previously unsampled island (Fogo). With the addition of these new data, the phylogenetic tree presented in Fig. III.2 now includes representatives of all known taxa from all the islands where this genus occurs. Most branches are now better supported and the relationships between the three new forms are revealed. Knowledge of a complete and robust phylogeny for the Cape Verdean *Tarentola* is also essential for future conservation of these endemic geckos as it defines the ESUs to be protected in the projected protected areas.

The results indicate that *T. caboverdiana nicolauensis*, which previously appeared as a sister taxon to *T. c. raziana* and *T. c. substituta*, *T. rudis* and *T. gigas*, is probably unrelated to the other specimens of *T. caboverdiana* present in the northwestern group, which form a well-supported group. Currently, *T. c. nicolauensis* appears to be most closely related to the *T. rudis* – *T. gigas* complex. It is also apparent that the *T. rudis protogigas* and *T. rudis hartogi* populations (from the southern islands of Fogo, Brava and Rombos islets) form a well-supported clade. In addition it is shown that *T. r. maioensis* from Maio, which belongs to the southern group but is ecologically and geologically closer to the eastern group, forms another clade that is weakly supported as a sister taxon of the latter. Furthermore, it is apparent that the detection of *T. 'gigas'* on São Nicolau by Jesus *et al.* (2002) was a misinterpretation due to the previous lack of samples from Maio Island – it is in fact a specimen of *T. r. maioensis* (Fig. III.3). This highlights the importance of a complete sampling to perform phylogenetic analyses.

The agreement between the phylogenetic structure within the different clades in this group and the three ecogeographical regions of the archipelago is also strongly evident. Thus, group 'A' is subdivided into three units, each of which is assigned to one of the eastern, north-western and southern regions (see Fig. III.1). Some *Tarentola* species, such as *T. caboverdiana*, which only appears in the north-western islands group, and *T. rudis*, which is present in all southern islands, are exclusive to one of these regions, as is the case with *Chioninia* and *Hemidactylus* endemic reptiles, two other radiations in this archipelago (Carranza *et al.* 2001; Arnold *et al.* 2008).

Figure III.3 Networks corresponding to cytochrome *b* sequence variation in endemic Cape Verde *Tarentola* geckos. Lines represent a mutational step, dots missing haplotypes and circles haplotypes. The circle area is proportional to the number of individuals. Dotted circles represent probable ancestral haplotypes and * represents individuals with ambiguous identification. For correspondences of sample and location codes, see Appendix III.2. **A)** *Tarentola 'rudis' boavistensis* from Boavista (1), *Tarentola darwini* from São Nicolau (2), Fogo (3) and Santiago (4); **B)** *Tarentola caboverdiana* from São Vicente (1), Santa Luzia, Branco and Raso islets (2) and Santo Antão (3); **C)** *Tarentola caboverdiana nicolauensis* from São Nicolau; **D)** *Tarentola gigas* from Branco and Raso (1), *Tarentola rudis* from Santiago (2), Fogo (3), Brava (4), Rombos islets (5), and Maio (6). Coloured dots correspond to taxa shown in Fig. III.1.


A
1
2
3
4 North
4 South
4
B
1
2
3
ISLANDS
Boavista (BV)
Fogo (F)
Santiago (ST)
Santa Maria (sm)
S. Nicolau (SN)
S. Vicente (SV)
Santa Luzia (SL)
Raso (ra)
Branco (br)
Santo Antão (SA)
Brava (B)
Rombos (ro)
Maio (M)
C
D
1
2
3
4
5
6

According to the new phylogenetic hypothesis and inferred dates (Fig. III.2), *Tarentola* colonized the Cape Verde archipelago from the western Canary Islands approximately 7.73 ± 1.8 Mya. The most parsimonious explanation is that the first island to be colonized was São Nicolau, which is part of the north-western island group (Fig. III.1). As São Nicolau consisted of two independent units until 4.7 – 2.6 Mya, when they were finally united by volcanic activity (Duprat *et al.* 2007), we hypothesize that the first speciation event that separated the ancestor of group 'A' (*T. darwini* + *T. 'rudis' boavistensis*) and the ancestor of groups 'B', 'C' and 'D' (*T. caboverdiana* + *T. rudis* from the southern islands, plus *T. gigas* from Raso and Branco) approximately 5.99 ± 1.6 Mya took place by allopatric speciation on this island. The ancestor of *T. caboverdiana* went on to colonize all the remaining north-western islands, whereas the ancestor of group 'A' colonized the eastern island of Boavista and the southern islands of Santiago and Fogo. The topology presented in Fig. III.2 also suggests that another colonization event took place from São Nicolau to Branco, Raso or Santa Luzia approximately 3.49 ± 1.2 Mya. This event gave rise to *T. gigas*, which nowadays only survives on the islets of Branco and Raso, where it coexists with the much smaller *T. caboverdiana*. The ancestor of the four subspecies of *T. rudis* present on all the southern islands arrived approximately 2.53 ± 0.9 Mya, also from the north.

Distribution of the genetic diversity

As the network analyses showed that not even the populations considered to belong to the same species could be linked together, it can be concluded, following Hart & Sunday (2007), that cryptic taxa have probably been overlooked. Geckos are often morphologically conservative (Harris *et al.* 2004), although mtDNA variation in *Tarentola* from the Cape Verde Islands is high between species relative to other reptiles from the same islands (Jesus *et al.* 2002), such as the endemic *Chioninia* skinks (Brehm *et al.* 2001).

This sampling confirmed that a population of the very distinct *T. darwini* form is indeed present on São Nicolau after a unique individual was reported by Carranza *et al.* (2000). Joger (1984) first reported the finding of *T. darwini* on São Nicolau, although Schleich (1987) considered this doubtful as Joger himself considered two of three animals found to be doubtfully assigned. This form therefore probably represents a new species. Extensive sampling identified its distribution, which is restricted to the eastern part of the island (Fig. III.1).

Examination of the networks within *T. darwini* shows little evidence for structuring within islands, except on Santiago. Here there are two geographically well delimited subgroups, one in the north and another one in the south of the island (A4North and A4South in Figs III.2 and III.3), which appear to be genetically differentiated according to the *Snn* test (Appendix III.3) and are considered here as independent ESUs.

As explained above, the presence of the two allopatric *Tarentola* species on São Nicolau (*T. darwini* and *T. caboverdiana*) can be explained by allopatric speciation, whereas the presence of two *Tarentola* species on Santiago (*T. rudis* and *T. darwini*) can be explained by two independent colonization events from the north, following the direction of the main currents and trade winds. Future GIS modelling of the species distributions may shed light on which factors constrain the current range of different species on the same island. The two species from Santiago are both morphologically and genetically distinct and occur in sympatry in the south of the island. This was first noticed by Schleich (1987) and is confirmed here, ruling out the parapatry suggested by Joger (1984). Ten of the 149 individuals sequenced, which had been assigned to *T. rudis* based on their morphology, presented *T. darwini* type mtDNA. This implies that limited hybridization may be occurring and that the movement of mtDNA across the species boundary may be unidirectional. However, detailed analyses of nuclear markers and morphological characters will be needed to confirm this.

The network analysis suggests that the presence of *T. r. maioensis* on São Nicolau is possibly due to an introduction, as it presents a haplotype only one mutational step away from that found in Maio (Fig. III.3.D6). Furthermore, despite extensive sampling, no other individual of that taxon was found on this island and the individual was found on the coast at Ponta Cachorro. Analogously, the two individuals of *T. c. nicolauensis* from São Vicente cited by Jesus *et al.* (2002) also seem to be the result of recent introductions as they present haplotypes common to those found on São Nicolau (Fig. III.3.C) and because they were found in Mindelo, which is a major port. Another possible introduction is of *T. c. substituta* (endemic to São Vicente) on Santo Antão, in Sinagoga, a fishing village (Fig. III.3.B). However, the presence of a common haplotype between *T. c. substituta* and *T. c. caboverdiana* (Fig. III.3.B) in this latter case could also be explained by the fact that Santo Antão and its neighbouring islands (São Vicente, Santa Luzia, Raso and Branco islets) were very close together during the Pleistocene sea-level falls, thus allowing gene flow between them. Geckos are often introduced from one island to another, for example the introduction of *T. mauritanica* from the island of Madeira to Porto Santo, in the same archipelago (Jesus *et al.* 2008), or the two independent introductions of *Hemidactulus angulatus* on Cape Verde from two different African sources (Arnold *et al.* 2008). Island endemics can even be introduced to the mainland, as in the case of *T. delalandii* from the Canaries to Cantabria (Gómez 2006), thus highlighting the need to consider this factor when assessing phylogeographic patterns of these species.

Biogeographical patterns

Deep molecular divergences between reptile lineages of the same island have been reported in Tenerife and Gran Canaria, Canary Islands (e.g. *Chalcides sexlineatus* and *Chalcides viridanus*: Pestano & Brown 1999, Brown *et al.* 2000, Carranza *et al.* 2008; *Tarentola delalandii* and *Tarentola boettgeri*: Nogales *et al.* 1998, Gübitz *et al.* 2005; *Gallotia galloti* and *Gallotia intermedia*/*Gallotia goliath*: Thorpe *et al.* 1996, Maca-Meyer *et al.* 2003). The main proposals to explain this pattern are geographical or ecological isolation, in other words, multiple geological origins and marked ecological differences between regions on the islands that enhanced opportunities to evolve allopatrically (Thorpe & Malhotra 1996). Likewise, homogeneity at the molecular level on the smaller islands of Fuerteventura, Lobos and Lanzarote has been explained by the absence of geographical barriers and ecological similarity within these islands (Nogales *et al.* 1998). Since the Cape Verde archipelago belongs to the same biogeographical region and presents islands of different sizes, a similar pattern of divergent new lineages following the extensive sampling would be expected for the larger and more mountainous islands, as it has been demonstrated that both area and elevation positively affect speciation rates (Rosenzweig 1995; Hobohm 2000). However, within the same form, different mitochondrial lineages were found only on Santiago. Furthermore, half of the median-joining networks revealed a 'star-like' haplotype network (Fig. III.3) and presented strongly negative F_S (Fu 1997) and significant SDD values, thus indicating that rapid recent expansions (Slatkin & Hudson 1991) preceded by strong bottlenecks occurring all over the archipelago (Table III.1).

Demographic analyses further demonstrate that six out of the seven expansion events inferred from our data set occurred between 55,000 and 147,000 years ago. One possible explanation is that these expansions occurred after volcanic eruptions that decimated the fauna. Indeed, volcanism younger than 1.1 Mya has occurred on several of the islands: São Vicente (0.3 Mya), Fogo (in 1995, with 26 volcanic eruptions since the 15th century), Santiago, Sal (0.4 Mya), Santo Antão (0.09 Mya) and São Nicolau (0.1 Mya) (Plesner *et al.* 2002; Torres *et al.* 2002; Knudsen *et al.* 2003; Schlüter 2006; Duprat *et al.* 2007). However, such events have not occurred recently on Maio or Boavista, for example (Stillman *et al.* 1982; Mitchell *et al.* 1983), and these present low intraspecific mitochondrial divergences too. Thus, recent volcanism could be a factor, although not the only factor, involved. Half of the Cape Verde Islands (Santiago, Fogo, Brava, Santo Antão and São Nicolau) have steep mountain areas, one reaching almost 3000 m, thus the presence of geographical barriers is unquestionable, especially since *Tarentola* species are typically found in dry areas at elevations below 1500 m (Barbadillo *et al.* 1999; R. Vasconcelos pers. obs.).

On the other hand, reduced ecological differences within an island were shown by the low number of 'floristic altitudinal zones' (used by many authors as an indicator of the macro habitat diversity), which is always lower than three for all islands (Duarte *et al.* 2007). This could explain why two mtDNA lineages with geographic structure were observed only on Santiago, the biggest island of the archipelago. This island also presents the highest number of ESUs and one of the highest haplotype diversities, followed by Santo Antão, which is the second biggest island (Appendix III.4). Both these islands exhibit a strong orography because erosion processes did not have enough time to flatten and aridify them as markedly as the older eastern islands and Maio, thus allowing an elevational ecological gradient. Moreover, based on the agro-ecological and vegetation zoning maps (Appendix III.1) and observations on the terrain (Appendix III.4), these islands present a relatively high habitat diversity (both climatic and topographic); this contrasts with their arid and semi-arid low and older eastern counterparts, where severe pluriannual droughts occur periodically and have been recorded since the 16th century (Langworthy & Finan 1997). This is also probably why *Tarentola* was found in low densities on Boavista (R. Vasconcelos & A. Perera pers. obs.), the third biggest island, and why this species is apparently not present on Sal (Carranza *et al.* 2000; R. Vasconcelos pers. obs.), even though an undetermined *Tarentola* species was reported from there by Angel (1935, 1937) and Mertens (1955). If those records are correct, we could even hypothesize an extinction scenario on this extremely arid island. Thus, the relatively fewer ecological niches and high ecological pressure in the Cape Verde Islands with respect to the Canaries have produced strong bottlenecks, which mean that *Tarentola* presents mtDNA networks with recent coalescent times.

The above findings are congruent with the general dynamic model (GDM) of oceanic island biogeography postulated by Whittaker *et al.* (2008). This model predicts that speciation rates peak when an island reaches its maximum area and elevational range, meaning that the maximum habitat diversity, and therefore the maximum opportunity for within-island allopatry, occurs during 'middle age' of the island. As only a snapshot of this archipelago can be analysed simultaneously, the Cape Verdes' 'middle age' corresponds to those islands that are in the mature phase of ontogeny, such as Santiago. The model also predicts that representatives on old, declining islands, such as Boavista, Sal and Maio, should gradually be lost because of loss of habitat, as could be the case of *Tarentola* from Sal. Furthermore, the model predicts that composite islands such as São Nicolau should have provided more opportunity for within-island allopatry, and should therefore contain sister species, as was found to be the case.

In conclusion, the *Tarentola* radiation has been clarified and the phylogenetic relationships found to be associated with historical island sizes, oceanic currents and trade winds, and distances between the three island groups. Two factors account for the low specific and intraspecific variation observed on each island of the Cape Verdes: (1) the recent volcanic activity and high ecological stress that could lead to population extinctions, and (2) the poor habitat diversity within some islands that could restrain opportunities for allopatric diversification. Some geological and ecological features of the islands, such as area, elevation and number of habitats have been found to be positively correlated with genetic diversity. The relationship between genetic diversity and age of the islands fits the predictions of the GDM of oceanic island biogeography.

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SUPPORTING INFORMATION

Appendix III.1 Types and total number of habitats for each island in the Cape Verde archipelago (adapted from Diniz & Matos, 1986, 1987, 1988 a, b, 1993, 1994, 1999 a, b, c).

Habitat type	**SV**	**SL**	**ra**	**br**	**SA**	**SN**	**B**	**ro**	**M**	**F**	**ST**	**sm**	**S**	**BV**
Beach	yes	yes	no	no	yes	yes	no	no	yes	yes	yes	no	yes	yes
Dunes and sandy areas	yes	yes	no	no	no	no	no	no	yes	no	no	no	yes	yes
Recent lavas	no	no	no	no	no	no	no	no	no	yes	no	no	no	no
Very arid flat areas	yes	yes	yes	no	yes	yes	no	no	yes	yes	no	no	yes	yes
Very arid and hilly areas	yes	yes	yes	yes	yes	yes	no	no	no	no	no	no	yes	yes
Very arid and mountain areas	yes	yes	yes	yes	no	yes	no	no	no	no	no	no	no	no
Arid and flat areas	no	no	no	no	no	yes	yes	yes	no	yes	yes	yes	no	no
Arid and hilly areas	yes	no	no	no	yes	yes	yes	yes	yes	no	yes	no	no	no
Arid and mountain areas	yes	no	no	no	yes	no	no	no	no	no	yes	no	no	no
Semi-arid and flat areas	no	no	no	no	no	yes	yes	no	no	yes	yes	no	no	no
Semi-arid and hilly areas	no	no	no	no	yes	yes	yes	no	no	yes	yes	no	no	no
Semi-arid and mountain areas	yes	no	no	no	yes	yes	no	no	no	no	yes	no	no	no
Sub-humid and flat areas	no	no	no	no	no	no	no	no	no	yes	no	no	no	no
Sub-humid and hilly areas	no	no	no	no	yes	no	yes	no	no	yes	yes	no	no	no
Sub-humid and mountain areas	yes	no	no	no	yes	yes	yes	no	no	yes	yes	no	no	no
Humid and mountains areas	no	no	no	no	yes	yes	yes	no	no	yes	yes	no	no	no
Water lines and floodplain areas	yes	yes	no	no	yes	yes	yes	no	yes	no	yes	no	yes	yes
Coastal-salty lowland areas	yes	no	no	no	no	no	no	no	yes	no	no	no	yes	yes
Cliffs	no	no	no	no	no	no	no	no	no	yes	yes	no	no	no
Urban	yes	no	no	no	yes	yes	yes	no	yes	yes	yes	no	yes	yes
Total number	12	6	3	2	12	13	9	2	7	12	13	1	7	7

SV, S. Vicente; SL, Sta. Luzia; ra, Raso; br, Branco; SA, Santo Antão; SN, S. Nicolau; B, Brava; ro, Rombos; M, Maio; F, Fogo; ST, Santiago; sm, Sta. Maria; S, Sal; BV, Boavista.

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Appendix III.2 Details of material and sequences used in the present study.

Code	Taxa	Island	Locality	GenBank codes 12S/ cyt *b* 1st/ cyt *b* 2nd
T001	*Tcs*	SV	Mindelo	GQ381037
T003	*Tcs*	SV	Mindelo	GQ381038
T010	*Tcs*	SV	Madeiral	GQ381039
T014	*Tcs*	SV	Calhau	GQ381040
T017	*Tcs*	SV	Calhau	GQ381041
T021	*Tcs*	SV	Calhau-Madeiral road	GQ381042
T026	*Tcs*	SV	Pico Alves Martinho	GQ381043
T032	*Tcs*	SV	Monte Verde	GQ381044
T033	*Tcs*	SV	Monte Verde	GQ381045
T035	*Tcs*	SV	Salamansa	GQ381046
T037	*Tcs*	SV	Salamansa	GQ381047
T038	*Tcs*	SV	Salamansa	GQ381048
T043	*Tcs*	SV	Salamansa	GQ381049
T045	*Tcs*	SV	Salamansa	GQ381050
T046	*Tcs*	SV	Salamansa	GQ381051
T047	*Tcs*	SV	Calhau	GQ381052
T048	*Tcs*	SV	S. Pedro	GQ381053
T051	*Tcs*	SV	S. Pedro	GQ381054
T055	*Tcs*	SV	S. Pedro	GQ381055
T059	*Tcs*	SV	S. Pedro	GQ381056
T064	*Tcs*	SV	Mindelo	GQ381057
T070	*Tcs*	SV	Mindelo	GQ381058
T077	*Tcs*	SV	Road to Madeiral	GQ381059
T084	*Tcs*	SV	Palha Carga	GQ381060
T092	*Tcs*	SV	Monte Verde	GQ381061
T094	*Tcs*	SV	Monte Verde	GQ381062
T095	*Tcs*	SV	Mato Inglês	GQ381063
T096	*Tcs*	SV	Mato Inglês	GQ381064
T097	*Tcs*	SV	Mato Inglês	GQ381065
T102	*Tcs*	SV	Mato Inglês	GQ381066
T105	*Tcs*	SV	Lazareto	GQ381067
T109	*Tcs*	SV	Lazareto	GQ381068
T110	*Tcs*	SV	Monte Cara	GQ381069
T116	*Tcs*	SV	Monte Cara	GQ381070
T122	*Tcs*	SV	road to S. Pedro	GQ381071
T124	*Tcs*	SV	road to S. Pedro	GQ381072
T125	*Tcs*	SV	road to S. Pedro	GQ381073
T126	*Tcs*	SV	road to S. Pedro	GQ381074
T128	*Tcs*	SV	road to S. Pedro	GQ381075
T129	*Tcs*	SV	Pico do Vento	GQ381076
T132	*Tcs*	SV	Pico do Vento	GQ381077
T133	*Tcs*	SV	Pico do Vento	GQ381078
T134	*Tcs*	SV	Pico do Vento	GQ381079
T135	*Tcs*	SV	Flamengos	GQ381080
T136	*Tcs*	SV	Flamengos	GQ381081
T137	*Tcs*	SV	Flamengos	GQ381082
T140	*Tcs*	SV	Flamengos	GQ381083
T142	*Tcs*	SV	Flamengos	GQ381084
T144	*Tcr*	SL	Água Doce	GQ381027
T145	*Tcr*	SL	Água Doce	GQ381017
T150	*Tcr*	SL	Água Doce	GQ381021
T151	*Tcr*	SL	Água Doce	GQ381018
T154	*Tcr*	SL	Ponta Salina	GQ381019
T158	*Tcr*	SL	Ponta de Praia	GQ381025
T162	*Tcr*	SL	Praia de Palmo a Tostão	GQ381026
T164	*Tcr*	SL	Monte Espia	GQ381020
T165	*Tcr*	SL	Topinho de Nhô Lopes	GQ381022
T166	*Tcr*	SL	Ribeira de Casa	GQ381023
T170	*Tcr*	SL	Morro da Prainha Branca	GQ381030
T172	*Tcr*	SL	Monte Creoulo	GQ381028
T174	*Tcr*	SL	Ribeira de Freira	GQ381024
T178	*Tcr*	SL	Ribeira de Freira	GQ381031
raT1	*Tcr*	ra	Ponta de Casa	GQ381032
raT2	*Tcr*	ra	Ponta de Casa	GQ381033
raT3	*Tcr*	ra	Ponta de Casa	GQ381029
raT5	*Tcr*	ra	Ponta de Casa	GQ381034
raT6	*Tcr*	ra	Ponta de Casa	GQ381035
raT7	*Tcr*	ra	Ponta de Casa	GQ381036
T181	*Tcc*	SA	Ponta do Sol	GQ381097
T182	*Tcc*	SA	Alto Mira	GQ381098
T183	*Tcc*	SA	Cova	GQ381099
T187	*Tcc*	SA	Cruzinha da Garça	GQ381108
T188	*Tcc*	SA	Coculi	GQ381117
T189	*Tcc*	SA	Lagoa	GQ381100
T192	*Tcc*	SA	Espongueiro cross	GQ381119
T193	*Tcc*	SA	Sinagoga	GQ381110
T194	*Tcc*	SA	Lombo Figueira	GQ381088
T196	*Tcc*	SA	Morro de Passagem	GQ381089
T198	*Tcc*	SA	Morro de Passagem	GQ381090
T199	*Tcc*	SA	Chã de Norte	GQ381091
T201	*Tcc*	SA	Chã de Norte village	GQ381092
T203	*Tcc*	SA	Aldeia	GQ381093
T204	*Tcc*	SA	Porto Novo	GQ381111
T206	*Tcc*	SA	Porto Novo	GQ381094
T207	*Tcc*	SA	Chã de Norte	GQ381095
T210	*Tcc*	SA	Chã de Lagoinha	GQ381096
T211	*Tcc*	SA	S.Tomé	GQ381109
T214	*Tcc*	SA	Porto Novo	GQ381101
T215	*Tcc*	SA	Rib de Bodes	GQ381102
T216	*Tcc*	SA	Chã do Brejo	GQ381103
T219	*Tcc*	SA	Chã de Banca	GQ381118
T222	*Tcc*	SA	Chã de Nhã Nica	GQ381112
T225	*Tcc*	SA	Chã de Nhã Nica	GQ381113
T228	*Tcc*	SA	Lombo do Meio	GQ381114
T230	*Tcc*	SA	Rabo de Gamboeza	GQ381085
T234	*Tcc*	SA	Curralete	GQ381115
T238	*Tcc*	SA	Curralete	GQ381086
T240	*Tcc*	SA	Curralete	GQ381116
T241	*Tcc*	SA	Ponte Sul	GQ381104
T248	*Tcc*	SA	Monte Trigo	GQ381087
T254	*Tcc*	SA	Covão	GQ381105
T256	*Tcc*	SA	Ponta Aguadinha	GQ381106
T259	*Tcc*	SA	Tarrafal de Monte Trigo	GQ381107
cv105	*Tcc*	SA	Dogoi	GQ380699/ GQ381120/GQ380712
cv107	*Tcc*	SA	Lagoa	GQ380703/ GQ381124/GQ380716
cv108	*Tcc*	SA	Lagoa	GQ380704/ GQ381125/GQ380717

Code	Taxa	Island	Locality	GenBank codes 12S/ cyt *b* 1st/ cyt *b* 2nd
cv110	*Tcc*	SA	Lagoa	GQ380705/ GQ381126/GQ380718
cv111	*Tcc*	SA	Lagoa	GQ380702/ GQ381123/GQ380715
cv113	*Tcc*	SA	Porto Novo	GQ380700/ GQ381121/GQ380713
cv114	*Tcc*	SA	Ribeira da Cruz	GQ380701/ GQ381122/GQ380714
T261	*Tcn*	SN	Tarrafal	GQ380980
T264	*Tcn*	SN	Praia Branca	GQ380981
T267	*Tcn*	SN	Praia Branca graveyard	GQ380974
T271	*Tcn*	SN	Praia Branca graveyard	GQ380983
T273	*Tcn*	SN	Monte Furado	GQ380975
T278	*Tcn*	SN	Chã do Curral	GQ380976
T280	*Tcn*	SN	Rb.ra da Prata	GQ380977
T281	*Tcn*	SN	Rb.ra da Prata	GQ380978
T283	*Tcn*	SN	Cabeçalinho	GQ380984
T285	*Tcn*	SN	Cabeçalinho	GQ380973
T286	*Tcn*	SN	Cabeçalinho	GQ380985
T287	*Tcn*	SN	Cabeçalinho	GQ380982
T288	*Tcn*	SN	Lombo de Morro	GQ380986
T294	*Tcn*	SN	Tarrafal	GQ380969
T295	*Tcn*	SN	Luís Afonso	GQ380998
T298	*Tcn*	SN	Luís Afonso	GQ380970
T306	*Tcn*	SN	Ribeira Brava	GQ380999
T307	*Tcn*	SN	Ribeira Brava	GQ381000
T308	*Tcn*	SN	Ribeira Brava	GQ381001
T309	*Tcn*	SN	Ribeira Brava	GQ381002
T311	*Tcn*	SN	Campinho	GQ380972
T313	*Tcn*	SN	Fajã de Baixo	GQ380987
T315	*Tcn*	SN	Estância Brás cross	GQ380994
T316	*Tcn*	SN	Estância Brás cross	GQ380995
T318	*Tcn*	SN	Cabeçalinho	GQ380991
T321	*Tcn*	SN	Praia de Baixo	GQ380966
T326	*Tcn*	SN	Campo do Porto	GQ380997
T327	*Tcn*	SN	Fajã de Baixo	GQ380988
T328	*Tcn*	SN	Assomada da Covada	GQ380996
T331	*Tcn*	SN	Preguiça Airport	GQ380965
T334	*Tcn*	SN	Caldeira da Preguiça	GQ380989
T337	*Tcn*	SN	Caldeira da Preguiça	GQ380964
T338	*Tcn*	SN	Caldeira da Preguiça	GQ380968
T339	*Tcn*	SN	Hortelão	GQ380979
T342	*Tcn*	SN	Ponta da Praia do Garfo	GQ380971
T346	*Tcn*	SN	Ponta Pataca	GQ380967
T353	*Tcn*	SN	Ponta Coruja	GQ380992
T355	*Tcn*	SN	Chã de Norte	GQ381003
T356	*Tcn*	SN	Chã de Norte	GQ381004
T366	*Tcn*	SN	Mombaixa	GQ380993
T367	*Tcn*	SN	Mombaixa	GQ380990
T301	*Td*	SN	Carriçal	GQ380949
T302	*Td*	SN	Carriçal	GQ380950
T303	*Td*	SN	Carriçal-Juncalinho road	GQ380951
T304	*Td*	SN	Carriçal-Juncalinho road	GQ380952
T348	*Td*	SN	Juncalinho	GQ380953
T349	*Td*	SN	Juncalinho	GQ380954
T351	*Td*	SN	Ponta Larga	GQ380955
T358	*Td*	SN	Aguada de Falcão	GQ380956
T359	*Td*	SN	Aguada de Falcão	GQ380957
T360	*Td*	SN	Aguada de Falcão	GQ380958
T361	*Td*	SN	Monte Vermelho	GQ380959
T362	*Td*	SN	Monte Vermelho	GQ380963
T363	*Td*	SN	Ponta Mota	GQ380960
T364	*Td*	SN	Ponta Mota	GQ380961
T365	*Td*	SN	Ponta Mota	GQ380962
T370	*Td*	ST	S. Lourenço dos Órgãos	GQ380825
T372	*Td* *	ST	Cidade Velha	GQ380841
T373	*Td*	ST	Cidade Velha	GQ380827
T374	*Td*	ST	Cidade Velha	GQ380831
T375	*Td*	ST	Cidade Velha	GQ380826
T376	*Td*	ST	Achada Pedra	GQ380845
T378	*Td*	ST	Ribeirão Chiqueiro	GQ380863
T379	*Td*	ST	Ribeirão Chiqueiro	GQ380864
T380	*Td* *	ST	Ribeirão Chiqueiro	GQ380833
T381	*Td* *	ST	Ribeirão Chiqueiro	GQ380832
T383	*Td* *	ST	Ribeirão Chiqueiro	GQ380836
T384	*Td* *	ST	S. Nicolau Tolentino	GQ380886
T389	*Td*	ST	Achada Fazenda	GQ380837
T390	*Td*	ST	Achada Fazenda	GQ380834
T391	*Td*	ST	Achada Fazenda	GQ380829
T392	*Td*	ST	Porto Gouveia	GQ380843
T394	*Td*	ST	Porto Gouveia	GQ380835
T395	*Td*	ST	Rb.ra Grande de Santiago	GQ380822
T397	*Td*	ST	Rb.ra Grande de Santiago	GQ380820
T398	*Td*	ST	Ponta Bombardeiro	GQ380842
T399	*Td*	ST	Ponta Bombardeiro	GQ380823
T400	*Td*	ST	Ponta Bombardeiro	GQ380824
T402	*Td*	ST	S. Martinho Pequeno	GQ380859
T403	*Td*	ST	João Varela	GQ380852
T404	*Td*	ST	João Varela	GQ380849
T405	*Td*	ST	João Varela	GQ380821
T406	*Td*	ST	João Varela	GQ380848
T407	*Td*	ST	João Varela	GQ380851
T409	*Td*	ST	S. Martinho Pequeno	GQ380844
T411	*Td*	ST	S. Martinho Pequeno	GQ380862
T412	*Td*	ST	Praia Baixo	GQ380850
T413	*Td*	ST	Praia Baixo	GQ380885
T414	*Td*	ST	Praia Baixo	GQ380876
T415	*Td*	ST	Praia Baixo	GQ380853
T416	*Td*	ST	Praia Baixo	GQ380857
T417	*Td*	ST	Praia Baixo	GQ380858
T418	*Td*	ST	Praia Baixo	GQ380878
T420	*Td*	ST	Nossa Sra da Luz	GQ380877
T421	*Td*	ST	Nossa Sra da Luz	GQ380856
T422	*Td*	ST	Cancelo	GQ380934
T423	*Td*	ST	Cancelo	GQ380901
T424	*Td*	ST	Cancelo	GQ380893
T425	*Td*	ST	Cancelo	GQ380900
T426	*Td*	ST	Cancelo	GQ380899
T428	*Td*	ST	Cancelo	GQ380894
T429	*Td*	ST	S. Lourenço dos Órgãos	GQ380860
T430	*Td*	ST	S. Lourenço dos Órgãos	GQ380879

Code	**Taxa**	**Island**	**Locality**	**GenBank codes** 12S/ cyt *b* 1st/ cyt *b* 2nd
T431	*Td*	ST	Calheta S. Miguel	GQ380910
T432	*Td*	ST	Calheta S. Miguel	GQ380942
T433	*Td*	ST	Calheta S. Miguel	GQ380919
T434	*Td*	ST	Calheta S. Miguel	GQ380938
T435	*Td* *	ST	S. Lourenço dos Órgãos	GQ380854
T436	*Td* *	ST	S. Filipe de Cima	GQ380855
T437	*Td*	ST	Ribeira da Barca	GQ380928
T438	*Td*	ST	Ribeira da Barca	GQ380911
T439	*Td*	ST	Ribeira da Barca	GQ380933
T440	*Td*	ST	Ribeira da Barca	GQ380927
T441	*Td* *	ST	Curral Grande	GQ380861
T443	*Td* *	ST	Curral Grande	GQ380840
T444	*Td*	ST	Pedra Barro	GQ380908
T445	*Td*	ST	Pedra Barro	GQ380920
T446	*Td*	ST	Calheta S. Miguel	GQ380902
T447	*Td*	ST	Calheta S. Miguel	GQ380935
T448	*Td*	ST	Ribeirão Galinha	GQ380880
T449	*Td*	ST	Achada Além	GQ380903
T451	*Td*	ST	Santa Ana	GQ380819
T452	*Td*	ST	Santa Ana	GQ380881
T453	*Td*	ST	Santa Ana	GQ380882
T454	*Td* *	ST	Santa Ana	GQ380883
T456	*Td*	ST	Santa Ana	GQ380818
T457	*Td*	ST	Santa Ana	GQ380884
T458	*Td*	ST	Santa Ana	GQ380847
T459	*Td*	ST	Santa Ana	GQ380838
T460	*Td*	ST	Santa Ana	GQ380839
T462	*Td*	ST	Praia	GQ380846
T464	*Td*	ST	Chão Bom	GQ380912
T465	*Td*	ST	Chão Bom	GQ380888
T468	*Td*	ST	S. Lourenço dos Órgãos	GQ380865
T469	*Td*	ST	Montanhinha	GQ380828
T470	*Td*	ST	Palha Carga	GQ380915
T471	*Td*	ST	S. Lourenço dos Órgãos	GQ380830
T472	*Td*	ST	S. Lourenço dos Órgãos	GQ380866
T473	*Td*	ST	S. Lourenço dos Órgãos	GQ380867
T474	*Td*	ST	Chão de Tanque	GQ380914
T475	*Td*	ST	Santa Catarina	GQ380917
T476	*Td*	ST	Santa Catarina	GQ380923
T477	*Td*	ST	Santa Catarina	GQ380925
T478	*Td*	ST	Santa Catarina	GQ380922
T479	*Td*	ST	Santa Catarina	GQ380918
T480	*Td*	ST	Santa Catarina	GQ380916
T482	*Td*	ST	Chão Bom	GQ380946
T483	*Td*	ST	Chão Bom	GQ380945
T484	*Td*	ST	Chão Bom	GQ380887
T486	*Td*	ST	Chão Bom	GQ380897
T487	*Td*	ST	Chão Bom	GQ380941
T488	*Td*	ST	Ponta do Lobrão	GQ380891
T489	*Td*	ST	Ponta do Lobrão	GQ380895
T490	*Td*	ST	Ponta do Lobrão	GQ380898
T491	*Td*	ST	Trás os Montes	GQ380921
T492	*Td*	ST	Trás os Montes	GQ380896
T493	*Td*	ST	Trás os Montes	GQ380889
T494	*Td*	ST	Trás os Montes	GQ380948
T495	*Td*	ST	Trás os Montes	GQ380913
T496	*Td*	ST	Trás os Montes	GQ380947
T497	*Td*	ST	Tarrafal	GQ380890
T499	*Td*	ST	Tarrafal	GQ380892
T500	*Td*	ST	Tarrafal	GQ380937
T501	*Td*	ST	Flamengos	GQ380904
T502	*Td*	ST	Flamengos	GQ380905
T503	*Td*	ST	Flamengos	GQ380907
T504	*Td*	ST	Flamengos	GQ380906
T505	*Td*	ST	Jalalo Ramos	GQ380940
T507	*Td*	ST	Serra Malagueta	GQ380943
T508	*Td*	ST	Serra Malagueta	GQ380909
T509	*Td*	ST	Serra Malagueta	GQ380936
T510	*Td*	ST	Serra Malagueta	GQ380924
T511	*Td*	ST	Serra Malagueta	GQ380939
T512	*Td*	ST	Porto Madeira	GQ380868
T513	*Td*	ST	Porto Madeira	GQ380869
T514	*Td*	ST	Barragem	GQ380870
T515	*Td*	ST	Barragem	GQ380871
T516	*Td*	ST	Barragem	GQ380872
T522	*Td*	ST	Praia Baixo	GQ380873
T523	*Td*	ST	Praia Baixo	GQ380874
T524	*Td*	ST	Praia Baixo	GQ380875
T526	*Td*	ST	Porto Rincão	GQ380929
T527	*Td*	ST	Porto Rincão	GQ380930
T528	*Td*	ST	Porto Rincão	GQ380931
T529	*Td*	ST	Entre Picos de Rede	GQ380932
T530	*Td*	ST	Entre Picos de Rede	GQ380926
T531	*Td*	ST	Entre Picos de Rede	GQ380944
T533	*Td*	F	Campanas de Baixo	GQ380784
T534	*Td*	F	Monte Calhau	GQ380785
T536	*Td*	F	Monte Calhau	GQ380786
T537	*Td*	F	Monte Calhau	GQ380787
T538	*Td*	F	Luzia Nunes	GQ380788
T539	*Td*	F	Luzia Nunes	GQ380789
T540	*Td*	F	Luzia Nunes	GQ380790
T577	*Td*	F	Campanas de Baixo	GQ380791
T578	*Td*	F	Campanas de Baixo	GQ380792
T579	*Td*	F	Campanas de Baixo	GQ380793
T581	*Td*	F	Velho Manuel	GQ380794
T583	*Td*	F	Lomba	GQ380795
T584	*Td*	F	Mosteiros	GQ380796
T585	*Td*	F	Mosteiros	GQ380797
T586	*Td*	F	Fonsaco	GQ380798
T587	*Td*	F	Fonsaco	GQ380799
T588	*Td*	F	Mosteiros	GQ380800
T589	*Td*	F	Mosteiros	GQ380801
T590	*Td*	F	Mosteiros	GQ380802
T591	*Td*	F	Santa Catarina do Fogo	GQ380803
T592	*Td*	F	Santa Catarina do Fogo	GQ380804
T593	*Td*	F	Santa Catarina do Fogo	GQ380805
T594	*Td*	F	S. Filipe	GQ380806
T595	*Td*	F	S. Filipe	GQ380807
T596	*Td*	F	S. Filipe	GQ380808
T597	*Td*	F	Monte Vermelho	GQ380809
T599	*Td*	F	S. Filipe	GQ380810
T600	*Td*	F	Cova Figueira	GQ380811
T601	*Td*	F	Cova Figueira	GQ380812
T602	*Td*	F	Cova Figueira	GQ380813

Code	**Taxa**	**Island**	**Locality**	**GenBank codes** 12S/ cyt *b* 1st/ cyt *b* 2nd
T603	*Td*	F	Monte Verde	GQ380814
T604	*Td*	F	Monte Verde	GQ380815
T605	*Td*	F	Monte Verde	GQ380816
T606	*Td*	F	S. Filipe	GQ380817
T661	*Trb*	BV	Caminho cruz João Santo	GQ381016
T662	*Trb*	BV	Caminho cruz João Santo	GQ381015
T663	*Trb*	BV	Caminho cruz João Santo	GQ381014
T664	*Trb*	BV	Monte Estância	GQ381013
T665	*Trb*	BV	Ervatão	GQ381012
T666	*Trb*	BV	Ervatão	GQ381011
T667	*Trb*	BV	Chão de Palhal	GQ381010
T668	*Trb*	BV	Salamansa	GQ381009
T669	*Trb*	BV	Salamansa	GQ381008
T671	*Trb*	BV	Lomba de Malva	GQ381007
T672	*Trb*	BV	Cabeça de Cachorro	GQ381006
T675	*Trb*	BV	Chã de Calheta	GQ381005
raTg2	*Tgg*	ra	Ponta de Casa	GQ381127
raTg3	*Tgg*	ra	Ponta de Casa	GQ381128
raTg4	*Tgg*	ra	Ponta de Casa	GQ381129
T371	*Trr*	ST	Cidade Velha	GQ380725
T377	*Trr*	ST	Ribeirão Chiqueiro	GQ380726
T382	*Trr*	ST	Ribeirão Chiqueiro	GQ380727
T385	*Trr*	ST	S. Nicolau Tolentino	GQ380732
T386	*Trr*	ST	S. Nicolau Tolentino	GQ380730
T387	*Trr*	ST	S. Nicolau Tolentino	GQ380731
T401	*Trr*	ST	S. Martinho Pequeno	GQ380742
T408	*Trr*	ST	S. Martinho Pequeno	GQ380741
T410	*Trr*	ST	S. Martinho Pequeno	GQ380733
T419	*Trr*	ST	Nossa Sra da Luz	GQ380739
T442	*Trr*	ST	Curral Grande	GQ380734
T455	*Trr*	ST	Santa Ana	GQ380728
T461	*Trr*	ST	Praiaaia	GQ380740
T463	*Trr*	ST	Praiaaia	GQ380729
T517	*Trr*	ST	Barnabé	GQ380735
T518	*Trr*	ST	Barnabé	GQ380736
T519	*Trr*	ST	Barnabé	GQ380737
T521	*Trr*	ST	Barnabé	GQ380738
T532	*Trp*	F	Lagariça	GQ380781
T535	*Trp*	F	Monte Calhau	GQ380706/ GQ380782/GQ380719
T598	*Trp*	F	Monte Vermelho	GQ380783
T541	*Trp*	B	Favatal	GQ380767
T544	*Trp*	B	Lima Doce	GQ380768
T545	*Trp*	B	EsPraiaadinha	GQ380769
T548	*Trp*	B	Fajã de Água	GQ380770
T549	*Trp*	B	Cova Rodela	GQ380771
T550	*Trp*	B	Porto de Ferreiros	GQ380772
T556	*Trp*	B	Palhal	GQ380773
T561	*Trp*	B	Chão de Sousa	GQ380774
T565	*Trp*	B	Chão de Aguada	GQ380775
T569	*Trp*	B	Baleia	GQ380776
T570	*Trp*	B	Cachaço	GQ380777
T571	*Trp*	B	Morro Largo	GQ380778
T575	*Trp*	B	Campo da Porca	GQ380779
T576	*Trp*	B	Chão Queimado	GQ380780
T607	*Trm*	M	Calheta de Cima	GQ380743
T610	*Trm*	M	Monte Batalha	GQ380744
T613	*Trm*	M	Rocha Albarda	GQ380746
T616	*Trm*	M	Volta Grande	GQ380745
T619	*Trm*	M	Morro	GQ380747
T621	*Trm*	M	Terras Salgadas	GQ380748
T625	*Trm*	M	Casas Velhas	GQ380749
T628	*Trm*	M	Fig. da Horta - Pilão Cão	GQ380750
T631	*Trm*	M	Ribeira D. João	GQ380751
T634	*Trm*	M	Cascabulho	GQ380752
T637	*Trm*	M	Laje Branca	GQ380753
T640	*Trm*	M	Monte Branco	GQ380754
T643	*Trm*	M	Pilão Cão de Cima	GQ380755
T645	*Trm*	M	Pêro Vaz	GQ380756
T647	*Trm*	M	Pêro Vaz	GQ380757
T650	*Trm*	M	Ponta Rabil	GQ380758
T651	*Trm*	M	Monte Batalha	GQ380759
T653	*Trm*	M	Monte Penoso	GQ380760
T657	*Trm*	M	Monte Vermelho	GQ380761
cv90	*Trm*	M	Morrinho	GQ380707/ GQ380762/GQ380720
cv91	*Trm*	M	Pêro Vaz	GQ380708/ GQ380763/GQ380721
cv92	*Trm*	M	Pilão Cão de Cima	GQ380711/ GQ380766/GQ380724
cv93	*Trm*	M	Ribeira D. João	GQ380710/ GQ380765/GQ380723
cv94	*Trm*	M	Ponta Pedrenau	GQ380709/ GQ380764/GQ380722

SV, S. Vicente; SL, Sta. Luzia; ra, Raso; br, Branco; SA, Santo Antão; SN, S. Nicolau; ST, Santiago; F, Fogo; B, Brava; M, Maio; BV, Boavista. Individuals marked with * have ambiguous identification.

Tcs, T. caboverdiana substituta; Tcr, T. caboverdiana raziana; Tcc, T. caboverdiana caboverdiana; Tcn, T. caboverdiana nicolauensis; Td, T. darwini; Trb, T. 'rudis' boavistensis; Tgg, T. gigas gigas; Trr, T. rudis rudis; Trp, T. rudis protogigas; Trm, T. rudis maioensis.

Appendix III.3 Genetic differentiation between *Tarentola* populations belonging to the same network: *Snn* values.

Populations		***Snn***
A4 North	A4 South	1.00000**
D2	D4	1.00000**
D2	D3	1.00000**
D2	D1	1.00000**
D4	D5	0.86087**
D4	D3	1.00000**
D4	D1	1.00000**
D3	D1	1.00000**
B3	B1	0.96716*
B3	B2	0.97386**
B1	B2	0.97368**

*$P < 0.05$, **$P < 0.01$

Appendix III.4 Variables used in the correlation analyses between genetic variability of Cape Verdean *Tarentola* and geographical and ecological features of the Cape Verde Islands.

		Genetic variability		Size (Km^2/ Km)		Elevation (m)			Location (decimal degrees)		Habitat diversity (No. habitats)
Island	***n***	***Hd***	**No. ESUs**	**Area**	**Perimeter**	**Max.**	**Mean**	**Median**	**Longitude**	**Latitude**	**Total**
M	24	0.540	1	273.55	109.15	392	46	159	-23.16140	15.21709	7
ST	159	0.903	3	1003.96	326.65	1339	275	586	-23.62470	15.08353	13
sm	2	0.000	1	0.07	1.44	24	4	8	-23.50750	14.90760	1
F	42	0.782	2	471.42	121.56	2781	865	1339	-24.38440	14.92816	12
B	19	0.532	1	62.87	71.16	959	382	459	-24.70560	14.85122	9
ro	4	0.000	1	3.03	35.91	97	3	34	-24.66100	14.96909	2
BV	17	0.654	1	630.95	134.93	360	57	164	-22.81440	16.09726	7
S	0	0.000	0	220.88	124.01	381	31	137	-22.93150	16.73702	7
SN	63	0.886	2	345.82	209.42	1282	269	563	-24.25690	16.59846	13
SV	52	0.632	1	225.40	113.75	711	119	318	-24.96790	16.84547	12
SL	15	0.629	1	34.72	34.90	351	21	144	-24.74520	16.76634	6
ra	12	0.864	2	5.79	9.60	135	22	55	-24.58770	16.61791	3
br	3	0.000	2	2.77	10.85	322	31	137	-24.67020	16.65844	2
SA	43	0.939	1	785.11	203.55	1971	654	969	-25.16990	17.05633	12

SV, S. Vicente; SL, Sta. Luzia; ra, Raso; br, Branco; SA, Santo Antão; SN, S. Nicolau; B, Brava; ro, Rombos; M, Maio; F, Fogo; ST, Santiago; sm, Sta. Maria; S, Sal; BV, Boavista.

n, number of samples; *Hd*, haplotype diversity; ESUs, evolutionarily significant units; location (latitude and longitude of the centroid of the island); number of habitats for each island adapted from Diniz & Matos (1986, 1987, 1988 a, b, 1993, 1994, 1999 a, b, c).

References

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ARTICLE IV

An integrative taxonomic revision of the *Tarentola* geckos (Squamata, Phyllodactylidae) of the Cape Verde Islands

R. Vasconcelos[1,2,3], A. Perera[1], P. Geniez[3], D.J. Harris[1,2] & S. Carranza[4]

[1] CIBIO-UP, Centro de Investigação em Biodiversidade e Recursos Genéticos da Universidade do Porto,
Campus Agrário de Vairão, R. Padre Armando Quintas, 4485-661 Vairão, Portugal;

[2] Departamento de Zoologia e Antropologia, Faculdade de Ciências da Universidade do Porto,
R. Campo Alegre, s/n, 4169-007 Porto, Portugal. E-mail: raquel.vasconcelos@mail.icav.up.pt

[3] Institute of Evolutionary Biology (CSIC-UPF) - Passeig Marítim de la Barceloneta, 37-49,
E-08003 Barcelona, España. E-mail: salvador.carranza@ibe.upf-csic.es

[4] 4EPHE - UMR 5175, Centre d'Ecologie Fonctionnelle et Evolutive,
1919 route de Mende, 34293 Montpellier cedex 05, France. E-mail: philippe.geniez@cefe.cnrs.fr

ABSTRACT

Recent phylogeographic analyses using mitochondrial DNA (mtDNA) sequences indicate that the *Tarentola* from the Cape Verde archipelago originated from a propagule that dispersed from the Canary Islands approximately 7.7 Mya and that underwent a fast evolutionary radiation. Molecular analyses carried out to date clearly show some incongruences with the current taxonomy of *Tarentola* from the Cape Verde Islands, with some species being paraphyletic, polyphyletic and several independently evolving lineages needing formal taxonomic recognition. The aim of this study is to clarify the systematics of this group to unravel its taxonomy by applying an integrative approach based on information from three independent sources: mtDNA, three nuclear genes and morphology. As a result of this taxonomic revision, two new species for the islands of S. Nicolau and Fogo are described and eight subspecies are upgraded to species level. Moreover, an identification key for the *Tarentola* from the Cape Verde archipelago is presented. This study reconciles taxonomy and phylogeny in this group and provides the basic framework for the future management and conservation of this unique reptile radiation.

KEY WORDS

Cape Verdean, geckonids, morphology, *n*DNA, species description.

INTRODUCTION

Delineating species boundaries is crucial because it is the first step toward discussing broader questions on biogeography, ecology, conservation or evolution. The communication gap between different disciplines currently related to the species recognition is an important but often overlooked problem. According to de Queiroz (2007) one of the main problems is that species delimitation has long been confused with that of species conceptualisation, leading to a half a century of controversy concerning both the definition of the species categories and methods for inferring the boundaries and the number of species. Recent intellectual progress in the field has been made to identify a common element among all the different species concepts in order to propose a single, more general, concept of species known as the General Lineage Species Concept (de Queiroz 1998). This unified species concept considers species as separately evolving metapopulation lineages and treats this property as the single requisite for delimiting species. Other properties, such as phenetic distinguishability, reciprocal monophyly, pre- and postzygotic reproductive isolation, are not part of the species concept but serve as important lines of evidence relevant to assess the separation of lineages and therefore to species delimitation (de Queiroz 2007). The divorce between conceptualisation and delimitation of species and the proposal of a unified species concept has shifted emphasis away from the controversy of species criteria, concentrating efforts in the development of new approaches for species delimitation as for instance ‘integrative taxonomy’ (Dayrat 2005; Padial *et al.* 2010; Cardoso *et al.* 2009). The goal of integrative taxonomy is to delimit the units of biotic diversity from multiple and complementary disciplines (e.g. phylogeography, population genetics, comparative morphology or ecology). Hence, molecular markers, population genetic tests, morphological features and ecological characteristics should be used as different complementary approaches to achieve reliable identifications of species. All sets of characters have the same weight during the process of recognising and diagnosing species and the goal is to use as many as possible. Species delineation is therefore regarded as an objective scientific process that results in a taxonomic hypothesis. In this way, the level of confidence in the taxonomic hypothesis supported by several independent character sets is much higher than for species supported by only one (Schlick-Steiner *et al.* 2010). Such integrative view is especially useful in the case of taxonomic groups that are morphologically conservative such as the geckos (Jesus *et al.* 2002), where cryptic species have been likely overlooked (Perera & Harris 2010).

Tarentola is a genus of the family Phyllodactylidae with around 20 species commonly called wall geckos. All of them present robust bodies, non-divided subdigital lamellae and well-developed claws on the third and fourth digits (Arnold & Ovenden 2002) and, with the only exception of *Tarentola chazaliae* (Mocquard, 1895), have a conservative morphology (Joger 1984a; Carranza *et al.* 2002; Harris *et al.* 2004). These climbing geckos are mostly active by night and typically inhabit dry, open and rocky areas but also artificial habitats (Arnold & Ovenden 2002). This genus is distributed across southern Europe, Mediterranean islands, North Africa and on many islands of the Macaronesian region, namely Madeira (including Selvagens), Canary and Cape Verde Islands (Arnold & Ovenden 2002; Sindaco 2008). On the other side of the Atlantic Ocean, three species are accepted: *T. americana* (Gray, 1831), from Cuba and the Bahamas; the recently described *T. crombiei* Díaz & Hedges, 2008 endemic to Cuba; and the probably extinct *T. albertschwartzi* Sprackland & Swinney, 1998, known from a single specimen allegedly from Jamaica.

Tarentola members were divided into five different subgenera based on anatomical, biochemical, immunological and phylogenetical data (Joger 1984a; Carranza *et al.* 2000). These are: *Sahelogecko* and *Saharogecko* in North Africa, *Tarentola sensu stricto* in North Africa, southern Europe and the eastern Canary Islands, *Neotarentola* which includes *T. americana*, *T. crombiei* and *T. albertschwartzi* (Weiss & Hedges, 2007), and *Makariogecko* in the Macaronesian Islands (Carranza *et al.* 2000; Weiss & Hedges 2007). The subgenus *Makariogecko* presents a synapomorphy: the supraciliar scales are larger than the remaining interorbital scales and they are divided (Joger 1984a). Nevertheless, recent molecular phylogenies including *Tarentola chazaliae* (previously *Geckonia chazaliae*) do not seem to support the monophyly of this subgenus (Carranza *et al.* 2002). Within this subgenus, the *Tarentola* from Cape Verde are especially interesting as they originated from a single colonisation event by a propagule that rafted southwards from the western Canary Islands (Carranza *et al.* 2000) around 7.7 million years (My) ago (Vasconcelos *et al.* 2010).

The Cape Verde Islands are a volcanic archipelago located approximately 500 km off the West African coast with 10 main islands, plus several islets, which are topologically divided into north-western, eastern and southern islands groups (Fig. IV.1). The radiation of the geckos after the single colonisation event gave origin to four currently accepted endemic species with several subspecies, some of them exclusive to one of these island groups: *T. darwini* Joger, 1984b, *T. caboverdiana* Schleich, 1984, *T. rudis* Boulenger, 1906 and *T. gigas* (Bocage, 1875). However, the most exhaustive recent revision regarding the genetic variability of *Tarentola* from the Cape Verde Islands using mitochondrial markers recovered 15 evolutionary significant units (ESUs) arranged into four main groups (Fig. IV.2; Vasconcelos *et al.* 2010) not completely congruent with the current taxonomy (Schleich 1987; Joger 1993). The first group included all *T. darwini* plus *T. rudis* from Boavista, although both the bootstrap and posterior probability (PP) values were low; the second one grouped *T. caboverdiana* from São Vicente, Santa Luzia, Raso, and Santo Antão; the third one was exclusively formed by *T. caboverdiana nicolauensis* from São Nicolau; finally, the fourth group included the remaining *T. rudis* populations. From all the accepted Cape Verdean *Tarentola*, only *T. gigas* and *T. darwini* are monophyletic based on mitochondrial data (Fig. IV.2), with *T. rudis* and *T. caboverdiana* being poly- and paraphyletic, respectively (Vasconcelos *et al.* 2010). As a result, previous molecular phylogenetic studies have always stressed that a review of the systematics of the Cape Verdean *Tarentola* was needed (Carranza *et al.* 2000, 2002; Vasconcelos *et al.* 2010). In the case of *T. rudis*, the mitochondrial lineages of each subspecies (*T. r. boavistensis*, *T. r. rudis*, *T. r. protogigas* and *T. r. maioensis*) seem to be quite divergent among them and from all other forms. Moreover, *T. r. boavistensis* mitochondrial lineage is closer to *T. darwini* clade than to *T. rudis* clade and *T. r. rudis* forms a clade with *T. gigas*, turning *T. rudis* into a polyphyletic species. Also *T. 'caboverdiana' nicolauensis* is more closely related to *T. gigas* and *T. rudis* than to the other *T. caboverdiana* subspecies (see Vasconcelos *et al.* 2010). As effective conservation measures depend largely on a good knowledge of the taxonomy of the species (Mace 2004), the present taxonomic revision is clearly needed not only to clarify the systematics of this group but also as a basic framework for the future conservation management of the *Tarentola* geckos from Cape Verde.

In order to describe new taxa, intraspecific variability should be studied and a taxonomical revision should be made, with all previous synonyms and chresonyms identified (Dayrat 2005). Genetic assessment regarding the *Tarentola* geckos of the Cape Verde Islands was accomplished in previous works (see Carranza *et al.* 2000; Vasconcelos *et al.* 2010), although using only mitochondrial markers. Therefore, in the present work, information from mitochondrial DNA (mtDNA), three nuclear markers and morphology is used following an 'integrative taxonomy' approach to revise the systematics of the genus *Tarentola* from the Cape Verde archipelago and to fully reconcile taxonomy with phylogeny. The results of this work are very relevant for the conservation of this unique island radiation.

MATERIALS AND METHODS

Origin of tissue samples and specimens

A total of 127 live specimens of Cape Verdean *Tarentola* were included in the genetic analyses of the nuclear data and 92 in the multivariate morphological analysis. All specimens were identified in the field using diagnostic characters published by Joger (1984b, 1993) and Schleich (1987) and a piece of tail was removed and stored in 96% ethanol. Before the animals were released, digital photographs (from dorsal, ventral and lateral parts) were taken to qualitatively analyse the colour pattern characteristics that may disappear in preserved specimens and

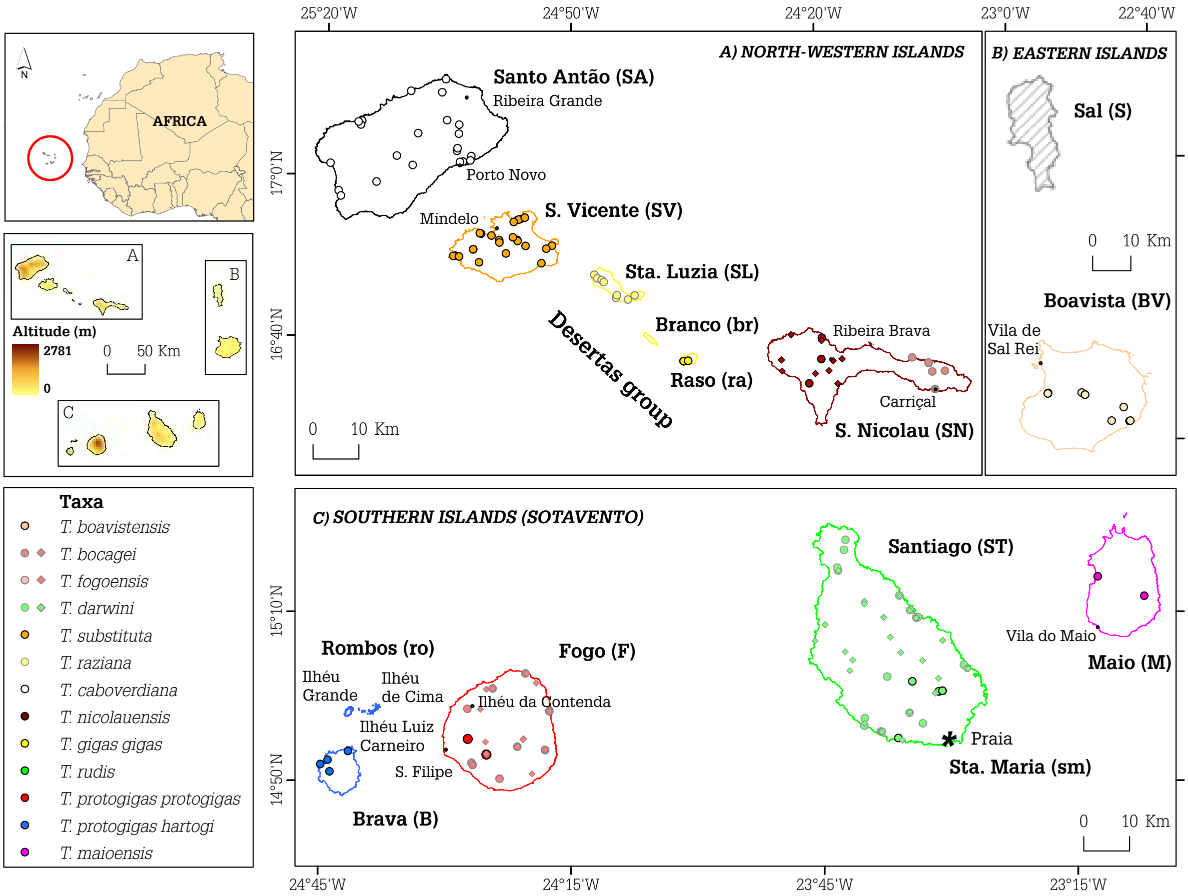

Figure IV.1 Map of the Cape Verde Islands showing the geographic location (latitudes and longitudes) and altitudes of the islands and the origins of the *Tarentola* samples included in the genetic (circles) and morphological (diamonds) analyses (Geographic Coordinate System, Datum WGS 84). Island and taxa colours match the colours used on the network analyses. No specimens were found on Sal.

to perform pholidotic counts *a posteriori*. Some of these photos have been deposited in MorphoBank (http://www.morphobank.org/; see Appendix IV.1).

Apart from to the morphological analysis of live specimens, a total of 115 Cape Verdean voucher specimens were also examined. Vouchers are deposited at the Natural History Museum, London (BMNH), at the Centre d'Ecologie Fonctionnelle et Evolutive, Montpellier, but previously housed at Laboratoire de Biogéographie et Ecologie des Vertebrés collection (BEV), Departamento de Biología de la Universidad de Las Palmas de Gran Canaria (DBULPGC), and at the Museum National d'Histoire Naturelle (MNHN) from Paris. Identification codes, localities and GenBank and MorphoBank accession numbers of the live and voucher specimens examined are listed in Appendix IV.1. In addition, specimen data from other authors used in the taxonomic revision are included in the 'Additional material and references' section under each taxon.

Genetic analyses

Total genomic DNA was extracted from small pieces of tail using standard methods. Three fragments of nuclear genes were analysed: phosducin (PDC), acetylcholinergic receptor M4 (ACM4) and melanocortin 1 receptor (MC1R). The sets of primers used were: PHOR1 and PHOF2, and *Tg-F* and *Tg-R* (Gamble *et al.* 2008) for the PDC and ACM4 fragments, respectively, and MC1R-F and MC1R-R (Pinho *et al.* 2010) for the MC1R fragment. For the amplification of these three fragments, an initial denaturation step of 95°C for 90s was used, followed by 35 cycles of 95ºC for 30 s, 50°C (annealing temperature) for 45 s, 72°C (extending temperature) for 90s and a final extension at 72°C for 7 min. Amplified nuclear DNA (nDNA) fragments were sequenced from both strands with the same primers used in the amplification process. Sequences were aligned manually using BIOEDIT v.7.0.4. (Hall 1999). The Bayesian algorithm implemented in the program PHASE 2.1.1 (Stephens *et al.* 2001) was used to reconstruct haplotypes from population genotyped data. Sequence pairs with probability lower than 0.7 were not included in posterior analyses.

Population analyses

The genealogical relationships between taxa were assessed with haplotype networks constructed using statistical parsimony (Templeton *et al.* 1992), implemented in the program TCS v.1.21 (Clement *et al.* 2000), with a connection limit of 95%. Haplotypes were then arranged in groups based on the 15 ESUs recovered in the mitochondrial study by Vasconcelos *et al.* (2010). Genetic differentiation between ESUs for the three nuclear genes was calculated using the nearest neighbour statistic, *Snn* (Hudson 2000), implemented in the program DnaSP v.5 (Rozas *et al.* 2003) and tested with 1000 permutations. Additionally, estimates of evolutionary divergence (*p*-dist) over 302 base pairs long of cytochrome *b* (cyt *b*) sequences among the 15 ESUs were calculated with Mega4 (Tamura *et al.* 2007). All cyt *b* sequences used (GenBank accession numbers Q380699-Q381129) were from Vasconcelos *et al.* (2010).

The IMa software (Hey & Nielsen 2007), which takes into account population divergence and gene flow in the same framework, was used to disentangle the relative effects of isolation and migration in shaping the patterns of variation among diverging cryptic species occurring on the same island and sharing nuclear haplotypes, as was the case of the two *Tarentola* from S. Nicolau. This software uses a Markov Chain Monte Carlo sampling of gene genealogies to estimate posterior probability (PP) distributions of rates of migration in either direction (m1 and m2) and time of divergence (*t*), among other parameters. The assumption made by IMa of no recombination was tested with DnaSP v.5 (Rozas *et al.* 2003) coalescent simulations. After two experimental runs to assess appropriate parameter settings and ensure proper mixing, IMa was run three times for the two-species data set for 50 million steps along the Markov Chain after 10 million steps of burn-in with 10 Metropolis-coupled chains with linear heating. The mixing properties of MCMC were checked by monitoring the values of the parameters and the trend-line plots of the parameters.

Morphological analyses

A multivariate analysis of the three populations previously described as *T. 'darwini'* from the islands of Fogo, S. Nicolau and Santiago (Fig. IV.2) was performed in order to assess if diversity existed and, if so, which level of morphological distinctiveness these populations presented. Several morphological characters from individuals (ind.) of other groups were also measured to disentangle complex relationships detected at the mitochondrial level, such as between *T. protogigas* from Fogo and Brava islands.

Since fixation and preservation in museums may deform bodies or some body parts making difficult the comparison with live specimens (Vervust *et al.* 2009), no vouchers were included in this analysis, and only live adult specimens that had been genetically confirmed using the cyt *b* mitochondrial marker were used. Sex was determined by the presence of enlarged spurs and more developed cloacal pouches in males (Barbadillo *et al.* 1999) and by their larger body size and robustness (Arnold & Oveden 2002). Details on the specimens examined are listed in Appendix IV.1. Morphological variation was assessed using both morphometric and meristic variables (14 linear body measurements and 7 pholidotic variables, respectively). Bilateral variables (Appendix IV.2 and IV.3) were taken from the same side of the animals whenever possible.

All 14 linear body measurements were recorded in the field by the same person (AP) using a ruler (for snout-vent length, SVL, with accuracy to the nearest 0.1 mm) and a digital calliper (all the remaining variables with accuracy to the nearest 0.01 mm) and were expressed in millimetres. Trunk length (TrL) was measured from the posterior edge of forelimb insertion to the anterior edge of hindlimb insertion and the tail width (TW) was recorded at its widest point. The total lengths of front (FLL) and hindlimbs (HLL) from the longest toe to the base of the limb were measured. Also the partial lengths of front (CFL) and hind (FFL) limbs were measured from the tip of the longest toe to the elbow or knee inflexion point, respectively. Head width (HW) was measured at its widest part, usually at the level of the temporal region and maximum head height (HH) was measured from occiput to jaws. Ear length (EL) and eye diameter (OD) were considered the longest dimension of ear and ocular orbit, respectively. Nostril-eye (NED) and snout-eye distances (SED) were measured from the anterior border of the ocular orbit to the posterior margin of the right nostril and snout, respectively. Ear-eye distance (EED) was measured from the anterior border of the ear to the posterior border of the ocular orbit.

Pholidotic (meristic) variables recorded included the number of supra- and infra-labial scales (SLS and ILS, respectively) counted until the limit of the mouth opening, and the number of non-divided enlarged side to side lamellae under the fourth hind toe (Lam). The number of transversal (Trow and Srow) and longitudinal (Tline and medS) tubercles and scales in the dorsum, respectively, were counted paramedially. The number of small scale rows (Srow) in the vertebral line was counted in the midbody, in a midline between the front and hindlimbs, between the upper and lower rows of tubercles. The number of small scales lines (medS) was estimated by the mean number of scales between tubercles on the intersection of the midbody line with the vertebral line.

Prior to the analysis, linear measurements were log transformed and checked for homoscedasticity (Lillieford test) and normality (Levene test). As linear body measurements are correlated to body size ($P<0.05$ in all cases), body-size corrected variables were estimated using an isometric correction (Somers 1986) to investigate the existence of possible differentiation patterns not related to body size. For this, an isometric vector was created where all linear measurements (log transformed) were projected, in order to obtain a multivariate representation of the isometric size of each individual (SIZE). After that, each variable was regressed on this isometric vector. The obtained residuals for each variable were used as size-corrected variables (Kaliontzopoulou *et al.* 2010). The multivariate representation of the isometric size (SIZE) was used as size estimator, while the remaining size-corrected variables were considered as shape estimators.MANOVAS were used to analyse the effect of sex, population, and their interaction (sex*population) on all linear (both sets, raw log-transformed and size-corrected) and pholidotic variables.

In order to assess the generalised morphological patterns within the different populations previously assigned as *T.* '*darwini*', a stepwise Canonical Discriminant Function Analysis (CDFA) was performed on all meristic and size-corrected linear variables. Due to the different degree of sexual dimorphism observed between populations in some of the variables, multivariate analysis was performed on males and females separately. This multivariate approach maximises differences between *a priori* defined groups from different island populations (mtDNA clades A2-A4) and classifies the individuals based on canonical discriminant functions (CDF). Only 30 of the 88 individuals from Santiago were randomly included in the analyses to avoid bias of results due to uneven samples sizes. The leave-one-out option was implemented to cross-validate the classification results. Since this procedure generates individual classifications using discriminate functions based on all observations except the given case, it provides a more accurate estimate of the classification values. Statistical analyses were performed using R (R Development Core Team 2010).

Museums Acronyms

Laboratoire de Biogéographie et Ecologie des Vertebrés collection (BEV), Montpellier; British Museum of Natural History (BNHM), London; Centro de Zoologia, Instituto de Investigação Científica Tropical (IICT), Lisbon; Departamento de Biología de la Universidad de Las Palmas de Gran Canaria (DB-ULPGC), Canary Islands; Museum der Universitat Helsingfors (MUH), Helsinki; Gabinete d'Ajuda, (GA), Lisbon; Hessisches Landesmuseum Darmstadt

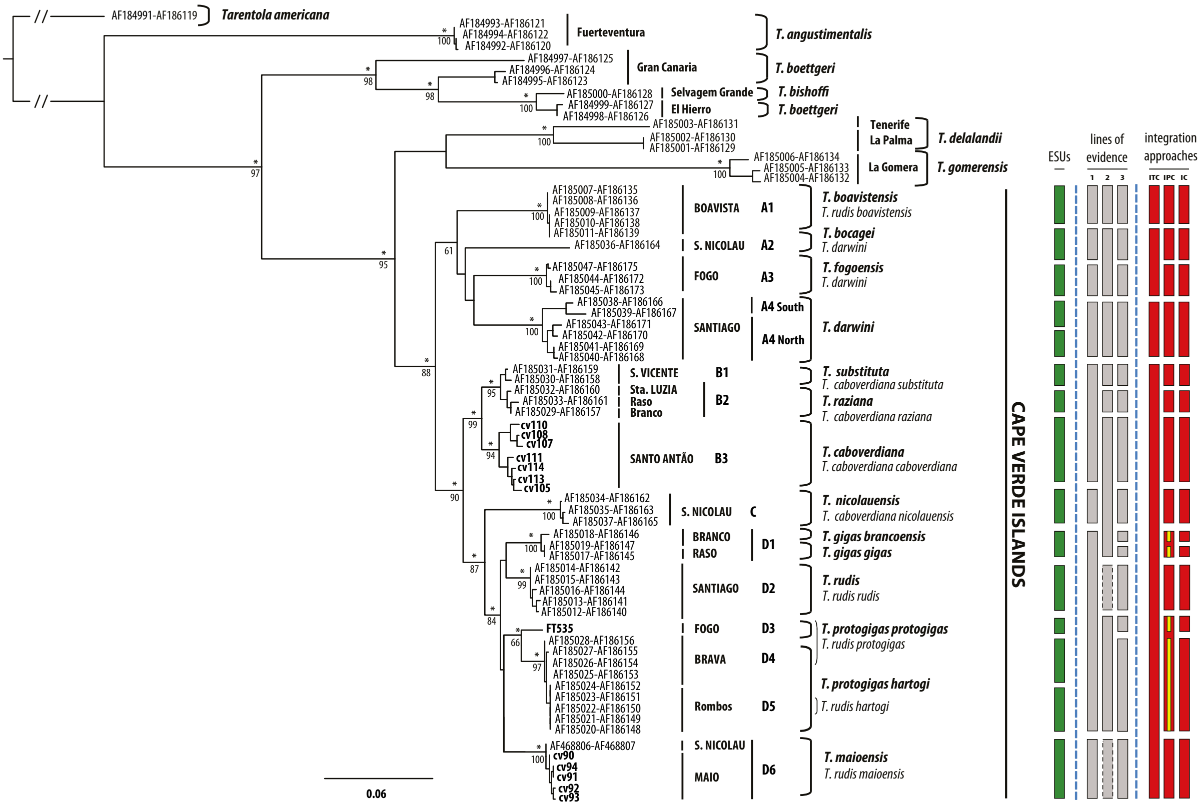

Figure IV.2 Phylogenetic relationships of endemic Cape Verde *Tarentola* taxa and their relatives from the Canary Islands modified from Vasconcelos *et al.* (2010) based on cytochrome *b* and 12S rRNA genes. Tree inferred using Maximum Likelihood (ML) and GTR+I+G model of sequence evolution (log likelihood = -6468.896) and rooted using *Tarentola americana*. Bootstrap support values above 60% for the ML analysis are shown below nodes. Posterior probability (PP) values higher than 95% for the Bayesian analysis are represented by an asterisk (*) and are shown above nodes. Names in bold follow the new taxonomic proposal and non-bold ones the taxonomy accepted in previous recent papers (Carranza *et al.* 2000; Jesus *et al.* 2002, Vasconcelos *et al.* 2010). For further details see Vasconcelos *et al.* (2010). Characters immediately to the right of island names correspond to the 15 evolutionarily significant units (ESUs) of A, B, C and D clades recognised in the present work and represented in split green bars. Lines of evidence (in grey): 1. Mitochondrial DNA (independent cyt *b* parsimony networks with a connection limit of 95%; see Appendix IV.4); 2. Nuclear DNA (absence of shared haplotypes in MC1R) and 3. Morphology (detection of any diagnostic morphological character). Integration approaches (in red) from the most conservative to the most inflationist: ITC stands for integration by total congruence (all lines of evidence should be congruent), IPC stands for integration by partial congruence, retained in the present study (at least two lines of evidence are necessary); IC stands for integration by cumulation (one line of evidence is sufficient). Species are represented in split red bars and subspecies in yellow.

(HLMD), Darmstadt; Hessisches Landesmuseum Wiesbaden (HLMW), Wiesbaden; Jon Boone collection (JB); Museu Civico 'G. Doria' di storia Naturale de Genova (MSNG), Genoa; Museu di Zoologia dell'Università degli Studi di Torino (MZUT), Turin; Muséum National d'Histoire Naturelle (MNHN), Paris; Institut Francais d'Afrique Noire (IFAN); Rijksmuseum van Natuurlijke Historie (RMNH), Leiden; Senckenberg-Museum Forschungsinstitut (SMF), Frankfurt; Universidade da Madeira (CCBG), Funchal; Zoologische Staatssammlung München (ZSM and ZSMH), Munich; Zoologisches Forschungsinstitut und Museum Alexander Koenig (ZFMK), Bonn; Zoologisches Museum Berlin (ZMB), Berlin; Zoologisches Museum der Universität Hamburg (ZMH), Hamburg.

Integrative approach

For consistency, the same approach used in the taxonomic revision of the endemic Cape Verdean skink genus *Chioninia* (Miralles *et al.* 2010) was followed in this study. The mitochondrial phylogenetic tree (Fig. IV.2) adapted from Vasconcelos *et al.* (2010) was used as a framework to investigate the taxonomy of the Cape Verdean *Taren-*

tola. Three lines of evidence have been defined on the basis of the alleged independence of their respective data sets (mtDNA, nDNA and morphology) to decide the taxonomic status of each ESU (see Fig. IV.2). Each of these lines represent equivalent, independent and combinable indicators able to detect splits between different species: (i) mtDNA – presence of independent cyt *b* parsimony networks with a connection limit of 95% (see Hart & Sunday 2007). The results of the cyt *b* networks analyses are from Vasconcelos *et al.* (2010) and are presented in Appendix IV.4; (ii) nDNA – absence of shared haplotypes in the MC1R nuclear gene (see Monaghan *et al.* 2009). The other two genes (PDC and ACM4) were not used as lines of evidence because both presented a very low level of genetic variability and a clear pattern of incomplete lineage sorting (see below); and (iii) morphology – detection of at least one fixed diagnostic character state (e.g. presence or absence for qualitative characters and non-overlapping values for meristic or allometric characters) that might be strong evidence of reduced or absence of gene flow (Wiens & Servedio 2000).

Different possible integration approaches are presented in Fig. IV.2, ranging from the most conservative to the most inflationist. The integration by total congruence (ITC) was achieved by retaining only the candidate species that are supported by all the three lines of evidence, whereas the integration by cumulation (IC) was calculated considering that one line of evidence was sufficient for splitting taxa. However, both methods have tendency to under- and overestimate the number of species, respectively (see Padial *et al.* 2010). Hence, a third approach was defined, the integration by partial congruence (IPC), which is intermediate between the two previous ones, as it retains only candidate species that are supported by the majority of independent lines of evidence. Also as in Miralles *et al.* (2010), splits supported by only one of these three lines of evidence within infraspecific allopatric ESUs have been considered as different subspecies.

RESULTS

Molecular data

The PDC and ACM4 networks recovered similar genealogies, with a similar number of haplotypes (13 and 14, respectively; Fig. IV.3) and a different topology to the one recovered with the MC1R fragment. PDC and ACM4 network analyses recovered the central and most common haplotype being the ancestral one, shared by many different taxa and surrounded by several singletons for most of the taxa groups. The only three exceptions were found in the PDC gene, which presented three non-ancestral haplotypes shared by geckos from S. Vicente and Santo Antão, specimens of lineage D3 and D4 from Fogo and Brava, respectively, and another one by some specimens from lineages A2 and C from S. Nicolau (see Fig. IV.3). On the other hand, the MC1R network recovered a higher number of haplotypes, 36 (including 23 for the same individuals sequenced for the other genes), and an increased level of substructuring among taxa, especially for the endemic *Tarentola* from Boavista and *T. darwini* from Santiago (lineages A1 and A4 in Fig. IV.2, respectively; see Fig. IV.3) and for each of the three *Tarentola* from clade B that do not share haplotypes. As expected from the results of the other two nuclear markers, MC1R also presents some sharing of ancestral haplotypes between specimens from S. Nicolau and Fogo (lineage A2 and A3 in Fig. IV.2, respectively) and also between most of the specimens analysed from the two species from S. Nicolau (lineages A2 and C in Fig. IV.2,) and some *T. caboverdiana* specimens from Santo Antão, *T. gigas* specimens from Raso and *T. protogigas* specimens from Brava and Fogo (lineages B3, D1, D3 and D4 in Fig. IV.2, respectively; see Fig. IV.3). Moreover, some recent haplotypes were shared by all specimens of *T. rudis* from Santiago and the *Tarentola* from Maio and by *T. protogigas* specimens from Fogo and Brava, respectively.

Three independent runs using IMa software converged on approximate marginal posterior probability distributions. Reliable estimates of m1, m2 and *t* between the two *Tarentola* taxa occurring on S. Nicolau were obtained to study the introgression versus ancestral polymorphism hypotheses. The migration rate curves, presented a clear peak although their tails did not reach zero, suggesting a high probability of no gene flow in either direction between these two populations and of *t* differing from zero (see Appendix IV.5). This *t*-value suggests that these two ESUs have indeed diverged.

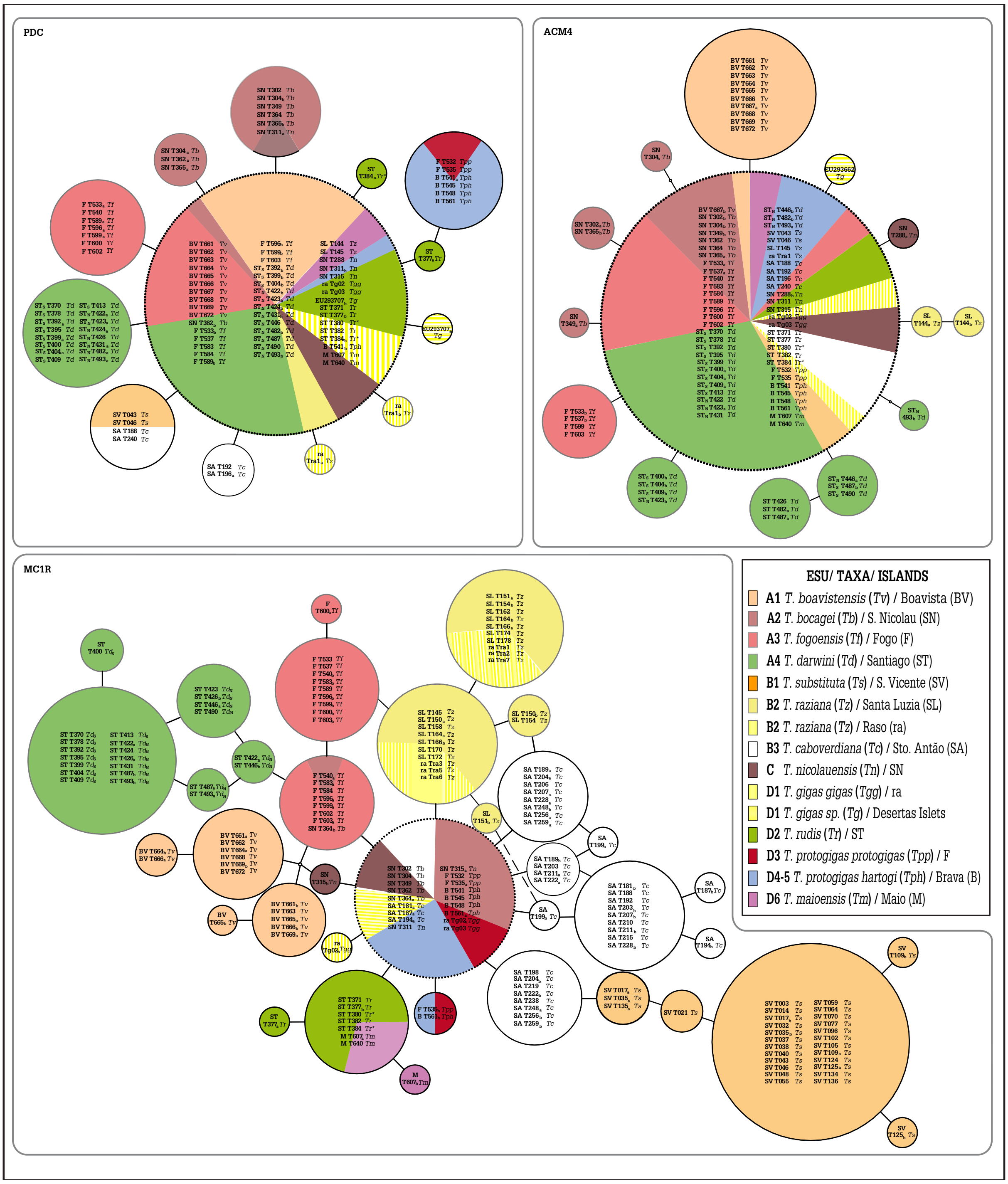

Figure IV.3 Parsimony networks corresponding to the PDC, ACM4 and MC1R nDNA sequence variation in *Tarentola* from the Cape Verde Islands. Lines represent a mutational step, circles haplotypes and dots missing haplotypes. The circle area is proportional to the number of haplotypes and colours to the number of individuals. The dotted circles represent the most probable ancestral haplotype. Samples from the same island are equally coloured but with different tonalities for different taxa. For correspondences of sample and location codes see Appendix IV.1.

Morphological data

In general, males and females were different in size (MANOVA $P<0.001$) but not in shape or pholidosis (in both cases MANOVA $P>0.05$), while the three populations (A2, A3 and A4) compared were different in all the datasets analysed (size, shape and pholidosis, in almost all cases MANOVA $P<0.001$; see Table IV.1). Populations had similar degree of sexual dimorphism (interaction sex*population) in pholidosis and shape (MANOVAs $P>0.005$ in both cases), but not in size (MANOVA $P<0.01$; see Table IV.1).

Regarding the linear measurements, the ANOVA analysis using raw log-transformed variables showed a clear sexual dimorphism in all the variables, except in OD (Table IV.1). However, such differences mostly disappeared when body size-corrected variables were compared, with the exception of TW, FFL and OD (Table IV.1). Regarding the differences between the three populations compared, all raw log-transformed variables were significantly different, even after correcting them for body size (Table IV.1). The interaction between sex*population was significant for most of the characters using log-transformed but not size-corrected variables. So, all raw log variables with the exception of FLL, CFL and EL were significant, but almost (with the exception of OD) all differences disappeared when considering size corrected variables (Table IV.1).

Regarding the meristic variables, males and females differed in the number of dorsal transversal rows of tubercles (Trow; Table IV.1, Appendix IV.2). All meristic variables, with the exception of Trow and Srow, were statistically different between populations (Table IV.1). However, all scale countings, with the exception of ILS and Srow, did not differ when interaction sex*population was considered (Table IV.1).

The stepwise Canonical Discriminant Function Analysis (CDFA) based on SIZE, shape and pholidosis showed a good discrimination among the three populations analysed. The first canonical discriminant function (CDF1) explained 66% and 76% of the variation in males and females, respectively (Table IV.2). The most contributing variables were TW and HLL in males and TW, OD and EL in females (Table IV.2). Regarding CDF2 (34% and 24% of the male and female variation, respectively), OD and SIZE in males and TW, SLS and OD in females were the most important variables (Table IV.2). The graphical representation of the factor scores across the two CDF axes showed a good separation of the three populations (Fig. IV.4). These results are confirmed by the classification scores obtained, with 92.0% males and 90.5% females correctly assigned to their populations (Table IV.3). In males, the population from S. Nicolau was the best discriminated (95.0% of the individuals correctly classified), while the species from Fogo (Table IV.3) presented the lowest classification score, although the values were still high (87.5%). Regarding females, the population from S. Nicolau had the highest score (100%), while *T. darwini* from Santiago had the lowest (80.0%, Table IV.3).

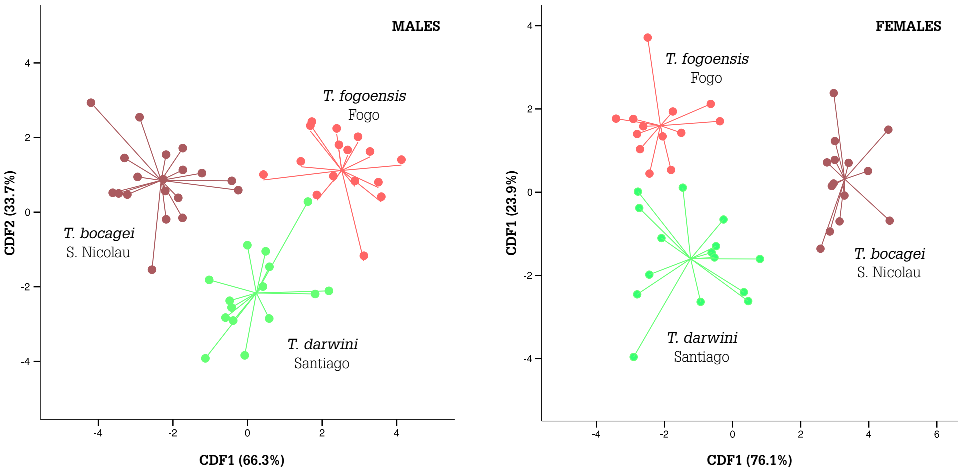

Figure IV.4 Discriminant analyses for males and females of the '*darwini*' clade. The total contribution of each of the two Canonical Discriminant Functions (CDF1 and CDF2) to explain the total morphological variation is also given. See material and methods for details.

Table IV.1 Summary of the ANOVA/MANOVA results regarding the effect of sex, population and their interaction (sex*population) on the morphological variables using two different sets: raw variables (after log-transformation), and size-corrected variables (using an isometric approach; SIZE). For each variable, F value and level of significance are provided (n.s., not significant, $P>0.05$; *, $0.01<P<0.05$; ** $P<0.01$). See material and methods for more details.

Variable codes	**Raw variables**			**Size-corrected variables**		
	sex	population	sex* population	sex	population	sex* population
SIZE				16.06 **	8.49 **	5.78 **
SVL	12.14 **	2.56 n.s.	5.68 **	0.00 n.s.	32.54 **	0.41 n.s.
TrL	5.73 *	9.40 **	4.74 **	1.11 n.s.	16.83 **	0.23 n.s.
TW	25.73 **	10.76 **	3.65 *	18.34 **	58.31 **	0.16 n.s.
FLL	15.57 **	19.94 **	2.37 n.s.	0.27 n.s.	11.25 **	2.70 n.s.
CFL	5.91 *	11.37 **	2.84 n.s.	1.86 n.s.	7.06 **	1.36 n.s.
HLL	12.77 **	31.09 **	5.39 **	0.15 n.s.	22.43 **	1.15 n.s.
FFL	10.77 **	22.22 **	6.19 **	0.52 n.s.	15.24 **	1.87 n.s.
HW	12.76 **	2.30 n.s.	4.84 **	0.61 n.s.	10.92 **	0.21 n.s.
HH	15.77 **	0.95 n.s.	6.11 **	3.16 n.s.	11.02 **	1.32 n.s.
OD	1.50 n.s.	23.05 **	5.21 *	5.39 *	39.58 **	4.11 *
EL	9.02 **	20.64 **	1.80 n.s.	1.60 n.s.	30.08 **	1.95 n.s.
NED	9.34 **	14.16 **	5.12 **	0.27 n.s.	5.28 *	1.26 n.s.
SED	9.20 **	18.32 **	4.25 *	0.24 n.s.	14.48 **	0.18 n.s.
EED	10.36 **	3.40 *	4.27 *	0.05 n.s.	5.80 **	0.07 n.s.
SLS	0.45 n.s.	11.66 **	1.58 n.s.			
ILS	1.75 n.s.	6.06 **	5.22 *			
Lam	0.81 n.s.	8.84 **	0.54 n.s.			
Trow	4.26 *	2.78 n.s.	0.07 n.s.			
Tline	1.92 n.s.	12.13 **	0.38 n.s.			
Srow	0.05 n.s.	2.96 n.s.	3.33 *			
medS	0.28 n.s.	14.99 **	0.05 n.s.			

Table IV.2 Summary of the stepwise Canonical Discriminant Function Analysis (CDFA) for size/shape dataset (obtained after using isometric approach) and pholidosis. For each analysis, the factor structure of the first two canonical discriminant functions, eigenvalues, and total explained and cumulative contribution (%) of each CDF to the total variation are also given. Analyses were done separately for males and females. Most contributing values (>0.35%) are indicated in bold. Scores in grey indicate the variables that were not selected by the stepwise CDFA. See text for more details regarding the meaning of the abbreviations of the variables.

	Males		**Females**	
Variables	CDF1	CDF2	CDF1	CDF2
SIZE	0.190	**0.374**	0.196	0.125
TrL	-0.118	-0.291	0.078	-0.199
TW	**-0.511**	-0.074	**0.468**	**-0.445**
FLL	0.275	-0.036	-0.379	0.290
CFL	0.036	-0.050	-0.041	0.469
HLL	**0.387**	0.293	-0.075	0.028
FFL	0.367	0.182	-0.057	0.041
HW	-0.102	-0.144	0.057	-0.199
HH	0.107	-0.131	0.043	-0.286
OD	-0.137	**0.511**	**0.442**	**0.362**
EL	-0.230	0.272	**0.426**	0.279
NED	-0.247	-0.014	-0.220	0.143
SED	0.198	0.097	-0.454	0.331
EED	-0.197	-0.111	-0.069	-0.275
SLS	-0.098	0.248	0.076	**0.465**
ILS	0.042	0.369	-0.295	0.298
Lam	0.190	0.196	0.039	0.142
Tline	0.246	-0.208	0.037	-0.319
Trow	-0.298	-0.270	-0.284	0.024
medS	-0.227	-0.004	0.016	0.189
Srow	-0.287	0.005	0.007	0.237
Eigenvalues	4.350	2.220	5.970	1.870
% explained	66.30	33.70	76.10	23.90
% cumulative	66.30	100.0	76.10	100.0

Table IV.3 Classification matrix retrieved from the canonical discriminant analyses (CDFA). For each population the percentage (%) and frequency (*n*; between brackets) of correctly classified individuals are provided.

Taxa		**% and *n* correct classification**	***T. bocagei***	***T. fogoensis***	***T. darwini***
Island	**Sex**		**S. Nicolau**	**Fogo**	**Santiago**
T. bocagei	Males	94.7 (19)	94.7 (18)	0 (0)	5.3 (1)
S. Nicolau	Females	100.0 (14)	100.0 (14)	0 (0)	0 (0)
T. fogoensis	Males	87.5 (16)	6.3 (1)	87.5 (14)	6.3 (1)
Fogo	Females	92.3 (13)	0 (0)	92.3 (12)	7.7 (1)
T. darwini	Males	93.3 (15)	0 (0)	6.7 (1)	93.3 (14)
Santiago	Females	80.0 (15)	0 (0)	20.0 (2)	80.0 (13)
Total	Males	92.0 (50)	38.0 (19)	30.0 (15)	32.0 (16)
	Females	90.5 (42)	33.3 (14)	33.3 (14)	33.3 (14)

Integrative approach

The IPC protocol recognises the existence of 12 species within the Cape Verdean *Tarentola* (Fig. IV.2). The distinctiveness of two species is supported by all lines of evidence, whereas the remaining ten species are supported by two. Also two subspecies supported by a single line of evidence are recognised for two out of the 12 species. Based on these results, a new taxonomy for the genus *Tarentola* from Cape Verde is proposed below. The different taxa are described following the order of the phylogenetic tree presented in Fig. IV.2 (from top to bottom).

Order Squamata
Family Gekkonidae
Type Genus *Tarentola* Gray, 1825

Tarentola boavistensis stat. nov. Joger, 1993

Figs. IV.1, IV.2A1, IV.3, IV.4, IV.5A1, IV.6A1, IV.7A1
MorphoBank M42539-M42659

Tarentola rudis boavistensis Joger, 1993: 438 (holotype: RMNH 24144, Boavista, unknown locality, 5 paratypes at RMNH and BMNH); Schleich 1996: 125; Andreone 2000: 21, 25; Carranza *et al.* 2000: 641; Köhler & Güsten 2007: 279

Tarentola delalandii delalandii Boulenger 1906: 200 (part.)

Tarentola delalandii Angel 1937: 1695 (part.)

Tarentola delalandii delalandii Loveridge 1947: 334 (part.); Schleich 1982a: 246 (part.)

Tarentola delalandii rudis Mertens 1954: 7 (part.)

Tarentola borneensis maioensis Joger 1984b: 102 (part.)

Tarentola maioensis López-Jurado, Mateo & Geniez 1999: 11 (part.); López-Jurado, Mateo & Fazeres 2005: 101 (part.)

Tarentola maioensis boavistensis López-Jurado *et al.* 2005: 101

Specimens examined. 11 live specimens and six voucher specimens (Appendix IV.1).

Additional material and references. Andreone (2000: 21, 25) refers to MSNG 49996, II.1898 and MSNG 37560. I.1898 (1 and 8 ind., respectively, all from Boavista, unknown locality, collected by Fea); Carranza *et al.* (2000: 641) to BMNH 1998.344, BMNH 1998.342, BMNH 1998.343 (Boavista, Vila de Sal Rei) and Köhler & Güsten (2007: 279) refer to HLMD-RA-1470 (Boavista, unknown locality).

Diagnosis. Medium to large-sized gecko (maximum SVL 79.0 mm, 65.2 mm on average; cf. Appendix IV.2); eye/ ear opening ratio averages 1.59; ear-eye/ eye-snout distance ratio averages 0.83. Eight to eleven supralabials; seven to nine infralabials; nine to 10 enlarged lamellae under the 4th finger; 112-143 midbody scales; narrow central keeled dorsal tubercles (Fig. IV.5A1) with 20-24 midbody longitudinal lines and 14-18 transversal rows; prominent tubercle above and anterior to the ear opening. Light orangey or yellowish to pinkish grey dorsal colouration slightly translucent with reduced pattern in adults (Figs. IV.6 and IV.7) and whitish below. A light vertebral stripe, interrupted or complete, appears on most individuals. Eye iris generally orange to orangey brown, contrasting with the rest of the head colouration. Juveniles with black tails with strongly marked white stripes. Most specimens with thin brown streaks arranged in different angles in front of and behind the ear. First supra and infralabials white followed by labials with very dark spots.

It differs from other taxa from clade A by presenting keeled dorsal tubercles and having an orangey, yellowish to pinkish grey dorsal colouration slightly translucent and an orangey eye iris. It differs from *T. caboverdiana*, clade B, and clade C by presenting light, reduced dorsal pattern. It differs from *T. gigas* by having smaller SVL and from *T. 'rudis'* from Santiago, Fogo, Brava, Rombos and Maio (taxa from clade D), by having a lower midbody scale count (112-143) but a higher number of interorbital scales (19-22).

Genetic and phylogeographic remarks. *Tarentola boavistensis* is monophyletic and phylogenetically not related to *T. 'rudis'* as it branches in a completely different clade (Fig. IV.2). It also presents a high level of genetic divergence compared to its sister taxa from clade A: A1-A2, A1-A3 and A1-A4 *p*-dist (cyt *b*)= 9.0±1.5/ 9.8±1.6/ 10.7±1.6%, respectively (Table IV.4). The *Snn* test values for PDC, ACM4 and MC1R performed with its sister taxa are all significant (Appendix IV.6). According to the presently selected protocol of integration (IPC), all lines of evidence clearly support the differentiation of the endemic *Tarentola* from Boavista from other taxa from clade A and from all the other *Tarentola* from Cape Verde (see Figs. IV.2, IV.3, IV.4 and Appendix IV.4). Consequently, this taxon is upgraded to the species level.
Distribution. Boavista Island and Sal Rei Islet, Cape Verde.

Conservation status. Listed as Data Deficient under the criteria of the First Red List of Cape Verde (Schleich 1996).

Tarentola bocagei **sp. nov.**

Figs. IV.1, IV.2A2, IV.3, IV.4, IV.5A2, IV.6A2, IV.7A2
MorphoBank M43461-M43781

Tarentola darwini Joger 1984b: 96 (part.), 1993: 443 (part.); Schleich 1996: 125 (part.); Carranza *et al.* 2000: 641 (part.); López-Jurado *et al.* 2005: 101 (part.); Köhler *et al.* 2007: 76 (part.)

Holotype. MNHNXXX, male from S. Nicolau Island (Cape Verde), Carriçal oasis, in the eastern part of the island (16.555289 N, 24.082165W, WGS84), collected on the 3rd of October 2009 by Vasconcelos, Perera and Harris (MorphoBank M43478-M43487). Paratypes: MNHNXXXX female, same data as for holotype (MorphoBank M55879-M55893); BMNH 1998-346 juvenile, Juncalinho (MorphoBank M55894-M55895).

Specimens examined. 34 live specimens and four voucher specimens (Appendix IV.1).

Additional material and references. Joger (1984b: 96) refers to ZSM 138/1981 (3 ind., 2 doubtful, S. Nicolau, unknown locality).

Diagnosis. Medium-sized gecko (maximum SVL 65.5 mm, 58.2 mm on average; Appendix IV.3); eye/ ear opening ratio averages 1.37; ear-eye/ eye-snout distance ratio averages 0.80. Ten to 13 supralabials; eight to 10 infralabials; eight to 10 enlarged lamellae under the 4th finger; 122-146 midbody scales; slightly keeled rounded dorsal tubercles (Fig. IV.5A2) with 17-24 midbody longitudinal lines and 14-18 transversal rows; no enlarged tubercles between the eye and the ear opening. Dorsal parts grey or greyish with four to six transversal bands generally asymmetrical and frequently Y-shaped on the flanks (Figs. IV.6 and IV.7), most of the dorsal tubercles darker than the ground colour while several other tubercles white, especially in subadults and young specimens, well-defined vertebral line without tubercles; pileus almost uniform contrasting with densely marked dorsum, two longitudinal light bands from snout to eye; labials and sides of the throat uniformly whitish or yellowish, without dark stains; eye iris blackish or dark brown.

It is characterised by the same general features of *T. darwini* (not presenting enlarged tubercles between the eye and ear opening and not strongly keeled dorsal tubercles), but in comparison with taxa from clade A3 and A4 by having, relatively to SVL, a shorter trunk length (22.2 mm on average; Appendix IV.3), larger ear opening, base of the tail proportionally wider, distance between nostrils or snout tip and eye significantly shorter, higher average number of small scales between dorsal tubercles (2.1 versus 1.6 for both A3 and A4 lineages; Appendix IV.3), profile of the forehead more concave, ventral part more yellowish and subdigital lamellae more grey than taxa from clade A3 and A4. In comparison with the strongly resembling *Tarentola* from clade C living on the same island, dorsal tubercles are less keeled and more rounded (Fig. IV.5), white tubercles are less numerous, not transversally aligned and usually placed on the flanks, iris more uniformly dark.

Etymology. The species epithet is a Latin noun to honour J.V. Barbosa du Bocage, one of the first naturalists to study the reptiles from the Cape Verde Islands.

Genetic and phylogeographic remarks. *Tarentola bocagei* is monophyletic (Fig. IV.2) in the mitochondrial phylogeny and presents a high level of genetic divergence when compared to its sister taxa: A2-A1, A2-A3, A2-A4 *p*-dist (cyt *b*)= 9.0±1.5/ 9.0±1.5/ 10.1±1.4%, respectively (Table IV.4). The *Snn* test values for PDC, ACM4 and MC1R between its sister taxa are all significant (Appendix IV.6). According to the presently selected protocol of integration (IPC), a minimum of two lines of evidence clearly support the differentiation of *T. bocagei* from other taxa from clade A and from all the other *Tarentola* from Cape Verde (see Figs. IV.2, IV.3, IV.4 and Appendix IV.4). Consequently, this taxon is considered a distinct species.

Distribution. Eastern part of S. Nicolau Island, Cape Verde.

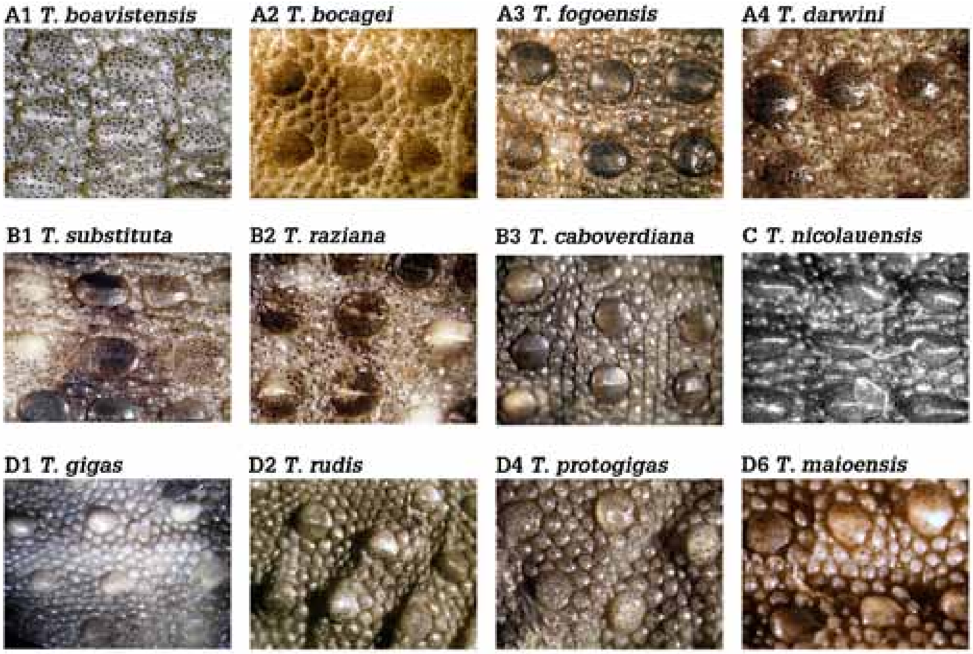

Figure IV.5 Magnified dorsal tubercles of *Tarentola* species of the Cape Verde Islands.

Table IV.4 Uncorrected *p*-distances between groups based on cyt *b* partial sequences (*p*-dist). All the results are based on the pairwise analysis of 459 sequences. Standard error estimates are shown in italics above the diagonal and were obtained by a bootstrap procedure (1000 replicates). Analyses were conducted in Mega4. All positions containing missing data were eliminated from the dataset. There were a total of 302 positions in the final dataset.

	Clade	**A1**	**A2**	**A3**	**A4**	**B1**	**B2**	**B3**	**C**	**D1**	**D2**	**D3**	**D4**	**D5**	**D6**
Clade	**Taxa**	*Tv*	*Tb*	*Tf*	*Td*	*Ts*	*Tr*	*Tc*	*Tn*	*Tg*	*Tr*	*Tpp*	*Tph*	*Tph*	*Tm*
A1	*Tv*		*1.5*	*1.6*	*1.6*	*1.4*	*1.4*	*1.5*	*1.6*	*1.6*	*1.6*	*1.6*	*1.6*	*1.7*	*1.7*
A2	*Tb*	9.0		*1.5*	*1.6*	*1.5*	*1.5*	*1.5*	*1.5*	*1.6*	*1.6*	*1.5*	*1.5*	*1.6*	*1.6*
A3	*Tf*	9.8	9.0		*1.4*	*1.4*	*1.4*	*1.4*	*1.6*	*1.6*	*1.6*	*1.6*	*1.5*	*1.6*	*1.8*
A4	*Td*	10.7	10.1	8.1		*1.6*	*1.6*	*1.5*	*1.6*	*1.6*	*1.7*	*1.7*	*1.6*	*1.7*	*1.8*
B1	*Tcs*	8.0	8.5	7.0	9.9		*0.4*	*0.7*	*1.4*	*1.2*	*1.2*	*1.2*	*1.1*	*1.1*	*1.5*
B2	*Tcr*	7.6	8.5	6.6	9.7	0.9		*0.8*	*1.4*	*1.2*	*1.2*	*1.2*	*1.1*	*1.1*	*1.5*
B3	*Tcc*	9.0	9.0	7.5	9.4	2.2	2.8		*1.4*	*1.2*	*1.3*	*1.2*	*1.2*	*1.2*	*1.5*
C	*Tn*	10.3	9.7	9.3	10.4	7.1	7.1	7.2		*1.3*	*1.5*	*1.4*	*1.4*	*1.4*	*1.5*
D1	*Tg*	9.1	9.2	9.1	10.7	4.6	4.6	5.8	6.4		*0.8*	*0.9*	*0.9*	*0.9*	*1.0*
D2	*Tr*	9.5	9.7	9.3	11.3	5.4	5.4	6.6	7.8	2.4		*1.0*	*0.9*	*0.9*	*1.2*
D3	*Tpp*	9.0	8.7	8.7	11.4	4.8	4.8	5.9	6.8	2.8	3.1		*0.8*	*0.8*	*1.3*
D4	*Tph*	9.1	8.8	8.1	10.3	4.2	4.3	5.3	6.5	2.6	2.6	2.1		*0.3*	*1.2*
D5	*Tph*	9.3	9.0	8.3	10.6	4.5	4.5	5.5	6.8	2.8	2.9	2.3	0.4		*1.3*
D6	*Tm*	10.9	10.2	11.9	13.1	7.4	7.5	8.0	8.7	3.9	5.3	5.7	5.3	5.6	

Tv, *T. boavistensis*; *Tb*, *T. bocagei*; *Tf*, *T. fogoensis*; *Td*, *T. darwini*; *Ts*, *T. substituta*; *Tr*, *T. raziana*; *Tc*, *T. caboverdiana*; *Tn*, *T. nicolauensis*; *Tg*, *T. gigas*; *Tr*, *T. rudis*; *Tpp*, *T. protogigas protogigas*; *Tph*, *T. protogigas hartogi*; *Tm*, *T. maioensis*.

Description of the holotype. A male gecko having the following morphometric features: SVL 63 mm, head 19.8 long, 13.7 mm wide, 8.29 mm height from occiput to jaws, distance between anterior eye and snout tip 5.1 mm, distance between anterior ear and posterior eye 6.13 mm, nostril-eye distance 16.69 mm, greatest orbital diameter 4.02 mm, longest dimension of ear 2.89 mm, total forelimb length 19.87 mm, crus forelimb length from base of palm to elbow 12.23 mm, hindlimb length 25.57 mm, crus length from base of heel to knee 14.49 mm, partially regenerated tail with 55.5 mm long (tip of the tail cut for DNA analyses) and 7.69 mm width at widest point. Dorsal tubercles slightly longer than wider, with one longitudinal smooth but well-defined keel, a straight vertebral line without tubercles of about 3 small scales wide, 14 longitudinal rows of dorsal tubercles at midbody, 19 tubercles along the vertebral line, these tubercles separated on average by 2.25 small scales, 11 supralabials on the left side, 10 supralabials on the right side, 8 infralabials on the left and right side, 44 gular scales counted from a line between the anterior margins of the ear openings to the mental scale, 9 enlarged lamellae under the fourth fingers, 9 enlarged lamellae under the fourth toes, 22 interorbital scales, nostrils in contact with rostral, the first supralabial and the three nasals, nasal scales separated by one scale, six tubercles on each verticillum. Colour in live specimen: mid-grey on the dorsum with four dark transversals bands, the third and fourth indistinct Y-shaped on the flanks, pileus with indistinct darker marks on the back, iris eyes blackish, scales bordering the anterior part of the eye light yellow, two longitudinal dark-faded stripes from snout to eye and one from snout to superior part of the ear opening enclosing a lighter stripe on each side; the six firsts supralabials yellowish, the four posterior ones whitish; lighter not well-marked vertebral line, most of the dorsal tubercles darker than ground colour, except 47 whitish ones, all dorsal tubercles and small scales dark dotted; upper part of the tail with three whitish transversal bands with lighter grey marks; ventral parts white-yellowish becoming yellow on the back; subdigital lamellae greyish. GenBank accession code (XXXXX).

Conservation status. Listed as Data Deficient under the criteria of the First Red List of Cape Verde (Schleich 1996).

Tarentola fogoensis sp. nov.

Figs. IV.1, IV.2A3, IV.3, IV.4, IV.5A3, IV.6A3, IV.7A3
MorphoBank M42945-M43220

Tarentola delalandii var. boettgeri Boulenger 1906: 200 (non Steindachner 1891);
Tarentola darwini Joger 1984b: 96 (part.); Joger 1993: 443 (part.); Schleich 1987: 40 (part.); Schleich 1996: 125 (part.); Carranza *et al.* 2000: 641 (part.); Carranza *et al.* 2002: 247 (part.); Jesus *et al.* 2002: 49 (part.); López-Jurado *et al.* 2005: 101 (part.).

Holotype. MNHNXXXX, male from Fogo Island (Cape Verde), Ilhéu de Contenda (14.983 N, 24.438 W, WGS84), collected on the 7th of December 1999 by S. Carranza (MorphoBank M55902-M55907). First paratype: BEVXXXX, female, same data as for holotype (MorphoBank M55908-M55911). Second paratype: BEVXXXX (MorphoBank M55912-M55919).

Specimens examined. 31 live specimens and nine voucher specimens (Appendix IV.1).

Additional material and references. Joger (1984b: 96; 1993: 443) refers to SMF 50015, 50016, BMNH 1906.3.30.27 (all from Fogo, Igreja) and HLMW 3280 (Fogo, S. Filipe), respectively; Carranza *et al.* (2000: 641, 2002: 247) to BMNH 1998.356 (Fogo, Ribeira Ilhéu) and BMNH 1998.354 (Fogo, S. Filipe) and Jesus *et al.* (2002: 49) to CCBG T23894 (Fogo, S. Filipe).

Diagnosis. Medium-sized gecko (maximum SVL 69.5 mm, 59.0 mm on average; Appendix IV.3); eye/ ear opening ratio averages 1.46; ear-eye/ eye-snout distance ratio averages 0.73. Ten to 12 supralabials; eight to 11 infralabials; nine to 11 enlarged lamellae under the 4th finger; 122-146 midbody scales; small numerous smooth rounded dorsal tubercles (Fig. IV.5A3) with 20-27 midbody longitudinal lines and 14-18 transversal rows; absence of enlarged tubercles between the eye and the ear opening. Dorsal parts grey or greyish and generally without a distinct vertebral stripe, with usually five transversal bands, indistinct or not, and sometimes Y-shaped on the flanks and sometimes forming one X-shape on the midbody (Figs. IV.6 and IV.7); two longitudinal faded light bands from snout to eye; ventral parts whitish or slightly yellowish; labials and sides of the throat with generally numerous dark stains; eye iris blackish and slightly golden on the upperparts.

It is characterised by the same general features of *T. darwini* (not presenting enlarged tubercles between the eye and ear opening and not strongly keeled dorsal tubercles), but in comparison with *T. darwini* from Santiago and *T. bocagei* by having, relatively to SVL, a narrower tail, limbs considerably longer, distance between nostrils and eye proportionally longer, profile of the forehead not concave. Certain individuals present a dark ring mark at the back, not observed in any other Cape Verdean *Tarentola*; vertebral line absent or less defined than in *T. bocagei*; pileus frequently vermiculate or marbled (more uniform in *T. bocagei*), sometimes ventral parts slightly yellowish but less than in *T. bocagei* and subdigital lamellae whiter.

Etymology. The species epithet refers to the island where the taxon is found, Fogo.

Genetic and phylogeographic remarks. *T. fogoensis* is monophyletic (Fig. IV.2) and presents a high level of genetic divergence when compared to *T. boavistensis*, *T. bocagei* and *T. darwini* from Santiago: A3-A1, A3-A2 and A3-A4 *p*-dist (cyt *b*)= 9.8±1.6/ 9.0±1.5/ 8.1±1.4%, respectively (Table IV.4). The *Snn* test values for PDC, ACM4 and MC1R are all significant among this clade (Appendix IV.6). According to the presently selected protocol of integration (IPC), a minimum of two lines of evidence clearly support the differentiation of *T. fogoensis* from other taxa from clade A and from all other *Tarentola* from Cape Verde (see Fig. IV.2, IV.3, IV.4 and Appendix IV.4). Consequently, this taxon is considered a distinct species.

Distribution. Fogo Island, Cape Verde.

Description of the holotype. A male gecko having the following morphometric features: SVL in alcohol 61 mm, head 21.0 long, 14.6 mm wide, 8.9 mm height from occiput to jaws, distance between anterior eye and snout tip 7.9 mm, distance between anterior ear and posterior eye 6.8 mm, greatest orbital diameter 3.6 mm, longest dimension of ear 1.9 mm, forelimb length 17.8 mm, forelimb length from base of palm to elbow 10.6 mm, hindlimb length 21.9 mm, crus length from base of heel to knee 11.0 mm, tail regenerated (tip of the tail cut for DNA analyses), 8.3 mm width at widest point. Dorsal tubercles slightly longer than wider, smooth and not keeled, not distinct vertebral line, 14 longitudinal rows of dorsal tubercles at midbody, 26 tubercles along the vertebral line, these tubercles separated on average by 1.5 small scales, 9 supralabials on the left side, 8 supralabials on the right side, 6 infralabials on the left and right side, 42 gular scales counted from a line between the anterior margins of the ear openings to the mental scale, 9 enlarged lamellae under the fourth fingers, 10 enlarged lamellae under the fourth toes, 20 interorbital scales, nostrils in contact with rostral, the first supralabial and the three nasals, nasal scales separated by one scale, four to six tubercles on each verticillium. Colour in preserved specimen: mid-grey on the dorsum with five dark asymmetric transversal bands, the third and fourth fusing into a X-shape on the vertebral region, pileus with transversal darker mark on the nape of the neck enclosing a distinct ring, scales bordering the anterior part of the eye lighter, supralabials grey light, dorsal tubercles with same colour as ground, all dorsal tubercles and small scales dark dotted, original part of tail with two darker marks at the base, regenerated part uniformly grey; ventral parts dirty whitish.

Conservation status. Listed as Low Risk under the criteria of the First Red List of Cape Verde (Schleich 1996).

Tarentola darwini **Joger, 1984b (restricted type species)**

Figs. IV.1, IV.2A4, IV.3, IV.4, IV.5A4, IV.6A4, IV.7A4
MorphoBank M44231-M44984

Tarentola darwini Joger, 1984b: 96 (part.) (holotype: ZFMK 37256; paratypes: ZFMK 37255, ZSM 365/78, 146/1981, 147/1981, 5 ind., MHNP 35-187,-188, all from Santiago, around Tarrafal), 1993: 443 (part.); Schleich 1987: 40 (part.), 1996: 124 (part.); Brygoo 1990: 51; Carranza *et al*. 2000: 641 (part.); Jesus *et al*. 2002: 49 (part.); López-Jurado *et al*. 2005: 101 (part.); Frazen & Glaw 2007: 219.
Tarentola delalandii delalandii Boulenger 1906: 200 (part.); Loveridge 1947: 334 (part.)
Tarentola delalandii rudis Mertens 1954: 6 (part.)
Tarentola sp. Schleich 1982a: 246; Schleich 1984: 102
Tarentola delalandii boettgeri Schleich 1984: 102

Specimens examined. 88 live specimens and 21 voucher specimens (Appendix IV.1).

Additional material and references. Schleich (1984: 102, 1987: 40) refers to ZFMK 37256 (Schleich collection 1978), ZSM 365/78, 146/81, 147/81, 29/8 (22 ind., all from Santiago, Tarrafal); Joger (1993: 443) to HLMW 3209 (Santiago, S. Domingos); Brygoo (1990:51) to MHNP 1935.187, 1935.188, G 944, ZFMK 37256 (Santiago, Pico Antónia, collected by Chevalier); Carranza *et al.* (2000: 641) to BMNH 1998.348 (Santiago, Rui Vaz), BMNH 1998.351 (Santiago, Tarrafal); Jesus *et al.* (2002: 49) to CCBG T23895 (Santiago, Tarrafal) and Frazen & Glaw (2007: 219) to ZSM 365/1978 (adult, Santiago, Tarrafal, collected by H.-H. Schleich in 1977), ZSM 147/1981/1-5 (5 ind., Santiago, Tarrafal, H.-H., collected by Schleich in 09.1981), ZSM 146/1981/1-2 (2 adults, Santiago, 5 km South from Tarrafal, collected by H.-H. Schleich, 09.1981).

Diagnosis. Medium-sized gecko (maximum SVL 65 mm, 56.4 mm on average; Appendix IV.3); eye/ ear opening ratio averages 1.49; ear-eye/ eye-snout distance ratio averages 0.77. Eight to 12 supralabials; seven to nine infralabials; eight to 12 enlarged lamellae under the 4th finger; 122-146 midbody scales; small numerous smooth rounded dorsal tubercles (Fig. IV.5A4) with 20-27 midbody longitudinal lines and 14-18 transversal rows; no enlarged tubercles between the eye and the ear opening. Dorsal pattern generally composed of 'silky' silver-grey diffuse dark or light spots, sometimes condensed to form an irregular marbling (Figs. IV.6 and IV.7) but sometimes forming indistinct transversal stripes, especially in juveniles; vertebral stripe absent or narrow and diffuse; light ventral parts; many dark spots on supralabials and some sublabials lighter but spotted; eye iris blackish wit upperparts slightly silver.

It differs from *T. boavistensis*, from clade A, and taxa from clade B, C and D by the diffuse dorsal pattern instead of composed of three to five dark or light symmetrical cross marks or bands pattern. Moreover, it also differs from *T. boavistensis* and from taxa from clade D by not presenting enlarged tubercles between the eye and ear opening or strongly keeled dorsal tubercles. Instead it has smooth flat oval to round tubercles with aligned cilia that produce a 'silky' silver-grey dorsal aspect. Differs from *T. bocagei* and *T. fogoensis* by presenting, relatively to SVL, an intermediate tail width at its widest point and snout-eye distance; orbital diameter and the longest dimension of the ear smaller. It also presents supralabial scales comparatively less numerous.

Genetic and phylogeographic remarks. *Tarentola darwini* is monophyletic (Fig. IV.2) and presents a high level of genetic divergence when compared to its sister taxa from clade A, *T. boavistensis*, *T. fogoensis* and *T. bocagei*: A4-A1, A4-A2 and A4-A3 *p*-dist (cyt *b*)= 10.7±1.6/ 10.1±1.6/ 8.1±1.4%, respectively (Table IV.4). The *Snn* test values for PDC, ACM4 and MC1R are all significant among this clade (Appendix IV.6). According to the presently selected protocol of integration (IPC), all lines of evidence clearly support the differentiation of *T. darwini* from other taxa from clade A and from all other *Tarentola* from Cape Verde (see Fig. IV.2, IV.3, IV.4 and Appendix IV.4). Consequently, this taxon is considered a distinct species.

Distribution. Santiago Island, Cape Verde.

Conservation status. Listed as Indeterminate under the criteria of the First Red List of Cape Verde (Schleich 1996).

Tarentola substituta **stat. nov. Joger, 1984b**

Figs. IV.1, IV.2B1, IV.3, IV.5B1, IV.6B1, IV.7B1
MorphoBank M44991-M44994, M55646-M55698

Tarentola caboverdiana substituta Joger, 1984b: 103 (holotype: ZMH-R 0167; paratypes: ZMH-R 01686, ZMH-R 01688-89, ZMNH 1935.5.11.1-8, 1922.11.23.11, 1970.2424-25; all from S. Vicente, unknown locality); Schleich 1987: 46; Joger 1993: 438; Schleich 1996: 124; Andreone 2000: 21, 25; Carranza *et al.* 2000: 641; Carranza *et al.* 2002: 247; Jesus *et al.* 2002: 49; López-Jurado *et al.* 2005: 101; Köhler *et al.* 2007: 76.

Tarentola delalandii Boulenger 1885: 199 (part.); Bocage 1896: 4 (part.); Bocage 1902: 209 (part.); Angel 1937: 1695 (part.)

Tarentola delalandii var. *rudis* Loveridge 1947: 334 (part.)
Tarentola delalandei delalandei Dekeyser & Villiers 1951: 1152 (part.)
Tarentola delalandii rudis Mertens 1954: 6 (part.)
Tarentola delalandii delalandii Schleich 1982a: 246 (part.)
Tarentola caboverdianus caboverdianus Schleich 1984: 98 (part.)

Specimens examined. 24 live specimens and 10 voucher specimens (Appendix IV.1).

Additional material and references. Boulenger (1885: 199) refers to BMNH (5 ind. collected by Rev. Lowe, J. Macgillivray and Dr. Cunningham, all from S. Vicente, unknown locality); Dekeyser & Villiers (1951: 1152) to IFAN 50-1-104 to 50-1-107, IFAN 50-1-108 to 50-1-120 (all from S. Vicente, Baía das Gatas and S. Pedro, respectively and collected by J. Cadenat in 1950); Mertens (1954: 6) to MUH 30.11.1953 (S. Vicente, B. de Norte), MUH 10.1.1954 (S. Vicente,

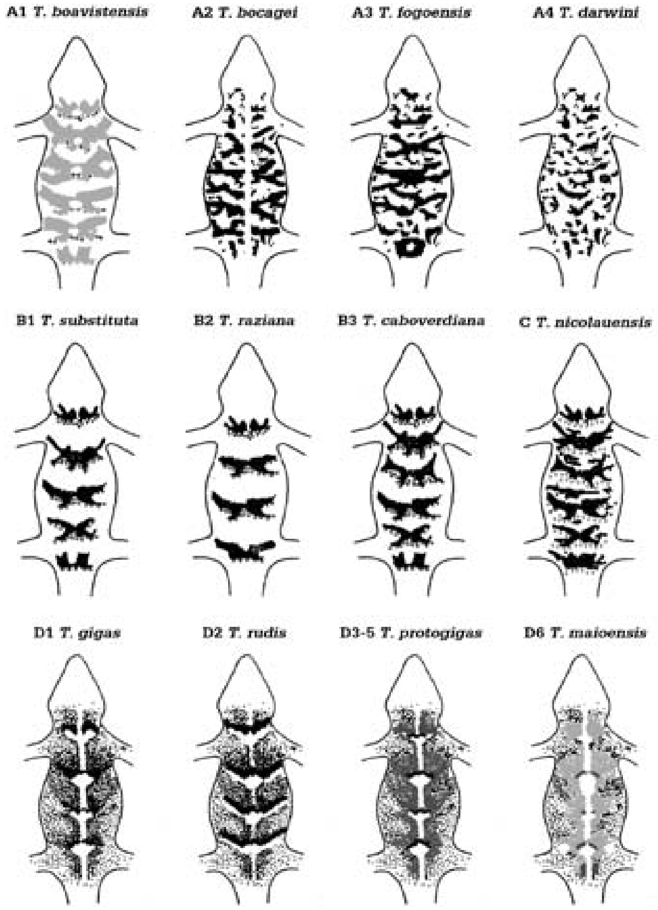

Figure IV.6 Typical dorsal patterns of *Tarentola* species of the Cape Verde Islands (adapted from Joger 1993).

Mindelo), MUH 26.11./2.12.1953, 9./11.3.1954 (S. Vicente, Ribeira Julião); Schleich (1984: 98, 1987: 46) to ZSM 371/78; 01-10.140/81 (S. Vicente, 3 km west from Madeiral); Joger (1993: 438) to RMNH 24118-122 (S. Vicente, S. Pedro Bay), HLMW 3279 (S. Vicente, airport); Andreone (2000: 21, 25) to MSNG 29221, MSNG 36007 (7 and 5 ind., respectively, S. Vicente, Mindelo) and MZUT R2555, R3233 (S. Vicente, unknown locality); Carranza *et al.* (2000: 641; 2002: 247) to BMNH 1998.364 (S. Vicente, Baía das Gatas), and Jesus *et al.* (2002: 49) to CCBG T23891-T23892 (S. Vicente, Madeiral).

Diagnosis. Medium-sized gecko (maximum SVL 65.5 mm, 51.6 mm on average), eye/ ear opening ratio between 1.5 and 2; ear-eye/ eye-snout distance ratio ≤1. Eight to 11 supralabials; seven to nine infralabials; eight to nine enlarged lamellae under the 4th finger; 146-167 midbody scales; oval to round conical and saddle-like more-or-less keeled dorsal tubercles (Fig. IV.5B1) with 14-20 longitudinal lines; no tubercles between the eye and the ear opening. Dorsal pattern with symmetrical butterfly- or x-shaped dark dorsal crossbands often lined with whitish tubercles posteriorly; vertebral stripe absent or reduced to a narrow light line (Figs. IV.6 and IV.7); cream to yellowish ventral parts; generally white labials; blackish eye iris with golden upperparts.

Smaller scales than the other *Tarentola* species from clades B and C, and though higher number of scales around midbody. It differs from *Tarentola* from clade B from Desertas (clade B2 in Fig. IV.2) by its larger SVL and higher number of dorsal bands; four to five from the neck to the caudal region sometimes surrounded by white tubercles; and from *Tarentola* from Santo Antão (clade B3 in Fig. IV.2) by the head length being longer than the anterior limbs and by presenting a higher number of interorbital scales, usually 21 or more, and from specimens from clade C by a lower number of scales and lamellae under the fifth toe.

Distribution. S. Vicente Island, Cape Verde.

Genetic and phylogeographic remarks. *Tarentola substituta* is monophyletic in the mtDNA tree from Fig. IV.2, although the support levels are low. Genetic divergence among taxa within clade B is lower than among members of clade A and D: B1-B2, B1-B3 and B2-B3 *p*-dist (cyt *b*)= 0.9±0.4/ 2.2±0.7/ 2.8±0.8%, respectively (Table IV.4), but most of the *Snn* test values for PDC, ACM4 and MC1R are significant within this clade (Appendix IV.6; see discussion below). According to the presently selected protocol of integration (IPC), a minimum of two lines of evidence support the differentiation of the different island populations and of the endemic *Tarentola* from S. Vicente from all the other *Tarentola* from Cape Verde (see Figs. IV.2, IV.3 and Appendix IV.4). Consequently, this taxon is upgraded to the species level.

Conservation status. Listed as Data Deficient under the criteria of the First Red List of Cape Verde (Schleich 1996).

Tarentola raziana stat. nov. Schleich, 1984

Figs. IV.1, IV.2B2, IV.3, IV.5B2, IV.6B2, IV.7B2
MorphoBank M44995-M44500, M55699-M55714

Tarentola caboverdianus razianus Schleich, 1984: 101 (holotype: ZSM 01.133/81, Santa Luzia, unknown locality; paratypes: 02-10.133/81, Santa Luzia, ZSM 01-10.134/81, Raso Islet)

Tarentola delalandii rudis Mertens 1954: 6 (part.); Schleich 1982a: 246 (part.)

Tarentola delalandii delalandii Schleich 1982a: 246 (part.)

Tarentola sp. Schleich & Wuttke 1983: 34, 42

Tarentola caboverdiana raziana Joger 1984b: 104; Schleich 1987: 44; Joger 1993: 438; Schleich 1996: 124; Andreone 2000: 21, 25; Carranza *et al.* 2000: 641; Jesus *et al.* 2002: 49; López-Jurado *et al.* 2005: 101; Frazen & Glaw 2007: 219.

Tarentola caboverdiana Mateo *et al.* 1997: 8

Specimens examined. 15 live specimens and 20 voucher specimens (Appendix IV.1).

Additional material and references. Mertens (1954: 6) refers to MUH 3.12.1953 (Santa Luzia, Água Doce); Joger (1984b: 104, 1993: 438) to ZSM 01/133/81 (Santa Luzia, unknown locality) and RMNH 24110-111 (Raso Islet), respectively; Schleich (1987: 44) to ZSM 01.133/81, 02-10.133/81 (Santa Luzia, unknown locality), ZSM 01-10.134/81 (Raso Islet); Andreone (2000: 21, 25) to MSNG 49273 (2 ind., Raso Islet); Carranza *et al.* (2000: 641) to BMNH 1998.362N (Santa Luzia); Jesus *et al.* (2002: 49) to IICT317* (Raso Islet) and Frazen & Glaw (2007: 219) to ZSM 133/1981/1 (given as ZSM 01.133/81 in the original description, male, Santa Luzia), ZSM 133/1981/2-10 (given as ZSM 02-10.133/81 in the original description, 9 ind., same data), ZSM 134/1981/1-9 (given as ZSM 01-10.134/81 in the original description, 9 ind., Raso Islet).

Diagnosis. Smallest Cape Verdean wall-gecko (maximum SVL lower than 60 mm, on average 48.2 mm; Appendix IV.2), eye/ ear opening ratio >2; ear-eye/ eye-snout distance ratio clearly ≤1. Nine to 11 supralabials (often 10); seven to nine infralabials (often 8,9); seven to 10 enlarged lamellae under the 4th finger; 116-156 midbody scales; oval to round conical and saddle-like more-or-less keeled dorsal tubercles (Fig. IV.5B2) with 16-18 longitudinal lines; no tubercles between the eye and the ear opening. Snout particularly pointed and forehead concave. Dorsal pattern with only three (sometimes four) symmetrical butterfly- or x-shaped broad dark dorsal crossbands often lined with whitish tubercles posteriorly (Figs. IV.6 and IV.7); light grey or beige to dark brown olive dorsal parts and cream to yellowish ventral parts; generally white labials; eye iris dark golden with a broad black horizontal band.

Besides of its smaller size, it has narrower fingers, lower number of lamellae under the first toe and lower number of gular scales than other *Tarentola* from clade B; usually only three dorsal transversal bands.

Distribution. Santa Luzia Island, Raso and Branco Islet, Cape Verde.

Figure IV.7 Photographs of the dorsal and lateral sides of *Tarentola* of the Cape Verde Islands. **A1)** *T. boavistensis,* **A2)** *T. bocagei*, **A3)** *T. fogoensis*, **A4)** *T. darwini;* **B1)** *T. substituta*, **B2)** *T. raziana*, **B3)** *T. caboverdiana*; **C)** *T. nicolauensis*; **D1)** *T. gigas*, **D2)** *T. rudis*, **D3)** *T. protogigas protogigas*, **D4)** *T. p. hartogi*, Brava Island, **D5)** *T. p. hartogi,* Rombos Islets, **D6)** *T. maioensis*.

Genetic and phylogeographic remarks. *Tarentola raziana* is monophyletic in the mtDNA tree from Fig. IV.2, although the support levels are low. Genetic divergence among taxa within clade B is lower than among members of clade A and D: B1-B2, B1-B3 and B2-B3 *p*-dist (cyt *b*)= 0.9±0.4/ 2.2±0.7/ 2.8±0.8%, respectively (Table IV.4), but most of the *Snn* test values for PDC, ACM4 and MC1R are significant among this clade (Appendix IV.6; see discussion below). According to the presently selected protocol of integration (IPC), a minimum of two lines of evidence clearly support the differentiation of the *Tarentola* populations from Sta. Luzia, Raso and Branco from all the other *Tarentola* from Cape Verde (see Figs. IV.2, IV.3 and Appendix IV.4). Consequently, it is upgraded to the species level.

Conservation status. Listed as Low Risk on the archipelago under the criteria of the First Red List of Cape Verde (Schleich 1996). Considered as Low Risk on Santa Luzia Island and as Rare on Raso Islet under this same criteria (Schleich 1996).

***Tarentola caboverdiana* stat. nov. Schleich, 1984**

Figs. IV.1, IV.2B3, IV.3, IV.5B3, IV.6B3, IV.7B3
MorphoBank M44501-M44514, M55715-M55761

Tarentola caboverdianus caboverdianus Schleich, 1984: 98 (part.) (holotype: ZSM 03.141/81, male; paratypes: 01-02.141/81; 04.141/81 - 17.141/81; all from Santo Antão, unknown locality)

Tarentola delalandii Bocage 1886: 4 (part.), 1902: 209 (part.); Angel 1937: 1695 (part.)

Tarentola delalandii var. *rudis* Loveridge 1947: 334 (part.)

Tarentola delalandei delalandei Dekeyser & Villiers 1951: 1152 (part.)

Tarentola delalandii rudis Mertens 1954: 6 (part.)

Tarentola delalandii delalandii Schleich 1982a: 246 (part.)

Tarentola caboverdiana caboverdiana Joger 1984b: 102; Schleich 1987: 42; Joger 1993: 443; Schleich 1996: 124; Jesus *et al*. 2002: 49; López-Jurado *et al*. 2005: 101; Frazen & Glaw 2007: 219 (part.).

Specimens examined. 22 live specimens and eight voucher specimens (Appendix IV.1).

Additional material and references. Bocage (1886: 4, 1902: 209) refers to individuals from GA (collected by Dr. Hopffer and lost during a fire); Dekeyser & Villiers (1951: 1152) to IFAN 50-1-87 to 50-1-93 and IFAN 50-1-94 to 50-1-103 (Santo Antão, unknown locality and Porto Novo, respectively, all collected by J. Cadenat in 1950); Mertens (1954: 6) to MUH 1.1.1954 and MUH 4./7.1.1954, 3.1.1954 (Santo Antão, Monte Conceição and Porto Novo, respectively); Joger (1984b: 102) to SMF 500011 (Santo Antão, Porto Novo); Schleich (1987: 42) to ZSM 03.141/81, 01-02.141/81, 04.141/81 - 17.141/81 (30 ind., Santo Antão, 4 to 10 km North of Porto Novo - Chã de Morte road, given as Chã do Monte); Jesus *et al*. (2002: 49) to CCBG T23855, CCBG T23839 (Santo Antão, Ponta do Sol and Porto Novo, respectively); Frazen & Glaw (2007: 219) to ZSM 141/1981/3 (female, given as ZSM 03.141/81 in the original description, Santo Antão, unknown locality), ZSM 141/1981/1-2, ZSM 141/1981/4-18 (17 ind. given as ZSM 01-02.141/81 and ZSM 04-17.141/81 [sic] in the original, same data).

Diagnosis. Medium-sized gecko (maximum SVL around 73.0 mm, 56.7 mm on average; Appendix IV.2), eye / ear opening ratio between 1.5 and 2; ear-eye/ eye-snout distance ratio ≤1. Nine to 13 supralabials; seven to 10 infralabials; eight to 10 enlarged lamellae under the 4th finger; 116-150 midbody scales; oval to round conical and saddle-like more-or-less keeled dorsal tubercles (Fig. IV.5B3) with 14-16 (often 16) longitudinal lines; no tubercles between the eye and the ear opening. Dorsal pattern with symmetrical butterfly- or x-shaped dark dorsal crossbands often lined with whitish tubercles posteriorly; vertebral stripe frequently present, but narrow and indistinct (Figs. IV.6 and IV.7); cream to yellow ventral parts; generally white labials; eye iris blackish.

It differs from other *Tarentola* from clades B and C by its tail length, which is smaller than SVL. It differs from *T. raziana* by its larger SVL and higher number of dorsal bands; from *T. substituta* by its lower number of interorbital scales and by the head length being comparatively shorter than hindlimb length. It differs from specimens from clade C by having a lower number of lamellae under the fifth toe.

Distribution. Santo Antão Island, Cape Verde.

Genetic and phylogeographic remarks. *Tarentola caboverdiana* is monophyletic in the mtDNA (Fig. IV.2). Genetic divergence among taxa within clade B is lower than among members of clade A and D: B1-B2, B1-B3 and B2-B3 *p*-dist (cyt *b*)= 0.9±0.4/ 2.2±0.7/ 2.8±0.8%, respectively (Table IV.4), but most of the *Snn* test values for PDC, ACM4 and MC1R are significant (Appendix IV.6) within this clade. According to the presently selected protocol of integration (IPC), a minimum of two lines of evidence clearly support the differentiation of the different island populations and of the endemic *Tarentola* from Santo Antão from all the other *Tarentola* from Cape Verde (see Figs. IV.2, IV.3 and Appendix IV.3). Consequently, it is upgraded to the species level.

Conservation status. Listed as Low Risk under the criteria of the First Red List of Cape Verde (Schleich 1996).

Tarentola nicolauensis **stat. nov. Schleich, 1984**

Figs. IV.1, IV.2C, IV.3, IV.4, IV.5C, IV.6C, IV.7C
MorphoBank M45011-M45992

Tarentola caboverdianus nicolauensis Schleich, 1984: 100 (holotype: ZSM 02.138/81; paratypes: ZSM 01 and 03 - 11.138/81; all from S. Nicolau, unknown locality)

Tarentola delalandii Bocage, 1902: 209 (part.); Angel, 1937: 1695 (part.)

Tarentola delalandii delalandii Boulenger, 1906: 200 (part.); Schleich, 1982a: 246 (part.)

Tarentola delalandii var. *rudis* Loveridge, 1947: 334 (part.)

Tarentola delalandii rudis Mertens, 1954: 6, 7 (part.)

Tarentola caboverdiana nicolauensis Joger, 1984b: 104; Schleich, 1987: 43; Joger, 1993: 443; Schleich, 1996: 124; Andreone, 2000: 21, 25; Carranza *et al*., 2000: 641; Jesus *et al*., 2002:49; López-Jurado *et al*., 2005: 101; Frazen & Glaw, 2007: 219; Köhler *et al*., 2007: 76.

Specimens examined. 39 live specimens and seven voucher specimens (Appendix IV.1).

Additional material and references. Bocage (1902: 209) refers to specimens from GA (S. Nicolau, Vila da Ribeira Brava, collected by F. Newton in 1901 and lost during a fire); Mertens (1954: 6, 7) to MUH 13./17.12.1954, S. Nicolau, Chã de Preguiça); Joger (1984b: 104) to ZSM 02.138/81 (S. Nicolau, unknown locality); Schleich (1987: 43) to ZSM 02.138/81, ZSM 01 and 03 - 11.138/81 (all from S. Nicolau, unknown locality); Andreone (2000: 21, 25) to MSNG 49998 (3 ind., S. Nicolau, unknown locality, collected by Fea in 1898); Carranza *et al*. (2000: 641) to BMNH 1998.358 (S. Nicolau, Tarrafal), BMNH 1998.359 (S. Nicolau, Tarrafal-Ribeira Brava); Jesus *et al*. (2002: 49) to CCBG T23848 (S. Nicolau, Ponta Cachorro), CCBG T23849*, CCBG T23847 (S. Nicolau, Vila da Ribeira Brava) and CCBG T23850* (S. Vicente, Mindelo) and Frazen & Glaw (2007: 219) to ZSM 138/1981/2 (given as ZSM 02.138/81 in the original description, male, S. Nicolau, collected by H.-H. Schleich & H.-J. Gruber, 02.1981), ZSM 138/1981/1, ZSM 138/1981/3-11 (10 ind., same data, given as ZSM 01.138/81 and ZSM 03-11.138/81 in the original description).

Diagnosis. Medium-sized gecko (maximum SVL 71.0 mm, 58.9 mm on average; Appendix IV.2); eye/ ear opening ratio averages 1.53; ear-eye/ eye-snout distance ratio averages 0.79. Nine to 12 supralabials; eight to 10 infralabials; eight to 11 enlarged lamellae under the 4th finger; 133-155 midbody scales; oblong asymmetrical angled dorsal tubercles (Fig. IV.5C) with 14-18 transversal rows; no enlarged tubercles between the eye and the ear opening. Dorsal pattern greyish presenting five clear symmetrical butterfly- or x-shaped dark dorsal crossbands often lined with whitish tubercles posteriorly (Figs. IV.6 and IV.7); white to yellowish light ventral parts; uniformly white labials; dark eye iris with golden upperparts.

It differs from *T. boavistensis*, *T. bocagei*, *T. fogoensis* and *T. darwini*, species from clade A, by butterfly- or x-shaped dorsal pattern and from all the species from clade D and *T. boavistensis* by not presenting enlarged tubercles between the eye and ear opening. It differs from *T. caboverdiana* and *T. substituta* by presenting a higher number of lamellae under the fourth and fifth toe and also from *T. bocagei* by generally presenting oblong apical tubercles. Finally, it differs from *T. raziana* by having a more massive head and a higher number of crossbands (generally five) on the dorsum.

Distribution. West and central part of S. Nicolau Island, Cape Verde.

Genetic and phylogeographic remarks. *Tarentola nicolauensis* is monophyletic (Fig. IV.2) and presents a high level of genetic divergence with species from clade B, *T. substituta*, *T. raziana* and *T. caboverdiana,* within which it was included before the present taxonomic revision: C-B1, C-B2 and C-B3 *p*-dist (cyt *b*)≈ 7.1±1.4%, and with *T. bocagei,* C-A2 *p*-dist (cyt *b*)= 9.7±1.5% (Table IV.4). It presents significant *Snn* test values for MC1R and most comparisons of PDC with *T. caboverdiana* and only of PCD with *T. bocagei* (Appendix IV.6). According to the presently selected protocol of integration (IPC), a minimum of two lines of evidence support the differentiation of *T. nicolauensis* from species from clade B and from all the other *Tarentola* from Cape Verde (Figs. IV.2, IV.3 and Appendix IV.4). Consequently, it is upgraded to the species level.

Conservation status. Listed as Low Risk under the criteria of the First Red List of Cape Verde (Schleich 1996).

Tarentola gigas (Bocage, 1875)

Diagnosis. Giant gecko with an SVL above 100 mm (maximum SVL 155 mm, 103.6 mm on average); eye/ ear opening ratio between 1.5-2.0; ear-eye/ eye-snout distance ratio slightly ≤1. Eight to 12 supralabials; seven to nine infralabials; eight to 12 enlarged lamellae under the 4th finger; 160-195 midbody scales; flatter apical dorsal tubercles (Fig. IV.5D1) with 16 transversal rows; several enlarged tubercles between the eye and the ear opening. Grey dorsal or olive greyish pattern with a broad light well-defined middorsal line with generally five large saddle-like marks (Figs. IV.6 and IV.7); cream ventral parts, yellow on the lower parts; big dark spots on the labials, creating an alternating light and dark pattern; eye iris dark grey with a typical vertical light area around the pupil, joining the upper and lower parts of the eye which are also light.

It differs from other *Tarentola* from the same clade D, *T. 'rudis'* from Santiago, Fogo, Brava, Rombos and Maio, besides from its size, by the absence of a keel on dorsal tubercles. Contrary to all other Cape Verdean *Tarentola*, strong vocalisations play a clear role in social behaviour. This species avoids vertical surfaces presumably due to its weight, and presents a robust body with typical extreme fat storage (Schleich 1987).

Distribution. Raso and Branco Islets, Cape Verde.

Genetic and phylogeographic remarks. *Tarentola gigas* is monophyletic in the mtDNA tree from Fig. IV.2. Genetic divergence with other taxa within clade D is higher than among taxa within clade B, although lower than among members of clade A: D1-D2, D1-D3, D1-D4, D1-D5 and D1-D6 *p*-dist (cyt *b*)= 2.4±0.8/ 2.8±0.9/ 2.6±0.9/ 2.8±0.9/ 3.9±1.0%, respectively (Table IV.4). Most of the *Snn* test values for PDC, ACM4 and MC1R are not significant among this clade (Appendix IV.6). According to the presently selected protocol of integration (IPC), a minimum of two lines of evidence differentiate *T. gigas* from all the other *Tarentola* from Cape Verde (Fig. IV.2). Consequently, it is considered a different species.

The two subspecies, *T. g. gigas* and *T. g. brancoensis*, are not reciprocally monophyletic (Fig. IV.2) and the level of genetic divergence is very low, *p*-dist (cyt *b*)= 0.2±0.2% (data not shown). Only one of the three lines of evidence (morphology) differentiates the two island populations. Consequently, according to the IPC protocol, these are considered distinct subspecies (Figs. IV.2, IV.3 and Appendix IV.4).

Tarentola gigas gigas (Bocage, 1875)

Figs. IV.1, IV.2D1, IV.3, IV.5D1, IV.6D1, IV.7D1
MorphoBank M45993-M45995

Ascalabotes gigas Bocage, 1875: 108 (holotype: from GA, collected by Dr. Hopffer in 1874, Raso Islet and lost due to a fire; paratype: ZMB Nr. 8998, Raso Islet, following Mertens 1954)

Tarentola gigas Boulenger 1885: 200, 414 (part.); Bocage 1896: 4; Bocage 1897: 194; Bocage 1902: 4; Boulenger 1906: 200; Angel 1937: 1695 (part.); Mateo *et al.* 1997: 9, 11 (part.); Gamble *et al.* 2008: 3 (part.)

Tarentola delalandii gigas Loveridge 1947: 330 (part.); Mertens 1954: 7; Greer 1976: 702 (part.); Schleich 1980: 147 (part.); Gruber & Schleich 1982: 309; Schleich 1982b: 82 (part.); Schleich & Wuttke 1983: 83

Tarentola 'delalandii' gigas Schleich 1982a: 246 (part.)

Tarentola borneensis gigas Joger 1984b: 100, 1993: 440

Tarentola borneensis Joger 1985: 308 (part.)

Tarentola gigas gigas Schleich 1984: 104, 1987: 48, 1996: 124; Andreone 2000: 21, 25; Carranza *et al.* 2000: 641; López-Jurado *et al*. 2005: 101.

Specimens examined. Two live specimens and one voucher specimen (Appendix IV.1).

Additional material and references. Bocage (1896: 4, 1897: 194, 1902: 4) refers to specimens from GA (Raso Islet, collected by Dr. Hopffer and Newton in 1874 and lost due to a fire); Gamble *et al.* (2008: 3) to JB 45 (unknown islet); Mertens (1954: 7) to cotype ZMB 8998 (Raso Islet); Schleich (1980: 147) ZSMH 362/1978 (unknown islet); Joger (1984b: 100, 1993: 440) to ZMB Nr. 8998 and RMNH 24148-163, respectively (Raso Islet); Schleich (1984: 104, 1987: 48) to ZSM 131/1981 (Raso Islet) and Andreone (2000: 21, 25) to MSNG 22150 (1 ind., Raso Islet, collected by Fea in X-XI.1898) and MSNG 37517 (1 ind., same data).

Diagnosis. Giant gecko SVL larger than 100 mm (maximum SVL 155 mm, 109.5 mm on average). It differs from *T. g. brancoensis* by the ratio between the width and length of the fourth toe being generally lower than 1:5, by presenting a higher scale count around midbody (180-213 versus 160-195) and a longer snout.

Distribution. Raso Islet, Cape Verde.

Genetic and phylogeographic remarks. See *T. gigas* above.

Conservation status. Listed as Endangered and so in need of urgent protection under the criteria of the First Red List of Cape Verde (Schleich 1996). Later, also the Cape Verde authorities considered the status of this population as Endangered (Anonymous 2002).

Tarentola gigas brancoensis **Schleich, 1984**

Figs. IV.1, IV.2D1, IV.3, IV.5D1, IV.6D1, IV.7D1

Tarentola gigas brancoensis Schleich, 1984: 104 (holotype: ZSM 01.362/78, Branco Islet; paratypes: 02.-06.362/78, 01.-12.19/82, same data), 1987: 49, 1996: 124; Carranza *et al.* 2000: 641, 2002: 247; López-Jurado *et al.* 2005: 101; Frazen & Glaw 2007: 220.

Tarentola borneensis Gray 1845: 165 (part.) (Borneo *ex errore pro* Branco, following Joger 1984b); Joger 1985: 307

Tarentola gigas Angel 1937: 1695 (part.); Mateo *et al.* 1997: 9, 11 (part.)

Tarentola delalandii gigas Loveridge 1947: 330 (part.); Greer 1976: 702 (part.); Schleich 1980: 147 (part.); Schleich 1982b: 82 (part.); Schleich & Wuttke 1983: 83

Tarentola 'delalandii' gigas Schleich 1982a: 246 (part.)

Tarentola borneensis gigas Joger 1984b: 100

Tarentola borneensis borneensis Joger 1993: 443

Specimens examined. Two vouchers specimens (Appendix IV.1).

Additional material and references. Schleich (1980: 147) refers to ZSMH 362/1978 (unknown islet); Joger (1984b: 100) to BMNH 1946.8.25.79-80 (Branco islet); Schleich 1987: 49 to ZSM 01.362/78; 02.-06.362/78, 01.-12.19/82 (Branco Islet); Frazen & Glaw (2007: 220) to ZSM 362/1978/1 (female, Branco Islet, given as ZSM 01.362/78 in the original description), ZSM 362/1978/2-8 (5 adults, 2 juveniles, same data, given as ZSM 02.-06.362/78 in the original description), ZSM 19/1982/1-7 (7 ind., same data, given as ZSM 01.-12.19/82 in the original description).

Diagnosis. Giant gecko with SVL above 100 mm (maximum SVL 113 mm, 98.0 mm on average).

It differs from *T. g. gigas* by its smaller body mass, by the ratio between the width and length of the fourth toe being generally higher than 1:5, by presenting a lower scale count around midbody (160-195 versus 180-213) and a shorter snout.

Distribution. Branco Islet, Cape Verde.

Genetic and phylogeographic remarks. See *T. gigas*, above.

Conservation status. Listed as Endangered and so in need of urgent protection under the criteria of the First Red List of Cape Verde (Schleich 1996). Later, also the Cape Verde authorities considered the status of this population as Endangered (Anonymous 2002).

Tarentola rudis **stat nov. Boulenger, 1906**

Figs. IV.1, IV.2D2, IV.3, IV.5D2, IV.6D2, IV.7D2
MorphoBank M45996-M46036

Tarentola delalandii var. rudis Boulenger, 1906: 200 (part.) [(lectotype: MCNG 28149/1, Santiago, unknown locality; later terra typica restricted to Santiago, Calheta de S. Martinho (Joger 1984b: 101)].

Tarentola borneensis rudis Joger 1984b: 101

Tarentola rudis rudis Schleich 1984: 97 (part.), 1987: 36; Joger 1993: 443; Schleich 1996: 124; Andreone 2000: 21, 25; Carranza *et al.* 2000: 641, 2002: 247; López-Jurado *et al.* 2005: 101

Specimens examined. 25 live specimens and 10 voucher specimens (Appendix IV.1).

Additional material and references. Joger (1984b: 101) refers to lectotype MCNG 28149/1 and paralectotype MCNG 28149/2 (Calheta de S. Martinho); Schleich (1984: 97, 1987: 36) to ZSM 372/1978 (1 ind., Santiago, Cidade Velha), ZSM 135/1981 (2 ind., Santiago, Praia), ZSM 139/1981 (3 ind., Santiago, Praia airport) and also to MCNG 28149/2 (Santiago, Calheta de S. Martinho), respectively; Andreone (2000: 21, 25) to MSNG 28149, MSNG 37561 (2 syntypes and 2 ind., respectively, Santiago, Calheta de S. Martinho) and MSNG 49997 (1 ind., Santiago, Pedra Badejo), all collected by Fea in 1898; Carranza *et al.* (2000: 641, 2002: 247) to BMNH 1998.369 (Santa Maria islet), DB-ULPGC-GG-12, BMNH 1998.368 (Santiago, Praia), also BMNH 1998.365 (Santiago, Cidade Velha).

Diagnosis. Medium to large-sized gecko (maximum SVL around 88 mm, Schleich 1987; 71.8 mm on average; Appendix IV.2); eye/ ear opening ratio averages 1.92; ear-eye/ eye-snout distance ratio averages 0.78. Nine to 11 supralabials (most 10-11); seven to 11 infralabials; nine to 13 enlarged lamellae under the 4th finger; 130-165 midbody scales; conical to apical prominent dorsal tubercles with a narrow central keel (Fig. IV.5D2), especially on the tail, with 16-18 transversal rows; several enlarged tubercles between the eye and the ear opening. Grey brownish-greenish dorsal pattern with a series of four to five (usually four) light middorsal patches, each preceded by a w-shaped dark mark, usually connected by a light middorsal line, which is situated in a tubercle-free space (Figs. IV.6 and IV.7); white ventral parts; clearly marked big dark spots on the labials, creating an alternating light and dark pattern; eye iris light grey with a broad horizontal dark area. Note that the insular specimens from Ilhéu Santa Maria are less robust and have the middorsal line generally more pronounced.

It differs from *T. bocagei*, *T. fogoensis*, *T. darwini*, *T. caboverdiana* and *T. nicolauensis* by presenting enlarged tubercles between the eye and ear opening and prominent dorsal tubercles with a narrow central keel and by presenting a w-shaped dorsal pattern limiting a white spot, instead of symmetrical or asymmetrical butterfly- or x-shaped dark dorsal crossbands or marbled patterns (Figs. IV.6 and IV.7). It differs from *T. gigas* by its smaller SVL (always below 100 mm), its smaller mass and eye iris colouration. It differs from *T. boavistensis* by generally presenting greyer dorsal colouration with frequently more contrasted pattern and eye iris not orangey, and from other taxa from clade D by the colouration and pattern of the labials (darker and/or more regularly creating an alternated dark and light pattern than *Tarentola* from Fogo, Brava, Rombos and Maio). It also differs from *Tarentola* from clade D from Brava, Rombos and Maio by a well-defined four to five w-shaped dorsal bands (Fig. IV.6); from *Tarentola* from Fogo, Brava, Rombos of the same clade by a whiter ventral colouration, and from *Tarentola* from Maio by a higher number of scales and lamellae under the fifth toe (22-24, rarely 21 versus 19-21, rarely 22; Joger 1984b).

Distribution. South of Santiago Island and Santa Maria Islet, Cape Verde.

Genetic and phylogeographic remarks. *Tarentola rudis* is monophyletic (Fig. IV.2) and genetically differentiated from other taxa from clade D: D2-D3, D2-D4, D2-D5 and D2-D6 *p*-dist (cyt *b*)= 3.1±1.0/ 2.6±0.9/ 2.9±0.9/ 5.3±1.2%, respectively (Table IV.4). However, the *Snn* test values for PDC, ACM4 and MC1R are not significant between *T. rudis* and *Tarentola* from Maio (Appendix IV.6). According to the presently selected protocol of integration (IPC), a minimum of two lines of evidence support the differentiation with sister taxa from clade D and differentiation of *T. rudis* from all the other *Tarentola* from Cape Verde (Figs. IV.2, IV.3 and Appendix IV.4). Consequently, *T. rudis* is considered a distinct species.

Conservation status. Listed as Indeterminate and in need of urgent protection under the criteria of the First Red List of Cape Verde (Schleich 1996). Later, also the Cape Verde authorities considered the status of this population as Indeterminate (Anonymous 2002).

Tarentola protogigas **Joger, 1984b**

Diagnosis. Medium to large-sized gecko (maximum SVL 98.5 mm, Schleich 1987; 64.9 mm on average, see Appendix IV.2); eye/ ear opening ratio averages 1.69; ear-eye/ eye-snout distance ratio averages 0.75. Eight to 12 supralabials; seven to nine infralabials; 10 to 13 enlarged lamellae under the 4th finger; 144-181 midbody scales; conical to apical prominent dorsal tubercles with a narrow central keel (Fig. IV.5D4), especially on the sacral region, with 12-15 transversal rows and 15-21 longitudinal rows; several enlarged tubercles between the eye and the ear opening. Grey, brownish to yellowish dorsal pattern with a series of four (sometimes five) light middorsal patches, each preceded by a more indistinct and lighter w-shaped dark mark, usually connected by a light middorsal line (Figs. IV.6 and IV.7); golden-yellowish grey ventral parts; dark spots on the labials, sometimes creating an alternating light and dark pattern; eye iris grey with an indistinct broad horizontal dark area.

It differs from *T. bocagei*, *T. fogoensis* and *T. darwini*, *T. caboverdiana*, *T. nicolauensis* by presenting prominent conical dorsal tubercles, enlarged tubercles between the eye and ear opening and a different dorsal pattern (Fig. IV.6), and from *T. gigas* by the presence of a narrow well-marked central keel, especially on the sacral region. It differs from *T. boavistensis*, *T. rudis* and *Tarentola* from Maio by its yellower ventral colouration. It also differs from *T. rudis* by a higher number of scales around midbody and interorbital scales (18-21 versus 16-19; Joger 1984b), by presenting four to five more indistinct and lighter w-shaped dorsal bands (Fig. IV.6), fader spots on the labials and less contrasted eye iris colouration (Fig. IV.7). It differs from *Tarentola* from Maio by a higher number of scales and lamellae under the fifth toe (22-26 versus 19-21, rarely 22; Joger 1984b) and interorbital scales (19-21 versus 16-18; Joger 1984b).

Distribution. The southern islands of Fogo, Brava and Rombos Islets, Cape Verde.

Genetic and phylogeographic remarks. *Tarentola protogigas* is monophyletic (Fig. IV.2) and presents a considerable level of genetic divergence with other sister taxa from clade D, as *T. gigas*, *T. rudis* and *Tarentola* from Maio: D3-D1, D3-D2, D3-D6 *p*-dist (cyt *b*)= 2.5±1.2/ 2.6±0.9/ 5.3±1.2%, respectively (Table IV.4). *Tarentola protogigas* population from Fogo presents a considerable level of genetic divergence with the populations from Brava and Rombos: D3-D4, D3-D5 *p*-dist (cyt *b*)= 2.1±0.8 and 2.3±0.8%, respectively. However, the *Snn* test values for PDC, ACM4 and MC1R are not significant between *T. protogigas* from Fogo versus Brava and Rombos (Appendix IV.6). The population from Brava presents very low values of genetic divergence with population from Rombos: D4-D5 *p*-dist (cyt *b*)= 0.4±0.3. Therefore, only one of the three lines of evidence (morphology) differentiates the population from Fogo from Brava and Rombos. Consequently, according to the IPC protocol, *T. p. protogigas* and *T. p. hartogi* comb. nov. are considered only distinct subspecies (Fig. IV.2). The lack of differentiation in at least two of the three lines of evidence precludes any further differentiation between the island populations from Brava and Rombos.

Tarentola protogigas protogigas **Joger, 1984b (restricted type subspecies)**

Figs. IV.1, IV.2D3, IV.3, IV.6D3-D5, IV.7D3
MorphoBank M46037-M46055

Tarentola borneensis protogigas Joger, 1984b: 100 (part.) (restricted holotype: ZSM 01/145/81, unknown locality; paratypes: ZSM 02/145/1981, unknown locality; BMNH 1906.3.30.28-29; MCNG C.E. 28149, S. Filipe; all from Fogo); Frazen & Glaw 2007: 219

Tarentola delalandii var. *rudis* Boulenger 1906: 200 (part.); Loveridge 1947: 332 (part.)

Tarentola delalandii rudis Mertens 1954: 6 (part.)

Tarentola 'delalandii' rudis Schleich 1982a: 246 (part.)

Tarentola rudis rudis Schleich 1984: 97 (part.)

Tarentola rudis protogigas Schleich 1987: 38 (part.), 1996: 124 (part.); Joger 1993: 439 (part.), 443; Andreone 2000: 21, 25 (part.); López-Jurado *et al.* 2005: 101 (part.); Frazen & Glaw 2007: 219

Specimens examined. Two live specimens (Appendix IV.1).

Additional material and references. Mertens (1954: 6) refers to MUH 16./21. 2. 1954 (5 ind., Fogo, unknown locality); Schleich (1984: 97, 1987: 38) to ZMS 145/1981.1-11 (Fogo, S. Filipe or S. Lourenço); Andreone (2000: 21, 25) to MSNG 28148 (1 ind., Fogo, Igreja), MSNG 37516, MSNG 37515, MSNG 49249, MSNG 49250 (1, 2, 2 and 3 ind., respectively, all from Fogo, S. Filipe) all collected by Fea in 1898 and Frazen & Glaw (2007: 219) to ZSM 145/1981/1 and ZSM 145/1981/2 (Fogo, S. Filipe, given as ZSM 01/145/81 and ZSM 02/145/1981 in the original, respectively, collected by H.-H. Schleich & H.-J. Gruber in 01.1981).

Diagnosis. Large-sized gecko (maximum SVL 98.5 mm, Schleich 1987; 80.0 mm on average, Appendix IV.2). It differs from *T. protogigas hartogi* by its longer SVL, its less yellowish and more marbled ventrum and more distinct w-shaped dorsal marks (Fig. IV.6).

Distribution. Fogo Island, Cape Verde.

Genetic and phylogeographic remarks. See *T. protogigas* above.

Conservation status. Considered Low Risk on Fogo Island under the criteria of the First Red List of Cape Verde (Schleich 1996).

Tarentola protogigas hartogi **comb. nov. Joger, 1993**

Figs. IV.1, IV.2D4-D5, IV.3, IV.5D4, IV.6D3-D5, IV.7D4-D5
MorphoBank M46056-M46091

Tarentola rudis hartogi Joger, 1993: 439 (holotype: RMNH 24131, collected on Cima Island, Rombos group – central plateau, in sandy area under shrub of Malvaceae – on 23/24 August, 1986 by J.C. Den Hartog; paratypes: HLMD RA-1471, RMNH 24116, Cima Island, easternmost tip, under rock; RMNH 24130, same locality as holotype, SMF 50012, Luiz Carneiro Islet, Rombos group); Schleich 1996: 124; Andreone 2000: 21, 25; Carranza *et al.* 2000: 641; López-Jurado *et al.* 2005: 101 (part.); Köhler & Güsten 2007: 279.

Tarentola delalandii delalandii Boulenger 1906: 200; Schleich 1982a: 246 (part.)

Tarentola delalandii Angel 1937: 1695 (part.)

Tarentola delalandii var. *rudis* Loveridge 1947: 332 (part.)

Tarentola delalandii rudis Mertens 1954: 6 (part.)

Tarentola 'delalandii' rudis Schleich 1982a: 246 (part.)

Tarentola delalandii ssp. Schleich 1982a: 246 (part.)

Tarentola borneensis protogigas Joger 1984b: 100 (part.)

Tarentola rudis protogigas Schleich 1987: 38 (part.), 1996: 124; Joger 1993: 439, 443; Andreone 2000: 21, 25; Carranza *et al.* 2000: 641; López-Jurado *et al.* 2005: 101

Specimens examined. 27 live specimens and 15 voucher specimens (Appendix IV.1).

Additional material and references. Mertens (1954: 6) refers to MUH 22./26.2.1954 (5 ind., Brava, unknown locality) and MUH 27.2.1954 (5 ind., Rombos, Luiz Carneiro and Cima Islet); Joger (1984: 100) to SMF 50013-014, Ilhéu de Contenda (14.983 N, 24.438 W, WGS84), collected in 1984 by Joger, Brava and SMF 50012, Luiz Islet, Rombos; Andreone (2000: 21, 25) to MSNG 28147, MSNG 49994, MSNG 49995 (3, 6 and 1 ind., respectively, all from Brava, unknown locality, collected by Fea in 1899) and to MSNG 37514 (5 ind., Rombos, unknown locality, collected by Fea in 1898); Carranza *et al.* (2000: 641) to BMNH 1998.374 (Brava, Porto da Furna), BMNH 1998.376, BMNH 1998.377 (Brava, Porto Ancião) and to BMNH 1998.372, BMNH 1998.373 (Rombos, unknown locality); Köhler & Güsten (2007: 279) to HLMD-RA-1471 (Rombos, Cima Islet, southernmost tip).

Diagnosis. Medium to large-sized gecko (maximum SVL 77.0 mm; 65.3 mm on average, Appendix IV.2). It differs from *T. protogigas protogigas* by presenting shorter SVL, more yellowish ventral colouration and less distinct w-shaped dorsal marks dorsal colouration on adults.

Distribution. Brava Islands and Rombos Islet group, Cima and Luiz Carneiro Islets, Cape Verde.

Genetic and phylogeographic remarks. See *T. protogigas* above.

Conservation status. Listed as Data Deficient on Brava and Rombos under the criteria of the First Red List of Cape Verde (Schleich 1996).

Tarentola maioensis **stat. nov. Schleich, 1984**

Figs. IV.1, IV.2D6, IV.3, IV.5D6, IV.6D6, IV.7D6
MorphoBank M46092-M46109

Tarentola rudis maioensis Schleich, 1984: 98 (holotype: ZSM 06.136/81; paratypes: ZSM 01.136/81 - 05.136/8, 07.136/8, 09.136/8; all from Maio, unknown locality), 1987: 37, 1996: 124; Joger 1993: 438; Frazen & Glaw 2007: 220
Tarentola delalandii rudis Schleich 1982a: 246 (part.); Mertens 1954: 6 (part.)
Tarentola delalandii ssp. Schleich 1982a: 246
Tarentola borneensis protogigas Joger 1984b: 102 (part.)
Tarentola maioensis maioensis López-Jurado *et al*. 2005: 101

Specimens examined. 16 live specimens and five voucher specimens (Appendix IV.1).

Additional material and references. Mertens (1954: 6) refers to MUH 3.2.1954 (2 ind., Maio, unknown locality); Joger (1984b: 102) to ZSM 06/136/81 (Maio, unknown locality); Schleich (1987: 37) to ZSM 136/81.1-9 (Maio, stream between Vila do Maio and Morro); Joger (1993: 438) to HLMW 3281, (2 ind., Maio, unknown locality) and RMNH 24112-113 (Maio, North of Vila do Maio) and Frazen & Glaw (2007: 220) to ZSM 136/1981/6 (male, Maio, unknown locality, given as ZSM 06.136/81 in the original description), ZSM 136/1981/1-5 and ZSM 136/1981/7-9 (8 ind., same data, given as ZSM 01.136/81-05.136/81 and 07.136/81-09.136/81, respectively in the original description).

Diagnosis. Medium-sized gecko (maximum SVL 71.0 mm, 60.8 mm on average, Appendix IV.2) with a wide and long head; distinct eye/ ear opening ratio ≥2; ear-eye/ eye-snout distance ratio averages ≤1. Seven to nine supralabials; seven to nine infralabials; eight to 10 enlarged lamellae under the 4th finger; 129-149 midbody scales; conical to apical prominent dorsal tubercles with a narrow central keel (Fig. IV.5D6) with 12-18 (often 14) transversal rows; several enlarged tubercles between the eye and the ear opening. Light grey-brownish dorsal colouration; dorsal pattern with a series of faint four to five light middorsal patches or/and a broad light middorsal line, each preceded by wide brown marks (Figs. IV.6 and 7); white ventral parts; usually faint dark spots on the labials sometimes alternating dark and light; pale grey eye iris with a faded horizontal darker area.

It differs from *T. bocagei*, *T. fogoensis* and *T. darwini*, from clade A, *T. caboverdiana* and *T. nicolauensis* by presenting conical dorsal slightly apical prominent tubercles (Fig. IV.5), enlarged tubercles between the eye and ear opening and a different dorsal pattern (Figs. IV.6 and 7). It differs from *T. gigas* by the well-marked central keel on dorsal tubercles (Fig. IV.5). It differs from *T. gigas*, *T. boavistensis*, *T. rudis* and *T. protogigas* by a lower maximum size (71 versus 115, 79, 83 and 83, respectively). Moreover, it differs from *T. boavistensis* by a greyer dorsal and eye iris colouration and from *T. rudis* and *T. protogigas* by generally presenting lower number of scales and lamellae under the fifth toe (19 to 21, rarely 22 versus 22 to 26; Joger 1984b). It also differs from *T. rudis* by presenting lighter dorsal colouration with wider and fainter dorsal bands and generally fainter colouration on the labials (Figs. IV.6 and 7). Finally, it also differs from *T. protogigas* by a lower number of interorbital scales (16-18 versus 19 to 21; Joger 1984b) and the whitish ventral colouration.

Distribution. Maio Island, Cape Verde. Recently introduced in S. Nicolau Island, Cape Verde (see Vasconcelos *et al*. 2010).

Genetic and phylogeographic remarks. *Tarentola maioensis* is a monophyletic lineage, genetically differentiated from other members of its clade, *T. gigas*, *T. rudis* and *T. protogigas*: D6-D1, D6-D2, D6-D3/4/5 *p*-dist (cyt *b*)= 3.9±1.0/ 5.3±1.2/ ≥5.3±1.2%, respectively (Table IV.4). Also *Snn* test values for MC1R were significant between *T. maioensis* and all other species of clade D, except *T. rudis* and all for PDC except with the latter and *T. gigas* (Appendix IV.6). According to the presently selected protocol of integration (IPC), all lines of evidence clearly support the differentiation of this taxon with all other taxa of clade D (see Figs. IV.2, IV.3 and Appendix IV.4), with the only exception of *T. rudis*, from which it differs by only two lines of evidence (mtDNA and morphology). Consequently, the endemic *Tarentola* from Maio is upgraded to the species level.

Conservation status. Listed as Low Risk under the criteria of the First Red List of Cape Verde (Schleich 1996).

IDENTIFICATION KEY

1.
Adults larger than or around 100 mm SVL .... *T. gigas*
Present in Raso Islet .... *T. gigas gigas*
Present in Branco Islet .... *T. gigas brancoensis*
Adults smaller than 100 mm SVL **2**

2.
Enlarged tubercles between the eye and ear opening and prominent keeled dorsal tubercles **3**
No enlarged tubercles between the eye and ear opening and rounded to oval, smoother or less apical dorsal tubercles **6**

3.
Dorsal pattern with a series of usually four light middorsal patches, each preceded by a dark mark, usually connected by a broad light middorsal line and apical tubercles **4**
Reduced dorsal pattern with light yellowish to grey dorsal colouration and apical tubercles **5**

4.
Present in Santiago Island; well-defined four to five w-shaped dorsal bands .... *T. rudis*
Present in Fogo, Brava Island and Rombos Islets .... *T. protogigas*
Present in Fogo Island .... *T. protogigas protogigas*
Present in Brava and Rombos Island .... *T. protogigas hartogi*

5.
Present in Boavista Island; orangey eye iris .... *T. boavistensis*
Present in Maio Island; grey eye iris .... *T. maioensis*

6.
Dorsal pattern with clear symmetrical butterfly- or x-shaped dark crossbands often lined with whitish tubercles posteriorly **7**
Dorsal pattern different **9**

7.
Oval to round dorsal tubercles **8**
Oblong dorsal tubercles, present in S. Nicolau .... *T. nicolauensis*
8.
Present in S. Vicente Island .... *T. substituta*
Present in Santa Luzia and Raso Islet, smaller than 60 mm SVL .... *T. raziana*
Present in Santo Antão Island .... *T. caboverdiana*

9.

Present in S. Nicolau, flat oval to round dorsal tubercles slightly keeled .... *T. bocagei*

Present in Santiago or Fogo, smooth and flat oval to round dorsal tubercles **10**

10.

Present in Santiago, dorsal pattern composed of diffuse dark or light spots, sometimes condensed to form an irregular marbling .... *T. darwini*

Present in Fogo, dorsal pattern composed of diffuse dark crossbands and spots, sometimes with a dark ring mark on the back .... *T. fogoensis*

DISCUSSION

The results of the molecular and morphological analyses are in accordance with previous reports of mitochondrial and morphological variation (Schleich 1984, 1987; Joger 1984b, 1993; Carranza *et al.* 2000; Vasconcelos *et al.* 2010). There is a remarkable degree of concordance between the units defined based on previously published mtDNA data and those observed by morphological analyses and multilocus nuclear data. The only exception is between *T. substituta* and *T. raziana*, which present low levels of mtDNA divergence but significant morphological and nuclear differentiation. For this reason a large number of samples were sequenced for MC1R (*n*=58), confirming that the absence of haplotype sharing between *T. substituta* and *T. raziana* was not a consequence of stochasticity due to low sample size. These two taxa may have been in partial contact and introgressed during the Pleistocene sea-level falls. The gene flow occurred as a consequence of the connection of the Desertas island group with S. Vicente during that period, and has left a signature in the population genetic structure of low mitochondrial divergence between *T. substituta* and *T. raziana* that would be misleading if systematics was based on a single line of evidence. Other studies on *Tarentola* have also shown that mtDNA alone can be misleading (Rato *et al.* 2010). These examples highlight the importance of multi-locus analyses and the choice of the IPC over the IC protocol used on the integrative taxonomy approach. Alternatively, extra lines of evidence might balance results differently, thus further investigation is needed.

Results of nuclear data analyses showed some differentiation between *T. bocagei*, *T. fogoensis* and *T. darwini* and amongst the *Tarentola* from clade B, especially on the MC1R gene. Nuclear data also supported the differentiation of *T. boavistensis* from the *T. gigas* + *T. rudis* clade D and between *T. nicolauensis* and *Tarentola* from clade B. Conversely, it always presented haplotype sharing among specimens of the same species but belonging to different ESUs, as *T. protogigas* from Fogo and Brava. However, nuclear genealogies do not support conclusively all the partitions observed in mtDNA, especially differentiation between *T. bocagei* and *T. nicolauensis* and *T. rudis* and *T. maioensis*. Discrepant results observed between mtDNA and nuclear genealogies are probably explained by incomplete lineage sorting of ancestral polymorphism, as nuclear markers are evolving at slower rates than mitochondrial ones. Another possible explanation could involve male-biased gene flow. Further assessment on faster evolving nuclear markers would be valuable to analyse this.

When haplotype sharing exists between two different species from separated islands that were never connected, most probably it is due to ancestral polymorphism, as gene flow is greatly reduced by the oceanic barrier. This is the case of haplotype sharing between *T. bocagei* and *T. caboverdiana*/ *T. protogigas*/ *T. gigas*/ *T. rudis*; between *T. rudis* and *T. maioensis*, and between *T. nicolauensis* and several species of clade D. In the case of the two *Tarentola* species present in S. Nicolau, the levels of gene flow were estimated to discriminate between the influence of ancestral polymorphism and migration scenarios in shaping the patterns of allele sharing detected by the nuclear markers. The data strongly suggests that the polyphyletic pattern of the nDNA networks derives from the incomplete lineage sorting of ancestral polymorphism as the most probable migration rates inferred with IMa software were zero (Appendix IV.5). When differentiation is recent, as is the case (see Carranza *et al.* 2002; Vasconcelos *et al.* 2010) it is probable that mitochondrial lineages may not be monophyletic with respect to nuclear genealogies. Another evidence is that, if gene flow was the main cause for the observed pattern, it would be expected that both ancestral and derived alleles (located in a central or marginal position in the haplotype network, respectively) to be equally transpecific, which is not the case (see Fig. IV.3). Although possibly allopatric, probably due to the geological history of S. Nicolau (see Vasconcelos *et al.* 2010), *T. bocagei* and *T. nicolauensis* are cryptic species difficult to distinguish in the field. This is probably due to patristic similarity or to convergence, as both species share evolutionary history and identical ecological pressures. Further morphological analyses, including colouration and other qualitative characters are needed to clearly identify these species in the field. It would also be interesting to focus on the possible contact zone between the two species to assess if hybridisation is occurring.

Considering clade D, it is important to note that despite the low differentiation in mtDNA between *T. gigas* and other species of this clade and between some of these species pairs in the nuclear genes, the alternative possibility of considering all these monophyletic lineages belonging to the same species has been refuted by several authors (see Joger 1993; Schleich 1887). The main reason for this is that *T. gigas* presents important morphological, bioacustical, ecological and behavioural differences and also a very distinct geographical distribution (north-western islands) in respect with the remaining species.

A 2.1% of genetic divergence in the cyt *b* was found between *T. protogigas* from Fogo and the populations from Brava and Rombos, while only a 0.4% was found between populations from Brava and Rombos (Table IV.4), the latter ones even sharing a mitochondrial haplotype (see Appendix IV.4). Despite the fact that populations from Brava and Rombos were regarded as different subspecies based on morphology (Joger 1993), the evidence was weak. The analysis was based on very variable pholidotic characters (midbody, toe and gular scale counts) with overlapping values and from very few specimens (two from Brava and five from Rombos). A reanalysis of four additional voucher specimens from Rombos and 27 live specimens from Brava using several characters clearly showed that the morphological variation of the individuals from Rombos falls within that of the specimens from Brava (data not shown). This result coincides with the lack of genetic differentiation between these two island populations and supports the conclusion that both populations should be regarded as part of the same subspecies. On the other hand, as shown in Tables IV.4 and IV.5, Appendixes IV.2 and IV.4, MorphoBank M46037-M46091 and explained in the 'Diagnosis' sections of the two subspecies of *T. protogigas*, *T. protogigas* from Fogo differs morphologically from the populations from Brava and Rombos and also presents distinct haplotypes in mitochondrial DNA. Furthermore, the geographic affinities between Fogo and those other populations are much weaker than between Brava and Rombos.

MANOVA analysis of the linear measurements indicated that males and females of *Tarentola* present sexual dimorphism in size but not in shape, as they became mostly not significant after size-correction. On the other hand, for studying differences among taxa, all linear measurements are important since these analyses proved that differences among populations are due to sizes and also shapes.

This taxonomic revision has considerable conservation implications for the Cape Verdean *Tarentola* since some clades were subdivided and now present more restricted areas of occupancy and extents of occurrence. Thus, a revision of the conservation status should follow. Presently, *Tarentola* is the most taxonomically diverse genus of all the endemic reptile genera occurring on the Cape Verde archipelago (*Hemidactylus*, *Tarentola* and *Chioninia*) and hence efforts should be made to ensure that the protected areas that are going to be implemented in a near future encompass all this richness.

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SUPPORTING INFORMATION

Appendix IV.1 Details of material and sequences used in the present study. CDFA refers to Canonical Discriminant Function Analysis.

Code	Taxa	ESU	Island	Lat.	Long.	Morphology	MorphoBank	mtDNA	nDNA	PDC	ACM4	MC1R
T661	*Tv*	A1	BV	16.10697	-22.89861	yes	M42539-M42547	GQ381016	yes	XXXXXX	XXXXXX	XXXXXX
T662	*Tv*	A1	BV	16.10645	-22.89908	yes	M42548-M42558	GQ381015	yes	XXXXXX	XXXXXX	XXXXXX
T663	*Tv*	A1	BV	16.10567	-22.89945	yes	M42559-M42572	GQ381014	yes	XXXXXX	XXXXXX	XXXXXX
T664	*Tv*	A1	BV	16.04173	-22.74916	yes	M42572-M42583	GQ381013	yes	XXXXXX	XXXXXX	XXXXXX
T665	*Tv*	A1	BV	16.04060	-22.70674	yes	M42584-M42592	GQ381012	yes	XXXXXX	XXXXXX	XXXXXX
T666	*Tv*	A1	BV	16.04135	-22.70532	yes	M42592-M42602	GQ381011	yes	XXXXXX	XXXXXX	XXXXXX
T667	*Tv*	A1	BV	16.10755	-22.81950	yes	M42605-M42616	GQ381010	yes	XXXXXX	XXXXXX	-
T668	*Tv*	A1	BV	16.10264	-22.81181	yes	M42617-M42625	GQ381009	yes	XXXXXX	XXXXXX	XXXXXX
T669	*Tv*	A1	BV	16.10264	-22.81181	yes	M42626-M42635	GQ381008	yes	XXXXXX	XXXXXX	XXXXXX
T672	*Tv*	A1	BV	16.07349	-22.72051	yes	M42636-M42645	GQ381007	yes	XXXXXX	XXXXXX	XXXXXX
T673	*Tv*	A1	BV	16.07349	-22.72051	yes	M42646-M42659	-	no	-	-	-
DB2532	*Tb*	A2	SN	16.61243	-24.12988	yes, CDFA	M43461-M43477	XXXXXX	no	-	-	-
DB2547	*Tb*	A2	SN	16.55529	-24.08217	yes, CDFA	M43478-M43487	XXXXXX	no	-	-	-
DB2561	*Tb*	A2	SN	16.55529	-24.08217	yes	M55879-M55888	XXXXXX	no	-	-	-
DB2596	*Tb*	A2	SN	16.61243	-24.12988	yes, CDFA	M43488-M43497	XXXXXX	no	-	-	-
DB2597	*Tb*	A2	SN	16.55529	-24.08217	yes, CDFA	M43498-M43506	XXXXXX	no	-	-	-
DB2607	*Tb*	A2	SN	16.61300	-24.15359	yes, CDFA	M43507-M43515	XXXXXX	no	-	-	-
DB2613	*Tb*	A2	SN	16.59156	-24.08601	yes, CDFA	M43516-M43524	XXXXXX	no	-	-	-
DB2622	*Tb*	A2	SN	16.61300	-24.15359	yes, CDFA	M43525-M43532	-	no	-	-	-
DB2765	*Tb*	A2	SN	16.55529	-24.08217	yes, CDFA	M43533-M43541	XXXXXX	no	-	-	-
DB2792	*Tb*	A2	SN	16.61243	-24.12988	yes, CDFA	M43542-M43550	XXXXXX	no	-	-	-
DB2796	*Tb*	A2	SN	16.55529	-24.08217	yes, CDFA	M43551-M43559	XXXXXX	no	-	-	-
DB2798	*Tb*	A2	SN	16.61140	-24.11905	yes, CDFA	M43560-M43568	-	no	-	-	-
DB2799	*Tb*	A2	SN	16.57828	-24.07568	yes, CDFA	M43569-M43577	XXXXXX	no	-	-	-
DB2800	*Tb*	A2	SN	16.61243	-24.12988	yes, CDFA	M43578-M43585	XXXXXX	no	-	-	-
DB2801	*Tb*	A2	SN	16.61243	-24.12988	yes, CDFA	M43586-M43594	XXXXXX	no	-	-	-
DB2803	*Tb*	A2	SN	16.61243	-24.12988	yes, CDFA	M43595-M43603	XXXXXX	no	-	-	-
DB2805	*Tb*	A2	SN	16.57828	-24.07568	yes, CDFA	M43604-M43612	XXXXXX	no	-	-	-
DB2808	*Tb*	A2	SN	16.59792	-24.09549	yes, CDFA	M43613-M43621	XXXXXX	no	-	-	-
DB2809	*Tb*	A2	SN	16.55529	-24.08217	yes, CDFA	M43622-M43630	XXXXXX	no	-	-	-
DB2812	*Tb*	A2	SN	16.61140	-24.11905	yes, CDFA	M43631-M43639	-	no	-	-	-
DB2815	*Tb*	A2	SN	16.61140	-24.11905	yes, CDFA	M43640-M43647	XXXXXX	no	-	-	-
DB2877	*Tb*	A2	SN	16.61953	-24.12920	yes, CDFA	M43648-M43657	XXXXXX	no	-	-	-
DB2881	*Tb*	A2	SN	16.55529	-24.08217	yes, CDFA	M43658-M43666	XXXXXX	no	-	-	-
DB2885	*Tb*	A2	SN	16.61140	-24.11905	yes, CDFA	M43667-M43675	XXXXXX	no	-	-	-
DB2888	*Tb*	A2	SN	16.61243	-24.12988	yes, CDFA	M43676-M43683	XXXXXX	no	-	-	-
DB2893	*Tb*	A2	SN	16.61300	-24.15359	yes, CDFA	M43684-M43691	XXXXXX	no	-	-	-
DB2898	*Tb*	A2	SN	16.61243	-24.12988	yes, CDFA	M43692-M43699	XXXXXX	no	-	-	-
DB2899	*Tb*	A2	SN	16.61300	-24.15359	yes, CDFA	M43700-M43707	XXXXXX	no	-	-	-
DB2934	*Tb*	A2	SN	16.59156	-24.08601	yes, CDFA	M43708-M43716	XXXXXX	no	-	-	-
DB2936	*Tb*	A2	SN	16.57828	-24.07568	yes, CDFA	M43717-M43724	XXXXXX	no	-	-	-
DB2938	*Tb*	A2	SN	16.61300	-24.15359	yes, CDFA	M43725-M43733	XXXXXX	no	-	-	-
DB2939	*Tb*	A2	SN	16.61243	-24.12988	yes, CDFA	M43734-M43742	XXXXXX	no	-	-	-
DB2950	*Tb*	A2	SN	16.59792	-24.09549	yes, CDFA	M43743-M43751	XXXXXX	no	-	-	-

Code	**Taxa**	**ESU**	**Island**	**Lat.**	**Long.**	**Morphology**	**MorphoBank**	**mtDNA**	**nDNA**	**PDC**	**ACM4**	**MC1R**
DB2955	*Tb*	A2	SN	16.55529	-24.08217	yes, CDFA	M43752-M43760	XXXXXX	no	-	-	-
T302	*Tb*	A2	SN	16.55476	-24.08140	no	-	GQ380950	yes	XXXXXX	XXXXXX	XXXXXX
T304	*Tb*	A2	SN	16.59085	-24.08757	SVL	M43761-M43763	GQ380952	yes	XXXXXX	XXXXXX	XXXXXX
T349	*Tb*	A2	SN	16.62020	-24.12912	SVL	M43764-M43767	GQ380954	yes	XXXXXX	XXXXXX	XXXXXX
T362	*Tb*	A2	SN	16.59264	-24.06122	SVL	M43768-M43771	GQ380963	yes	XXXXXX	XXXXXX	XXXXXX
T364	*Tb*	A2	SN	16.60834	-24.09522	SVL	M43772-M43775	GQ380961	yes	XXXXXX	XXXXXX	XXXXXX
T365	*Tb*	A2	SN	16.60964	-24.09524	SVL	M43776-M43781	GQ380962	yes	XXXXXX	XXXXXX	-
T533	*Tf*	A3	F	15.01382	-24.40431	yes, CDFA	M42945-M42952	GQ380784	yes	XXXXXX	XXXXXX	XXXXXX
T534	*Tf*	A3	F	14.88365	-24.41666	yes, CDFA	M42953-M42963	GQ380785	no	-	-	-
T536	*Tf*	A3	F	14.88400	-24.41676	yes, CDFA	M42964-M42973	GQ380786	no	-	-	-
T537	*Tf*	A3	F	14.88530	-24.41710	yes, CDFA	M42974-M42983	GQ380787	yes	XXXXXX	XXXXXX	XXXXXX
T538	*Tf*	A3	F	14.86594	-24.44522	yes, CDFA	M42984-M42992	GQ380788	no	-	-	-
T539	*Tf*	A3	F	14.86594	-24.44522	yes, CDFA	M42993-M43002	GQ380789	no	-	-	-
T540	*Tf*	A3	F	14.86753	-24.44612	yes, CDFA	M43003-M43012	GQ380790	yes	XXXXXX	XXXXXX	XXXXXX
T578	*Tf*	A3	F	15.01291	-24.41703	yes, CDFA	M43013-M43021	GQ380792	no	-	-	-
T579	*Tf*	A3	F	15.01291	-24.41703	yes, CDFA	M43022-M43030	GQ380793	no	-	-	-
T581	*Tf*	A3	F	14.97345	-24.42914	yes, CDFA	M43031-M43039	GQ380794	no	-	-	-
T583	*Tf*	A3	F	14.97379	-24.45443	yes	M43040-M43046	GQ380795	yes	XXXXXX	XXXXXX	XXXXXX
T584	*Tf*	A3	F	15.04369	-24.33996	yes, CDFA	M43047-M43055	GQ380796	yes	XXXXXX	XXXXXX	XXXXXX
T585	*Tf*	A3	F	15.04397	-24.33767	yes, CDFA	M43056-M43063	GQ380797	no	-	-	-
T586	*Tf*	A3	F	15.02519	-24.31852	yes, CDFA	M43064-M43072	GQ380798	no	-	-	-
T587	*Tf*	A3	F	15.02519	-24.31852	yes, CDFA	M43073-M43080	GQ380799	no	-	-	-
T588	*Tf*	A3	F	14.96933	-24.29293	yes, CDFA	M43080-M43087	GQ380800	no	-	-	-
T589	*Tf*	A3	F	14.96884	-24.29262	yes, CDFA	M43088-M43096	GQ380801	yes	XXXXXX	XXXXXX	XXXXXX
T590	*Tf*	A3	F	14.96884	-24.29262	yes, CDFA	M43097-M43105	GQ380802	no	-	-	-
T591	*Tf*	A3	F	14.91507	-24.34401	yes, CDFA	M43106-M43115	GQ380803	no	-	-	-
T592	*Tf*	A3	F	14.91362	-24.34490	yes, CDFA	M43116-M43124	GQ380804	no	-	-	-
T593	*Tf*	A3	F	14.91362	-24.34490	yes, CDFA	M43125-M43133	GQ380805	no	-	-	-
T594	*Tf*	A3	F	14.90025	-24.35563	yes, CDFA	M43134-M43143	GQ380806	no	-	-	-
T595	*Tf*	A3	F	14.90025	-24.35563	yes, CDFA	M43144-M43152	GQ380807	no	-	-	-
T596	*Tf*	A3	F	14.89915	-24.35590	yes, CDFA	M43153-M43161	GQ380808	yes	XXXXXX	XXXXXX	XXXXXX
T597	*Tf*	A3	F	14.84548	-24.32733	yes, CDFA	M43162-M43170	GQ380809	no	-	-	-
T599	*Tf*	A3	F	14.86309	-24.44382	yes, CDFA	M43171-M43179	GQ380810	yes	XXXXXX	XXXXXX	XXXXXX
T600	*Tf*	A3	F	14.89229	-24.30076	yes, CDFA	M43180-M43188	GQ380811	yes	XXXXXX	XXXXXX	XXXXXX
T601	*Tf*	A3	F	14.89229	-24.30076	yes, CDFA	M43189-M43197	GQ380812	no	-	-	-
T602	*Tf*	A3	F	14.89283	-24.30111	yes, CDFA	M43198-M43206	GQ380813	yes	XXXXXX	XXXXXX	XXXXXX
T603	*Tf*	A3	F	14.83589	-24.39089	yes	M43207-M43209	GQ380814	yes	XXXXXX	XXXXXX	XXXXXX
T606	*Tf*	A3	F	14.90883	-24.41889	yes, CDFA	M43210-M43218	GQ380817	no	-	-	-
T370	*Td*	A4	ST	15.03740	-23.62620	yes	M44231-M44239	GQ380825	yes	XXXXXX	XXXXXX	XXXXXX
T373	*Td*	A4	ST	14.91247	-23.59675	yes, CDFA	M44240-M44248	GQ380827	no	-	-	-
T374	*Td*	A4	ST	14.91247	-23.59675	yes, CDFA	M44249-M44255	GQ380831	no	-	-	-
T375	*Td*	A4	ST	14.91247	-23.59675	yes	M44256-M44265	GQ380826	no	-	-	-
T378	*Td*	A4	ST	15.00739	-23.52359	yes	M44266-M44273	GQ380863	yes	XXXXXX	XXXXXX	XXXXXX
T389	*Td*	A4	ST	15.10945	-23.51747	yes, CDFA	M44274-M44281	GQ380837	no	-	-	-
T390	*Td*	A4	ST	15.10945	-23.51747	yes	M44282-M44288	GQ380834	no	-	-	-
T392	*Td*	A4	ST	14.94052	-23.67154	yes	M44289-M44296	GQ380843	yes	XXXXXX	XXXXXX	XXXXXX
T394	*Td*	A4	ST	14.94524	-23.67117	yes, CDFA	M44297-M44304	GQ380835	no	-	-	-
T395	*Td*	A4	ST	14.95536	-23.67062	yes, CDFA	M44305-M44312	GQ380822	yes	XXXXXX	XXXXXX	XXXXXX
T397	*Td*	A4	ST	14.95567	-23.67068	yes	M44313-M44320	GQ380820	no	-	-	-
T398	*Td*	A4	ST	14.92932	-23.63896	yes	M44321-M44329	GQ380842	no	-	-	-

Code	Taxa	ESU	Island	Lat.	Long.	Morphology	MorphoBank	mtDNA	nDNA	PDC	ACM4	MC1R
T399	*Td*	A4	ST	14.92932	-23.63896	yes, CDFA	M44330-M44337	GQ380823	yes	XXXXXX	XXXXXX	XXXXXX
T400	*Td*	A4	ST	14.92871	-23.63700	yes, CDFA	M44338-M44345	GQ380824	yes	XXXXXX	XXXXXX	XXXXXX
T404	*Td*	A4	ST	14.96614	-23.58241	yes	M44346-M44353	GQ380849	yes	XXXXXX	XXXXXX	XXXXXX
T405	*Td*	A4	ST	14.96760	-23.58226	yes, CDFA	M44354-M44361	GQ380821	no	-	-	-
T406	*Td*	A4	ST	14.96760	-23.58226	yes, CDFA	M44362-M44369	GQ380848	no	-	-	-
T409	*Td*	A4	ST	14.94532	-23.55602	yes	M44370-M44377	GQ380844	yes	XXXXXX	XXXXXX	XXXXXX
T411	*Td*	A4	ST	14.94532	-23.55602	yes	M44379-M44388	GQ380862	no	-	-	-
T412	*Td*	A4	ST	15.06036	-23.47457	yes	M44389-M44396	GQ380850	no	-	-	-
T413	*Td*	A4	ST	15.06079	-23.47494	yes	M44397-M44405	GQ380885	yes	XXXXXX	XXXXXX	XXXXXX
T414	*Td*	A4	ST	15.05783	-23.47778	yes	M44406-M44414	GQ380876	no	-	-	-
T415	*Td*	A4	ST	15.05433	-23.47058	yes	M44415-M44422	GQ380853	no	-	-	-
T416	*Td*	A4	ST	15.05367	-23.47090	yes	M44423-M44430	GQ380857	no	-	-	-
T417	*Td*	A4	ST	15.05367	-23.47090	yes, CDFA	M44431-M44438	GQ380858	no	-	-	-
T420	*Td*	A4	ST	15.03371	-23.52336	yes	M44439-M44446	GQ380877	no	-	-	-
T421	*Td*	A4	ST	15.03451	-23.52552	yes, CDFA	M44447-M44454	GQ380856	no	-	-	-
T422	*Td*	A4	ST	15.15363	-23.56845	yes, CDFA	M44455-M44465	GQ380934	yes	XXXXXX	XXXXXX	XXXXXX
T423	*Td*	A4	ST	15.15382	-23.56897	yes, CDFA	M44471-M44480	GQ380901	yes	XXXXXX	XXXXXX	XXXXXX
T424	*Td*	A4	ST	15.15382	-23.56897	yes	M44481-M44488	GQ380893	yes	XXXXXX	-	XXXXXX
T425	*Td*	A4	ST	15.15378	-23.56922	yes	M44489-M44496	GQ380900	no	-	-	-
T426	*Td*	A4	ST	15.15492	-23.56569	yes	M44977-M44984	GQ380899	yes	XXXXXX	XXXXXX	XXXXXX
T428	*Td*	A4	ST	15.15492	-23.56569	yes	M44497-M44504	GQ380894	no	-	-	-
T431	*Td*	A4	ST	15.16898	-23.58145	yes	M44505-M44512	GQ380910	yes	XXXXXX	XXXXXX	XXXXXX
T432	*Td*	A4	ST	15.16898	-23.58145	yes	M44513-M44521	GQ380942	no	-	-	-
T433	*Td*	A4	ST	15.16814	-23.58249	yes, CDFA	M44522-M44528	GQ380919	no	-	-	-
T437	*Td*	A4	ST	15.13990	-23.74731	yes	M44529-M44536	GQ380928	no	-	-	-
T438	*Td*	A4	ST	15.13990	-23.74731	yes	M44537-M44543	GQ380911	no	-	-	-
T439	*Td*	A4	ST	15.14013	-23.74904	yes	M44544-M44551	GQ380933	no	-	-	-
T440	*Td*	A4	ST	15.14013	-23.74904	yes, CDFA	M44552-M44559	GQ380927	no	-	-	-
T444	*Td*	A4	ST	15.15475	-23.63381	yes, CDFA	M44560-M44568	GQ380908	no	-	-	-
T445	*Td*	A4	ST	15.15442	-23.63362	yes	M44569-M44576	GQ380920	no	-	-	-
T446	*Td*	A4	ST	15.19741	-23.60256	yes, CDFA	M44577-M44584	GQ380902	yes	XXXXXX	XXXXXX	XXXXXX
T451	*Td*	A4	ST	14.94624	-23.62375	yes	M44585-M44592	GQ380819	no	-	-	-
T452	*Td*	A4	ST	14.94624	-23.62375	yes	M44593-M44600	GQ380881	no	-	-	-
T453	*Td*	A4	ST	14.99202	-23.62272	yes	M44601-M44608	GQ380882	no	-	-	-
T462	*Td*	A4	ST	14.94774	-23.49853	yes	M44609-M44616	GQ380846	no	-	-	-
T464	*Td*	A4	ST	15.26524	-23.75379	yes	M44617-M44625	GQ380912	no	-	-	-
T468	*Td*	A4	ST	15.06631	-23.60313	yes	M44626-M44634	GQ380865	no	-	-	-
T469	*Td*	A4	ST	15.08512	-23.60028	yes, CDFA	M44635-M44643	GQ380828	no	-	-	-
T470	*Td*	A4	ST	15.07021	-23.69503	yes, CDFA	M44644-M44651	GQ380915	no	-	-	-
T471	*Td*	A4	ST	15.03814	-23.59595	yes	M44652-M44659	GQ380830	no	-	-	-
T472	*Td*	A4	ST	15.05110	-23.57769	yes	M44660-M44669	GQ380866	no	-	-	-
T473	*Td*	A4	ST	15.06663	-23.61430	yes	M44670-M44675	GQ380867	no	-	-	-
T474	*Td*	A4	ST	15.09981	-23.71310	yes	M44676-M44683	GQ380914	no	-	-	-
T475	*Td*	A4	ST	15.09981	-23.71310	yes	M44684-M44692	GQ380917	no	-	-	-
T476	*Td*	A4	ST	15.09592	-23.76615	yes	M44693-M44700	GQ380923	no	-	-	-
T477	*Td*	A4	ST	15.09592	-23.76615	yes	M44701-M44708	GQ380925	no	-	-	-
T478	*Td*	A4	ST	15.09592	-23.76615	yes	M44709-M44716	GQ380922	no	-	-	-
T480	*Td*	A4	ST	15.10786	-23.76891	yes	M44717-M44725	GQ380916	no	-	-	-
T482	*Td*	A4	ST	15.24671	-23.72318	yes, CDFA	M44726-M44733	GQ380946	yes	XXXXXX	XXXXXX	-
T483	*Td*	A4	ST	15.24688	-23.72321	yes	M44734-M44741	GQ380945	no	-	-	-

Code	**Taxa**	**ESU**	**Island**	**Lat.**	**Long.**	**Morphology**	**MorphoBank**	**mtDNA**	**nDNA**	**PDC**	**ACM4**	**MC1R**
T484	*Td*	A4	ST	15.25059	-23.72422	yes	M44742-M44749	GQ380887	no	-	-	-
T486	*Td*	A4	ST	15.25258	-23.72522	yes	M44750-M44758	GQ380897	no	-	-	-
T487	*Td*	A4	ST	15.25247	-23.72516	yes	M44759-M44766	GQ380941	yes	XXXXXX	XXXXXX	XXXXXX
T488	*Td*	A4	ST	15.30745	-23.70952	yes	M44767-M44775	GQ380891	no	-	-	-
T489	*Td*	A4	ST	15.30745	-23.70952	yes	M44776-M44785	GQ380895	no	-	-	-
T490	*Td*	A4	ST	15.30746	-23.70870	yes	M44786-M44794	GQ380898	yes	XXXXXX	XXXXXX	XXXXXX
T492	*Td*	A4	ST	15.28715	-23.71260	yes	M44795-M44803	GQ380896	no	-	-	-
T493	*Td*	A4	ST	15.28716	-23.71167	yes	M44804-M44812	GQ380889	yes	XXXXXX	XXXXXX	XXXXXX
T494	*Td*	A4	ST	15.08660	-23.70932	yes, CDFA	M44813-M44821	GQ380948	no	-	-	-
T495	*Td*	A4	ST	15.28076	-23.73057	yes	M44822-M44829	GQ380913	no	-	-	-
T496	*Td*	A4	ST	15.28076	-23.73057	yes	M44830-M44838	GQ380947	no	-	-	-
T501	*Td*	A4	ST	15.16521	-23.62645	yes	M44839-M44847	GQ380904	no	-	-	-
T502	*Td*	A4	ST	15.16288	-23.62428	yes	M44848-M44856	GQ380905	no	-	-	-
T503	*Td*	A4	ST	15.14243	-23.65662	yes	M44857-M44865	GQ380907	no	-	-	-
T505	*Td*	A4	ST	15.11527	-23.62050	yes, CDFA	M44867-M44876	GQ380940	no	-	-	-
T508	*Td*	A4	ST	15.18607	-23.67201	yes, CDFA	M44877-M44885	GQ380909	no	-	-	-
T509	*Td*	A4	ST	15.18607	-23.67201	yes, CDFA	M44886-M44895	GQ380936	no	-	-	-
T510	*Td*	A4	ST	15.18099	-23.67165	yes, CDFA	M44896-M44904	GQ380924	no	-	-	-
T511	*Td*	A4	ST	15.18275	-23.67104	yes	M44905-M44913	GQ380939	no	-	-	-
T512	*Td*	A4	ST	15.00521	-23.53196	yes	M44914-M44922	GQ380868	no	-	-	-
T513	*Td*	A4	ST	15.00521	-23.53196	yes, CDFA	M44923-M44931	GQ380869	no	-	-	-
T516	*Td*	A4	ST	15.06959	-23.55709	yes, CDFA	M44932-M44940	GQ380872	no	-	-	-
T523	*Td*	A4	ST	15.05336	-23.46686	yes, CDFA	M44941-M44949	GQ380874	no	-	-	-
T524	*Td*	A4	ST	15.05336	-23.46686	yes, CDFA	M44950-M44958	GQ380875	no	-	-	-
T526	*Td*	A4	ST	15.06558	-23.76531	yes	M44959-M44967	GQ380929	no	-	-	-
T529	*Td*	A4	ST	15.04916	-23.70036	yes, CDFA	M44968-M44976	GQ380932	no	-	-	-
T003	*Tcs*	B1	SV	16.87172	-24.99760	no		GQ381038	yes	-	-	XXXXXX
T014	*Tcs*	B1	SV	16.85089	-24.87269	no		GQ381039	yes	-	-	XXXXXX
T017	*Tcs*	B1	SV	16.84454	-24.88425	no		GQ381040	yes	-	-	XXXXXX
T021	*Tcs*	B1	SV	16.85035	-24.92702	no		GQ381041	yes	-	-	XXXXXX
T032	*Tcs*	B1	SV	16.86289	-24.94440	no		GQ381042	yes	-	-	XXXXXX
T035	*Tcs*	B1	SV	16.90569	-24.93826	no		GQ381043	yes	-	-	XXXXXX
T037	*Tcs*	B1	SV	16.90390	-24.94287	no		GQ381044	yes	-	-	XXXXXX
T038	*Tcs*	B1	SV	16.90492	-24.94089	no		GQ381045	yes	-	-	XXXXXX
T043	*Tcs*	B1	SV	16.90851	-24.92862	SVL	-	GQ381049	yes	XXXXXX	XXXXXX	XXXXXX
T046	*Tcs*	B1	SV	16.89993	-24.95152	SVL	M44991-M44994	GQ381051	yes	XXXXXX	XXXXXX	XXXXXX
T048	*Tcs*	B1	SV	16.83013	-25.07208	no		GQ381053	yes	-	-	XXXXXX
T055	*Tcs*	B1	SV	16.82982	-25.07634	no		GQ381055	yes	-	-	XXXXXX
T059	*Tcs*	B1	SV	16.82848	-25.06429	no		GQ381056	yes	-	-	XXXXXX
T064	*Tcs*	B1	SV	16.86241	-24.98141	no		GQ381057	yes	-	-	XXXXXX
T070	*Tcs*	B1	SV	16.85721	-24.98110	no		GQ381058	yes	-	-	XXXXXX
T077	*Tcs*	B1	SV	16.83474	-24.96736	no		GQ381059	yes	-	-	XXXXXX
T096	*Tcs*	B1	SV	16.86031	-24.94325	no		GQ381064	yes	-	-	XXXXXX
T102	*Tcs*	B1	SV	16.86817	-24.95305	no		GQ381066	yes	-	-	XXXXXX
T105	*Tcs*	B1	SV	16.87582	-25.01886	no		GQ381067	yes	-	-	XXXXXX
T109	*Tcs*	B1	SV	16.87695	-25.02152	no		GQ381068	yes	-	-	XXXXXX
T124	*Tcs*	B1	SV	16.84348	-25.03513	no		GQ381072	yes	-	-	XXXXXX
T125	*Tcs*	B1	SV	16.84348	-25.03513	no		GQ381073	yes	-	-	XXXXXX
T134	*Tcs*	B1	SV	16.81443	-24.89439	no		GQ381079	yes	-	-	XXXXXX
T136	*Tcs*	B1	SV	16.81633	-25.02315	no		GQ381081	yes	-	-	XXXXXX

Code	Taxa	ESU	Island	Lat.	Long.	Morphology	MorphoBank	mtDNA	nDNA	PDC	ACM4	MC1R
T144	*Tcr*	B2	SL	16.79072	-24.78505	SVL	M44995-M44997	GQ381027	yes	XXXXXX	XXXXXX	-
T145	*Tcr*	B2	SL	16.78341	-24.77890	SVL	M44998-M45000	GQ381017	yes	XXXXXX	XXXXXX	XXXXXX
T150	*Tcr*	B2	SL	16.61249	-24.60066	no		GQ381021	yes	-	-	XXXXXX
T164	*Tcr*	B2	SL	16.74295	-24.74024	no		GQ381020	yes	-	-	XXXXXX
T166	*Tcr*	B2	SL	16.74838	-24.73827	no		GQ381023	yes	-	-	XXXXXX
T170	*Tcr*	B2	SL	16.73945	-24.71607	no		GQ381030	yes	-	-	XXXXXX
T172	*Tcr*	B2	SL	16.74792	-24.70182	no		GQ381028	yes	-	-	XXXXXX
T174	*Tcr*	B2	SL	16.77977	-24.77000	no		GQ381024	yes	-	-	XXXXXX
T178	*Tcr*	B2	SL	16.77584	-24.76580	no		GQ381031	yes	-	-	XXXXXX
Tra1	*Tcr*	B2	ra	16.61249	-24.60066	no	-	GQ381032	yes	XXXXXX	XXXXXX	XXXXXX
Tra2	*Tcr*	B2	ra	16.61249	-24.60066	no		GQ381033	yes	-	-	XXXXXX
Tra3	*Tcr*	B2	ra	16.61249	-24.60066	no		GQ381029	yes	-	-	XXXXXX
Tra5	*Tcr*	B2	ra	16.61249	-24.60066	no		GQ381034	yes	-	-	XXXXXX
Tra6	*Tcr*	B2	ra	16.61249	-24.60066	no		GQ381035	yes	-	-	XXXXXX
Tra7	*Tcr*	B2	ra	16.61249	-24.60066	no		GQ381036	yes	-	-	XXXXXX
T181	*Tcc*	B3	SA	17.19484	-25.09118	no		GQ381097	yes	-	-	XXXXXX
T187	*Tcc*	B3	SA	17.17077	-25.16326	no		GQ381108	yes	-	-	XXXXXX
T188	*Tcc*	B3	SA	17.16766	-25.09881	SVL	M45001-M45003	GQ381117	yes	XXXXXX	XXXXXX	XXXXXX
T189	*Tcc*	B3	SA	17.08340	-25.14861	no		GQ381100	yes	-	-	XXXXXX
T192	*Tcc*	B3	SA	17.11002	-25.08886	SVL	M45004-M45007	GQ381119	yes	XXXXXX	XXXXXX	XXXXXX
T194	*Tcc*	B3	SA	17.10095	-25.06384	no		GQ381088	yes	-	-	XXXXXX
T198	*Tcc*	B3	SA	17.04673	-25.06845	no		GQ381090	yes	-	-	XXXXXX
T196	*Tcc*	B3	SA	17.05217	-25.06745	SVL	M45008-M45010	GQ381089	yes	-	XXXXXX	-
T199	*Tcc*	B3	SA	17.10948	-25.26420	no		GQ381091	yes	-	-	XXXXXX
T203	*Tcc*	B3	SA	17.10122	-25.26699	no		GQ381093	yes	-	-	XXXXXX
T204	*Tcc*	B3	SA	17.02456	-25.05634	no		GQ381111	yes	-	-	XXXXXX
T206	*Tcc*	B3	SA	17.02392	-25.06249	no		GQ381094	yes	-	-	XXXXXX
T207	*Tcc*	B3	SA	17.10742	-25.27155	no		GQ381095	yes	-	-	XXXXXX
T211	*Tcc*	B3	SA	16.98320	-25.23454	no		GQ381109	yes	-	-	XXXXXX
T219	*Tcc*	B3	SA	17.03717	-25.19258	no		GQ381118	yes	-	-	XXXXXX
T222	*Tcc*	B3	SA	17.08197	-25.06486	no		GQ381112	yes	-	-	XXXXXX
T228	*Tcc*	B3	SA	17.01747	-25.16001	no		GQ381114	yes	-	-	XXXXXX
T238	*Tcc*	B3	SA	17.03588	-25.03919	no		GQ381086	yes	-	-	XXXXXX
T240	*Tcc*	B3	SA	17.02712	-25.04083	no	M45011-M45014	GQ381116	yes	XXXXXX	XXXXXX	-
T248	*Tcc*	B3	SA	17.02214	-25.32942	no		GQ381087	yes	-	-	XXXXXX
T256	*Tcc*	B3	SA	16.96542	-25.31289	no		GQ381106	yes	-	-	XXXXXX
T259	*Tcc*	B3	SA	16.95450	-25.30810	no		GQ381107	yes	-	-	XXXXXX
DB1544	*Tn*	C	SN	16.61756	-24.27407	yes	M45653-M45661	XXXXXX	no	-	-	-
DB2422	*Tn*	C	SN	16.61490	-24.39946	yes	M45662-M45671	XXXXXX	no	-	-	-
DB2535	*Tn*	C	SN	16.65512	-24.31653	yes	M45672-M45681	XXXXXX	no	-	-	-
DB2540	*Tn*	C	SN	16.61369	-24.29219	yes	M45682-M45689	XXXXXX	no	-	-	-
DB2562	*Tn*	C	SN	16.58686	-24.32895	yes	M45690-M45698	XXXXXX	no	-	-	-
DB2580	*Tn*	C	SN	16.59210	-24.39728	yes	M45699-M45707	XXXXXX	no	-	-	-
DB2589	*Tn*	C	SN	16.58686	-24.32895	yes	M45708-M45716	XXXXXX	no	-	-	-
DB2591	*Tn*	C	SN	16.61490	-24.39946	yes	M45717-M45726	XXXXXX	no	-	-	-
DB2605	*Tn*	C	SN	16.61756	-24.27407	yes	M45727-M45733	XXXXXX	no	-	-	-
DB2610	*Tn*	C	SN	16.59275	-24.30092	yes	M45734-M45743	XXXXXX	no	-	-	-
DB2624	*Tn*	C	SN	16.61490	-24.39946	yes	M45744-M45752	XXXXXX	no	-	-	-
DB2773	*Tn*	C	SN	16.65512	-24.31653	yes	M45753-M45761	XXXXXX	no	-	-	-
DB2794	*Tn*	C	SN	16.66732	-24.37939	yes	M45762-M45770	XXXXXX	no	-	-	-

Code	**Taxa**	**ESU**	**Island**	**Lat.**	**Long.**	**Morphology**	**MorphoBank**	**mtDNA**	**nDNA**	**PDC**	**ACM4**	**MC1R**
DB2795	*Tn*	C	SN	16.65512	-24.31653	yes	M45771-M45780	XXXXXX	no	-	-	-
DB2804	*Tn*	C	SN	16.61369	-24.29219	yes	M45781-M45789	XXXXXX	no	-	-	-
DB2806	*Tn*	C	SN	16.61490	-24.39946	yes	M45790-M45798	XXXXXX	no	-	-	-
DB2816	*Tn*	C	SN	16.58686	-24.32895	yes	M45799-M45807	XXXXXX	no	-	-	-
DB2817	*Tn*	C	SN	16.66732	-24.37939	yes	M45808-M45816	XXXXXX	no	-	-	-
DB2824	*Tn*	C	SN	16.61756	-24.27407	yes	M45817-M45825	XXXXXX	no	-	-	-
DB2828	*Tn*	C	SN	16.61369	-24.29219	yes	M45826-M45834	XXXXXX	no	-	-	-
DB2829	*Tn*	C	SN	16.61490	-24.39946	yes	M45835-M45843	XXXXXX	no	-	-	-
DB2840	*Tn*	C	SN	16.56649	-24.28285	yes	M45844-M45852	XXXXXX	no	-	-	-
DB2880	*Tn*	C	SN	16.58686	-24.32895	yes	M45853-M45861	XXXXXX	no	-	-	-
DB2884	*Tn*	C	SN	16.56649	-24.28285	yes	M45862-M45870	XXXXXX	no	-	-	-
DB2892	*Tn*	C	SN	16.66732	-24.37939	yes	M45871-M45880	XXXXXX	no	-	-	-
DB2894	*Tn*	C	SN	16.61756	-24.27407	yes	M45881-M45889	XXXXXX	no	-	-	-
DB2895	*Tn*	C	SN	16.61756	-24.27407	yes	M45890-M45899	XXXXXX	no	-	-	-
DB2902	*Tn*	C	SN	16.56649	-24.28285	yes	M45900-M45908	XXXXXX	no	-	-	-
DB2903	*Tn*	C	SN	16.59275	-24.30092	yes	M45909-M45917	XXXXXX	no	-	-	-
DB2932	*Tn*	C	SN	16.66732	-24.37939	yes	M45918-M45926	XXXXXX	no	-	-	-
DB2935	*Tn*	C	SN	16.65512	-24.31653	yes	M45927-M45935	-	no	-	-	-
DB2940	*Tn*	C	SN	16.56649	-24.28285	yes	M45936-M45944	XXXXXX	no	-	-	-
DB2941	*Tn*	C	SN	16.56649	-24.28285	yes	M45945-M45953	XXXXXX	no	-	-	-
DB2945	*Tn*	C	SN	16.59275	-24.30092	yes	M45954-M45963	XXXXXX	no	-	-	-
DB2957	*Tn*	C	SN	16.65512	-24.31653	yes	M45964-M45973	-	no	-	-	-
DB2958	*Tn*	C	SN	16.65512	-24.31653	yes	M45974-M45983	XXXXXX	no	-	-	-
T288	*Tn*	C	SN	16.56635	-24.34141	SVL	M45984-M45986	GQ380986	yes	XXXXXX	XXXXXX	-
T311	*Tn*	C	SN	16.61661	-24.31657	SVL	M45987-M45989	GQ380972	yes	XXXXXX	XXXXXX	XXXXXX
T315	*Tn*	C	SN	16.66047	-24.31520	SVL	M45990-M45992	GQ380994	yes	XXXXXX	XXXXXX	XXXXXX
Tg02	*Tgg*	D1	ra	16.61249	-24.60066	no	M45993-M45994	GQ381127	yes	XXXXXX	XXXXXX	XXXXXX
Tg03	*Tgg*	D1	ra	16.61249	-24.60066	no	M45995	GQ381128	yes	XXXXXX	XXXXXX	XXXXXX
EU293662	*Tg*	D1	Desertas	-	-	no	-	-	yes	XXXXXX	-	-
EU293707	*Tg*	D1	Desertas	-	-	no	-	-	yes	-	XXXXXX	-
T371	*Tr*	D2	ST	14.91610	-23.60448	SVL	M45996-M46002	GQ380725	yes	XXXXXX	XXXXXX	XXXXXX
T377	*Tr*	D2	ST	15.00821	-23.52470	SVL	M46003-M46011	GQ380726	yes	XXXXXX	XXXXXX	XXXXXX
T380	*Tr*	D2	ST	15.00948	-23.51746	SVL	M46012-M46020	GQ380833	yes	XXXXXX	XXXXXX	XXXXXX
T382	*Tr*	D2	ST	15.00948	-23.51746	SVL	M46021-M46028	GQ380727	yes	XXXXXX	XXXXXX	XXXXXX
T384	*Tr*	D2	ST	15.02817	-23.57685	SVL	M46029-M46036	GQ380886	yes	XXXXXX	XXXXXX	XXXXXX
T532	*Tpp*	D3	F	14.91455	-24.45351	yes	M46037-M46046	GQ380781	yes	XXXXXX	XXXXXX	XXXXXX
T535	*Tpp*	D3	F	14.88365	-24.41666	yes	M46047-M46055	GQ380782	yes	XXXXXX	XXXXXX	XXXXXX
T541	*Tph*	D4	B	14.89053	-24.68965	yes	M46056-M46064	GQ380767	yes	XXXXXX	XXXXXX	XXXXXX
T545	*Tph*	D4	B	14.86478	-24.74425	yes	M46065-M46073	GQ380769	yes	XXXXXX	XXXXXX	XXXXXX
T548	*Tph*	D4	B	14.87332	-24.73007	yes	M46074-M46082	GQ380770	yes	XXXXXX	XXXXXX	XXXXXX
T561	*Tph*	D4	B	14.85044	-24.72604	yes	M46083-M46091	GQ380774	yes	XXXXXX	XXXXXX	XXXXXX
T542	*Tph*	D4	B	14.89134	-24.68932	yes	-	-	no	-	-	-
T546	*Tph*	D4	B	14.86455	-24.74429	yes	-	-	no	-	-	-
T547	*Tph*	D4	B	14.86341	-24.74533	yes	-	-	no	-	-	-
T549	*Tph*	D4	B	14.87241	-24.70266	yes	-	GQ380771	no	-	-	-
T553	*Tph*	D4	B	14.83135	-24.73407	yes	-	-	no	-	-	-
T554	*Tph*	D4	B	14.83135	-24.73407	yes	-	-	no	-	-	-
T555	*Tph*	D4	B	14.83216	-24.73434	yes	-	-	no	-	-	-
T558	*Tph*	D4	B	14.84299	-24.73560	yes	-	-	no	-	-	-
T559	*Tph*	D4	B	14.84314	-24.73609	yes	-	-	no	-	-	-

Code	Taxa	ESU	Island	Lat.	Long.	Morphology	MorphoBank	mtDNA	nDNA	PDC	ACM4	MC1R
T560	*Tph*	D4	B	14.84299	-24.73560	yes	-	-	no	-	-	-
T563	*Tph*	D4	B	14.85233	-24.72713	yes	-	-	no	-	-	-
T564	*Tph*	D4	B	14.85233	-24.72713	yes	-	-	no	-	-	-
T565	*Tph*	D4	B	14.84556	-24.67676	yes	-	GQ380775	no	-	-	-
T566	*Tph*	D4	B	14.84583	-24.67625	yes	-	-	no	-	-	-
T567	*Tph*	D4	B	14.84568	-24.67580	yes	-	-	no	-	-	-
T568	*Tph*	D4	B	14.84414	-24.67431	yes	-	-	no	-	-	-
T569	*Tph*	D4	B	14.85590	-24.68782	yes	-	GQ380776	no	-	-	-
T571	*Tph*	D4	B	14.83178	-24.70087	yes	-	GQ380778	no	-	-	-
T572	*Tph*	D4	B	14.83148	-24.70070	yes	-	-	no	-	-	-
T573	*Tph*	D4	B	14.83148	-24.70070	yes	-	-	no	-	-	-
T574	*Tph*	D4	B	14.83706	-24.71593	yes	-	-	no	-	-	-
T575	*Tph*	D4	B	14.83691	-24.71569	yes	-	GQ380779	no	-	-	-
T576	*Tph*	D4	B	14.84658	-24.71339	yes	-	GQ380780	no	-	-	-
T607	*Tm*	D6	M	15.23536	-23.21131	SVL	M46092-M46100	GQ380743	yes	XXXXXX	XXXXXX	XXXXXX
T640	*Tm*	D6	M	15.19690	-23.11949	SVL	M46101-M46109	GQ380754	yes	XXXXXX	XXXXXX	XXXXXX

Code (Vouchers)	Taxa	ESU	Island	Lat.	Long.	Morphology	MorphoBank	mtDNA	nDNA	PDC	ACM4	MC1R
BMNH 1998.346	*Tb*	A2	SN	16.61	-24.13	no	M55894-M55895	AF185036	no	-	-	-
DB2547	*Tb*	A2	SN	16.56	-24.08	no	M55896-M55901	XXXXXX	no	-	-	-
DB2561	*Tb*	A2	SN	16.56	-24.08	no	M55889-M55893	XXXXXX	no	-	-	-
MOR 69	*Tb*	A2	SN	16.61	-24.13	no	no	no	no	-	-	-
DB-ULPGC-GG-6	*Tf*	A3	F	14.90	-24.50	no	no	AF185044	no	-	-	-
MOR 19	*Tf*	A3	F	15.03	-24.32	no	no	no	no	-	-	-
MOR 20	*Tf*	A3	F	14.85	-24.31	no	no	no	no	-	-	-
MOR 21	*Tf*	A3	F	14.85	-24.31	no	no	no	no	-	-	-
TF1/T97	*Tf*	A3	F	14.86	-24.39	no	no	no	no	-	-	-
TF2/T98	*Tf*	A3	F	14.89	-24.49	no	no	no	no	-	-	-
TF3	*Tf*	A3	F	14.98	-24.44	no	M55912-M55919	no	no	-	-	-
TF4/T96	*Tf*	A3	F	14.98	-24.44	no	M55902-M55907	no	no	-	-	-
TF5	*Tf*	A3	F	14.98	-24.44	no	M55908-M55911	no	no	-	-	-
TF6/T99	*Tf*	A3	F	14.98	-24.44	no	no	no	no	-	-	-
TF7	*Tf*	A3	F	14.98	-24.44	no	no	no	no	-	-	-
DB-ULPGC-GG-3	*Td*	A4	ST	15.09	-23.66	no	no	no	no	-	-	-
DB-ULPGC-GG-4	*Td*	A4	ST	15.09	-23.66	no	no	no	no	-	-	-
DB-ULPGC-GG-5	*Td*	A4	ST	15.25	-23.72	no	no	no	no	-	-	-
MOR 260	*Td*	A4	ST	15.28	-23.75	no	no	no	no	-	-	-
MOR 500	*Td*	A4	ST	-	-	no	no	no	no	-	-	-
MOR 501	*Td*	A4	ST	-	-	no	no	no	no	-	-	-
MOR 502	*Td*	A4	ST	-	-	no	no	no	no	-	-	-
MOR 503	*Td*	A4	ST	-	-	no	no	no	no	-	-	-
MOR 504	*Td*	A4	ST	-	-	no	no	no	no	-	-	-
MOR 505	*Td*	A4	ST	-	-	no	no	no	no	-	-	-
MOR 506	*Td*	A4	ST	-	-	no	no	no	no	-	-	-
MOR 507	*Td*	A4	ST	-	-	no	no	no	no	-	-	-
MOR 508	*Td*	A4	ST	-	-	no	no	no	no	-	-	-
MOR 509	*Td*	A4	ST	-	-	no	no	no	no	-	-	-
MOR 510	*Td*	A4	ST	-	-	no	no	no	no	-	-	-
MOR 511	*Td*	A4	ST	-	-	no	no	no	no	-	-	-
MOR 512	*Td*	A4	ST	-	-	no	no	no	no	-	-	-

Code (Vouchers)	**Taxa**	**ESU**	**Island**	**Lat.**	**Long.**	**Morphology**	**MorphoBank**	**mtDNA**	**nDNA**	**PDC**	**ACM4**	**MC1R**
MOR 513	*Td*	A4	ST	-	-	no	no	no	no	-	-	-
MOR 514	*Td*	A4	ST	-	-	no	no	no	no	-	-	-
MOR 515	*Td*	A4	ST	-	-	no	no	no	no	-	-	-
MOR 516	*Td*	A4	ST	-	-	no	no	no	no	-	-	-
MOR 517	*Td*	A4	ST	-	-	no	no	no	no	-	-	-
MOR 518	*Td*	A4	ST	-	-	no	no	no	no	-	-	-
MOR 519	*Td*	A4	ST	-	-	no	no	no	no	-	-	-
MOR 520	*Td*	A4	ST	-	-	no	no	no	no	-	-	-
T100/Td1	*Td*	A4	ST	15.28	-23.75	no	no	no	no	-	-	-
T101/Td3	*Td*	A4	ST	15.28	-23.75	no	no	no	no	-	-	-
Td4	*Td*	A4	ST	15.28	-23.75	no	no	no	no	-	-	-
DB-ULPGC-GG-10	*Tcs*	B1	SV	16.87	-24.94	no	no	no	no	-	-	-
MOR 103	*Tcs*	B1	SV	16.87	-24.94	no	no	no	no	-	-	-
MOR 104	*Tcs*	B1	SV	16.87	-24.94	no	no	no	no	-	-	-
MOR 105	*Tcs*	B1	SV	16.87	-24.94	no	no	no	no	-	-	-
MOR 106	*Tcs*	B1	SV	-	-	no	no	no	no	-	-	-
MOR 107	*Tcs*	B1	SV	-	-	no	no	no	no	-	-	-
MOR 108	*Tcs*	B1	SV	-	-	no	no	no	no	-	-	-
Tc12	*Tcs*	B1	SV	16.87	-24.94	no	no	no	no	-	-	-
Tc13	*Tcs*	B1	SV	16.87	-24.94	no	no	no	no	-	-	-
Tc14	*Tcs*	B1	SV	16.85	-24.87	no	no	no	no	-	-	-
MOR 76	*Tcr*	B2	ra	16.62	-24.59	no	no	no	no	-	-	-
MOR 77	*Tcr*	B2	ra	16.62	-24.59	no	no	no	no	-	-	-
MOR 78	*Tcr*	B2	ra	16.62	-24.59	no	no	no	no	-	-	-
MOR 79	*Tcr*	B2	ra	16.62	-24.59	no	no	no	no	-	-	-
MOR 80	*Tcr*	B2	ra	16.62	-24.59	no	no	no	no	-	-	-
MOR 81	*Tcr*	B2	ra	16.62	-24.59	no	no	no	no	-	-	-
MOR 82	*Tcr*	B2	ra	16.62	-24.59	no	no	no	no	-	-	-
MOR 83	*Tcr*	B2	ra	16.62	-24.59	no	no	no	no	-	-	-
MOR 84	*Tcr*	B2	ra	16.62	-24.59	no	no	no	no	-	-	-
MOR 85	*Tcr*	B2	ra	16.62	-24.59	no	no	no	no	-	-	-
MOR 86	*Tcr*	B2	ra	16.62	-24.59	no	no	no	no	-	-	-
BMNH 1998.346	*Tb*	A2	SN	16.61	-24.13	no	M55894-M55895	AF185036	no	-	-	-
DB2547	*Tb*	A2	SN	16.56	-24.08	no	M55896-M55901	XXXXXX	no	-	-	-
DB2561	*Tb*	A2	SN	16.56	-24.08	no	M55889-M55893	XXXXXX	no	-	-	-
MOR 69	*Tb*	A2	SN	16.61	-24.13	no	no	no	no	-	-	-
DB-ULPGC-GG-6	*Tf*	A3	F	14.9	-24.5	no	no	AF185044	no	-	-	-
MOR 19	*Tf*	A3	F	15.03	-24.32	no	no	no	no	-	-	-
MOR 20	*Tf*	A3	F	14.85	-24.31	no	no	no	no	-	-	-
MOR 21	*Tf*	A3	F	14.85	-24.31	no	no	no	no	-	-	-
TF1/T97	*Tf*	A3	F	14.86	-24.39	no	no	no	no	-	-	-
TF2/T98	*Tf*	A3	F	14.89	-24.49	no	no	no	no	-	-	-
TF3	*Tf*	A3	F	14.98	-24.44	no	M55912-M55919	no	no	-	-	-
TF4/T96	*Tf*	A3	F	14.98	-24.44	no	M55902-M55907	no	no	-	-	-
TF5	*Tf*	A3	F	14.98	-24.44	no	M55908-M55911	no	no	-	-	-
TF6/T99	*Tf*	A3	F	14.98	-24.44	no	no	no	no	-	-	-
TF7	*Tf*	A3	F	14.98	-24.44	no	no	no	no	-	-	-
DB-ULPGC-GG-3	*Td*	A4	ST	15.09	-23.66	no	no	AF185038	no	-	-	-
DB-ULPGC-GG-4	*Td*	A4	ST	15.09	-23.66	no	no	AF185040	no	-	-	-
DB-ULPGC-GG-5	*Td*	A4	ST	15.25	-23.72	no	no	AF185043	no	-	-	-

Code (Vouchers)	Taxa	ESU	Island	Lat.	Long.	Morphology	MorphoBank	mtDNA	nDNA	PDC	ACM4	MC1R
MOR 260	*Td*	A4	ST	15.28	-23.75	no	no	no	no	-	-	-
MOR 500	*Td*	A4	ST	-	-	no	no	no	no	-	-	-
MOR 501	*Td*	A4	ST	-	-	no	no	no	no	-	-	-
MOR 502	*Td*	A4	ST	-	-	no	no	no	no	-	-	-
MOR 503	*Td*	A4	ST	-	-	no	no	no	no	-	-	-
MOR 504	*Td*	A4	ST	-	-	no	no	no	no	-	-	-
MOR 505	*Td*	A4	ST	-	-	no	no	no	no	-	-	-
MOR 506	*Td*	A4	ST	-	-	no	no	no	no	-	-	-
MOR 507	*Td*	A4	ST	-	-	no	no	no	no	-	-	-
MOR 508	*Td*	A4	ST	-	-	no	no	no	no	-	-	-
MOR 509	*Td*	A4	ST	-	-	no	no	no	no	-	-	-
MOR 510	*Td*	A4	ST	-	-	no	no	no	no	-	-	-
MOR 511	*Td*	A4	ST	-	-	no	no	no	no	-	-	-
MOR 512	*Td*	A4	ST	-	-	no	no	no	no	-	-	-
MOR 513	*Td*	A4	ST	-	-	no	no	no	no	-	-	-
MOR 514	*Td*	A4	ST	-	-	no	no	no	no	-	-	-
MOR 515	*Td*	A4	ST	-	-	no	no	no	no	-	-	-
MOR 516	*Td*	A4	ST	-	-	no	no	no	no	-	-	-
MOR 517	*Td*	A4	ST	-	-	no	no	no	no	-	-	-
MOR 518	*Td*	A4	ST	-	-	no	no	no	no	-	-	-
MOR 519	*Td*	A4	ST	-	-	no	no	no	no	-	-	-
MOR 520	*Td*	A4	ST	-	-	no	no	no	no	-	-	-
T100/Td1	*Td*	A4	ST	15.28	-23.75	no	no	no	no	-	-	-
T101/Td3	*Td*	A4	ST	15.28	-23.75	no	no	no	no	-	-	-
Td4	*Td*	A4	ST	15.28	-23.75	no	no	no	no	-	-	-
DB-ULPGC-GG-10	*Tcs*	B1	SV	16.87	-24.94	no	no	AF185030	no	-	-	-
MOR 103	*Tcs*	B1	SV	16.87	-24.94	no	no	no	no	-	-	-
MOR 104	*Tcs*	B1	SV	16.87	-24.94	no	no	no	no	-	-	-
MOR 105	*Tcs*	B1	SV	16.87	-24.94	no	no	no	no	-	-	-
MOR 106	*Tcs*	B1	SV	-	-	no	no	no	no	-	-	-
MOR 107	*Tcs*	B1	SV	-	-	no	no	no	no	-	-	-
MOR 108	*Tcs*	B1	SV	-	-	no	no	no	no	-	-	-
Tc12	*Tcs*	B1	SV	16.87	-24.94	no	no	no	no	-	-	-
Tc13	*Tcs*	B1	SV	16.87	-24.94	no	no	no	no	-	-	-
Tc14	*Tcs*	B1	SV	16.85	-24.87	no	no	no	no	-	-	-
MOR 76	*Tcr*	B2	ra	16.62	-24.59	no	no	no	no	-	-	-
MOR 77	*Tcr*	B2	ra	16.62	-24.59	no	no	no	no	-	-	-
MOR 78	*Tcr*	B2	ra	16.62	-24.59	no	no	no	no	-	-	-
MOR 79	*Tcr*	B2	ra	16.62	-24.59	no	no	no	no	-	-	-
MOR 80	*Tcr*	B2	ra	16.62	-24.59	no	no	no	no	-	-	-
MOR 81	*Tcr*	B2	ra	16.62	-24.59	no	no	no	no	-	-	-
MOR 82	*Tcr*	B2	ra	16.62	-24.59	no	no	no	no	-	-	-
MOR 83	*Tcr*	B2	ra	16.62	-24.59	no	no	no	no	-	-	-
MOR 84	*Tcr*	B2	ra	16.62	-24.59	no	no	no	no	-	-	-
MOR 85	*Tcr*	B2	ra	16.62	-24.59	no	no	no	no	-	-	-
MOR 86	*Tcr*	B2	ra	16.62	-24.59	no	no	no	no	-	-	-
MOR 87	*Tcr*	B2	ra	16.62	-24.59	no	no	no	no	-	-	-
MOR 88	*Tcr*	B2	ra	16.62	-24.59	no	no	no	no	-	-	-
MOR 89	*Tcr*	B2	ra	16.62	-24.59	no	no	no	no	-	-	-
MOR 90	*Tcr*	B2	ra	16.62	-24.59	no	no	no	no	-	-	-

Code (Vouchers)	**Taxa**	**ESU**	**Island**	**Lat.**	**Long.**	**Morphology**	**MorphoBank**	**mtDNA**	**nDNA**	**PDC**	**ACM4**	**MC1R**
MOR 91	*Tcr*	B2	ra	16.62	-24.59	no	no	no	no	-	-	-
MOR 92	*Tcr*	B2	ra	16.62	-24.59	no	no	no	no	-	-	-
T69/cv39/ 1998.361/ DB-ULPGC -GG-9	*Tcr*	B2	ra	16.62	-24.59	no	no	AF185033	no	-	-	-
MOR 94	*Tcr*	B2	SL	16.77	-24.75	no	no	no	no	-	-	-
MOR 96	*Tcr*	B2	SL	16.77	-24.75	no	no	no	no	-	-	-
MOR 97	*Tcr*	B2	SL	16.77	-24.75	no	no	no	no	-	-	-
MOR 98	*Tcr*	B2	SL	16.77	-24.75	no	no	no	no	-	-	-
MOR 99	*Tcr*	B2	SL	16.77	-24.75	no	no	no	no	-	-	-
Tc1	*Tcc*	B3	SA	17.02	-25.07	no	no	no	no	-	-	-
Tc10/cv105	*Tcc*	B3	SA	16.99	-25.19	no	no	GQ380712	no	-	-	-
Tc11/cv106	*Tcc*	B3	SA	-	-	no	no	no	no	-	-	-
Tc2	*Tcc*	B3	SA	17.09	-25.14	no	no	no	no	-	-	-
Tc3	*Tcc*	B3	SA	17.09	-25.14	no	no	no	no	-	-	-
Tc4	*Tcc*	B3	SA	17.09	-25.14	no	no	no	no	-	-	-
Tc5	*Tcc*	B3	SA	17.09	-25.14	no	no	no	no	-	-	-
Tc6	*Tcc*	B3	SA	17.09	-25.14	no	no	no	no	-	-	-
Tc7	*Tcc*	B3	SA	17.02	-25.09	no	no	no	no	-	-	-
Tc8	*Tcc*	B3	SA	17.11	-25.24	no	no	no	no	-	-	-
Tc9	*Tcc*	B3	SA	17.11	-25.24	no	no	no	no	-	-	-
DB-ULPGC-GG-8	*Tn*	C	SN	-	-	no	no	no	no	-	-	-
MOR 64	*Tn*	C	SN	16.61	-24.42	no	no	no	no	-	-	-
MOR 65	*Tn*	C	SN	16.64	-24.32	no	no	no	no	-	-	-
MOR 66	*Tn*	C	SN	16.64	-24.32	no	no	no	no	-	-	-
MOR 67	*Tn*	C	SN	16.64	-24.32	no	no	no	no	-	-	-
MOR 68	*Tn*	C	SN	16.56	-24.28	no	no	no	no	-	-	-
MOR 70	*Tn*	C	SN	16.56	-24.28	no	no	no	no	-	-	-
BEV9190 T87/Tg11	*Tgb*	D1	br	16.66	-24.67	no	no	no	no	-	-	-
BEV9191 T89/ TgDBr	*Tgb*	D1	br	16.66	-24.67	no	no	no	no	-	-	-
BEV6120 T88/Tgra	*Tgg*	D1	Ro	16.62	-24.59	no	no	no	no	-	-	-
DB-ULPGC-GG-11	*Tr*	D2	sm	14.91	-23.51	no	no	AF185013	no	-	-	-
ST001cv/MOR 001	*Tr*	D2	sm	14.91	-23.51	no	no	no	no	-	-	-
ST003cv	*Tr*	D2	sm	14.91	-23.51	no	no	no	no	-	-	-
ST004cv	*Tr*	D2	sm	14.91	-23.51	no	no	no	no	-	-	-
ST010cv	*Tr*	D2	sm	14.91	-23.51	no	no	no	no	-	-	-
ST011cv	*Tr*	D2	sm	14.91	-23.51	no	no	no	no	-	-	-
ST013cv	*Tr*	D2	sm	14.91	-23.51	no	no	no	no	-	-	-
ST015cv	*Tr*	D2	sm	14.91	-23.51	no	no	no	no	-	-	-
ST016cv	*Tr*	D2	sm	14.91	-23.51	no	no	no	no	-	-	-
ST017cv	*Tr*	D2	sm	14.91	-23.51	no	no	no	no	-	-	-
DB-ULPGC-GG - 12	*Tr*	D2	ST	14.92	-23.51	no	no	AF185014	no	-	-	-
DB-ULPGC-GG-15	*Tth*	D4	B	-	-	no	no	AF185025	no	-	-	-
DB-ULPGC-GG-16	*Tth*	D4	B	-	-	no	no	AF185028	no	-	-	-
MOR 32	*Tth*	D4	B	14.88	-24.7	no	no	no	no	-	-	-
MOR 33	*Tth*	D4	B	14.88	-24.69	no	no	no	no	-	-	-
MOR 34	*Tth*	D4	B	14.84	-24.72	no	no	no	no	-	-	-
MOR 35	*Tth*	D4	B	14.84	-24.72	no	no	no	no	-	-	-
MOR 36	*Tth*	D4	B	14.81	-24.71	no	no	no	no	-	-	-

Code (Vouchers)	Taxa	ESU	Island	Lat.	Long.	Morphology	MorphoBank	mtDNA	nDNA	PDC	ACM4	MC1R
MOR 37	*Trh*	D4	B	14.83	-24.7	no	no	no	no	-	-	-
MOR 38	*Trh*	D4	B	14.83	-24.7	no	no	no	no	-	-	-
MOR 39	*Trh*	D4	B	14.83	-24.7	no	no	no	no	-	-	-
MOR 40	*Trh*	D4	B	14.83	-24.7	no	no	no	no	-	-	-
DB-ULPGC-GG-13	*Trh*	D4	ro	-	-	no	no	AF185020	no	-	-	-
DB-ULPGC-GG-14	*Trh*	D4	ro	-	-	no	no	AF185021	no	-	-	-
MOR 302	*Trh*	D4	ro	-	-	no	no	no	no	-	-	-
MOR 303	*Trh*	D4	ro	-	-	no	no	no	no	-	-	-
T90/cv90/Tr1	*Tm*	D6	M	15.27	-23.2	no	no	no	no	-	-	-
T91/cv91/Tr2	*Tm*	D6	M	15.25	-23.11	no	no	no	no	-	-	-
T92/cv92/Tr5	*Tm*	D6	M	15.21	-23.11	no	no	no	no	-	-	-
T93/cv93/Tr6	*Tm*	D6	M	15.15	-23.13	no	no	no	no	-	-	-
T94/cv94/Tr7	*Tm*	D6	M	15.32	-23.12	no	no	no	no	-	-	-
Tr3	*Tm*	D6	M	15.31	-23.15	no	no	no	no	-	-	-
Tr4	*Tm*	D6	M	15.27	-23.12	no	no	no	no	-	-	-

SV, S. Vicente; SL, Sta. Luzia; ra, Raso; br, Branco; SA, Santo Antão; SN, S. Nicolau; ST, Santiago; F, Fogo; B, Brava; M, Maio; BV, Boavista. Individuals marked with * have introgressed mtDNA.

Tv, T. boavistensis; Tb, T. bocagei; Tf, T. fogoensis; Td, T. darwini; Ts, T. substituta; Tz, T. raziana; Tc, T. caboverdiana; Tn, T. nicolauensis; Tgg, T. gigas gigas; Tr, T. rudis; Tp, T. protogigas; Tm, T. maioensis.

Appendix IV.2 Descriptive statistics for all the linear measurements and meristic variables of adult specimens of the different *Tarentola* taxa included in this study. For each variable mean± standard deviation (SD), range, and sample size (*n*) is given.

	T. boavistensis						***T. nicolauensis***					
	Boavista						**São Nicolau**					
	Males (*n*=6)		Females (*n*=5)		All (*n*=11)		Males (*n*=18)		Females (*n*=18)		All (*n*=36)	
	mean±SD	Range	mean±SD	Range	mean±SD	Range	mean±SD	Range	mean±SD	Range	mean±SD	Range
SVL	69.67±7.09	60.00–79.00	59.9±4.01	53.50–64.00	65.23±7.59	53.50–79.00	58.97±5.16	51.50–71.00	58.31±4.51	50.00–65.50	58.64±4.79	50.00–71.00
TrL	27.94±3.26	23.28–31.09	24.79±2.01	22.07–27.73	26.51±3.1	22.07–31.09	22.70±2.67	19.61–30.33	23.46±2.08	20.04–27.49	23.08±2.39	19.61–30.33
TW	6.73±0.74	5.68–7.52	5.56±0.57	4.93–6.42	6.20±0.88	4.93–7.52	6.75±0.94	5.45–9.11	6.43±0.90	5.07–8.30	6.59±0.92	5.07–9.11
FLL	26.56±2.92	23.37–31.81	23.22±1.11	21.25–23.86	25.04±2.79	21.25–31.81	20.33±1.83	17.42–23.93	19.70±1.68	16.80–22.88	20.02±1.76	16.80–23.93
CFL	16.94±2.31	13.06–19.66	14.12±0.86	13.19–15.24	15.65±2.27	13.06–19.66	12.98±1.26	10.52–15.83	12.48±1.26	10.63–14.65	12.73±1.27	10.52–15.83
HLL	32.60±3.65	27.04–36.83	27.82±2.35	24.55–30.66	30.43±3.89	24.55–36.83	25.09±2.07	22.36–29.39	24.61±1.97	20.69–28.17	24.86±2.01	20.69–29.39
FFL	19.02±1.93	16.28–21.75	16.21±1.01	15.22–17.45	17.74±2.10	15.22–21.75	14.77±1.19	12.79–16.64	14.64±0.98	12.90–16.21	14.71±1.08	12.79–16.64
HW	15.94±1.02	14.75–17.13	14.02±0.54	13.33–14.76	15.07±1.28	13.33–17.13	13.54±1.39	11.40–16.99	12.91±1.05	11.29–14.78	13.23±1.26	11.29–16.99
HH	9.63±0.92	8.45–10.80	8.58±0.34	8.10–8.99	9.16±0.88	8.10–10.80	8.18±0.75	7.25–10.27	7.92±0.75	6.89–9.17	8.05±0.75	6.89–10.27
OD	4.09±0.34	3.62–4.54	3.79±0.33	3.36–4.20	3.96±0.35	3.36–4.54	3.68±0.21	3.32–4.19	3.76±0.28	3.35–4.21	3.72±0.25	3.32–4.21
EL	2.70±0.38	2.28–3.31	2.32±0.36	1.88–2.82	2.53±0.40	1.88–3.31	2.44±0.33	1.93–3.19	2.49±0.29	1.78–2.94	2.46±0.31	1.78–3.19
NED	6.75±0.55	6.26–7.74	6.11±0.38	5.70–6.54	6.46±0.57	5.70–7.74	5.51±0.45	4.80–6.45	5.44±0.45	4.39–6.07	5.47±0.45	4.39–6.45
SED	8.43±0.68	7.70–9.53	7.69±0.52	7.23–8.32	8.09±0.69	7.23–9.53	6.74±0.87	5.24–8.93	6.44±0.89	5.06–8.02	6.59±0.88	5.06–8.93
EED	7.47±0.83	6.55–8.68	5.91±0.43	5.36–6.52	6.76±1.04	5.36–8.68	5.23±0.47	4.55–6.20	5.24±0.50	4.35–6.08	5.23±0.48	4.35–6.20
SLS	9.67±1.03	8–11	9.40±1.14	8–11	9.55±1.04	8–11	11.00±0.84	9–12	10.22±0.65	9–12	10.61±0.84	9–12
ILS	7.50±0.55	7–8	7.80±0.84	7–9	7.64±0.67	7–9	9.11±0.58	8–10	8.67±0.69	8–10	8.89±0.67	8–10
Lam	9.67±0.52	9–10	9.67±0.58	9–10	9.67±0.50	9–10	9.11±0.68	8–10	9.35±0.70	8–11	9.23±0.69	8–11
Trow	15.33±1.03	14–16	16.40±1.14	15–18	15.82±1.17	14–18	15.67±1.03	14–17	15.67±1.19	14–18	15.67±1.10	14–18
Tline	22.17±1.33	20–24	23.40±1.34	21–24	22.73±1.42	20–24	20.56±1.85	18–24	21.61±2.33	18–26	21.08±2.14	18–26
Srow	2.17±0.26	2.00–2.50	2.20±0.84	1.00–3.00	2.18±0.56	1.00–3.00	2.56±0.57	2.00–4.00	2.42±0.46	2.00–3.00	2.49±0.51	2.00–4.00
medS	1.25±0.32	0.75–1.50	1.15±0.38	0.75–1.75	1.20±0.33	0.75–1.75	2.10±0.38	1.25–2.75	2.14±0.50	1.50–3.00	2.12±0.44	1.25–3.00

T. substituta (*n*=167): Mean SLV = 51.60±3.64; Range= 46.00–65.50 (Vasconcelos *et al.* submitted);

T. raziana (*n*=8): Mean SLV = 48.20±3.70; Range= 44.00–53.50;

T. caboverdiana (*n*=11): Mean SLV = 56.70±3.70; Range= 51.50–64.50

T. maioensis (*n*=16): Mean SLV = 60.80±3.70; Range= 52.00–71.00

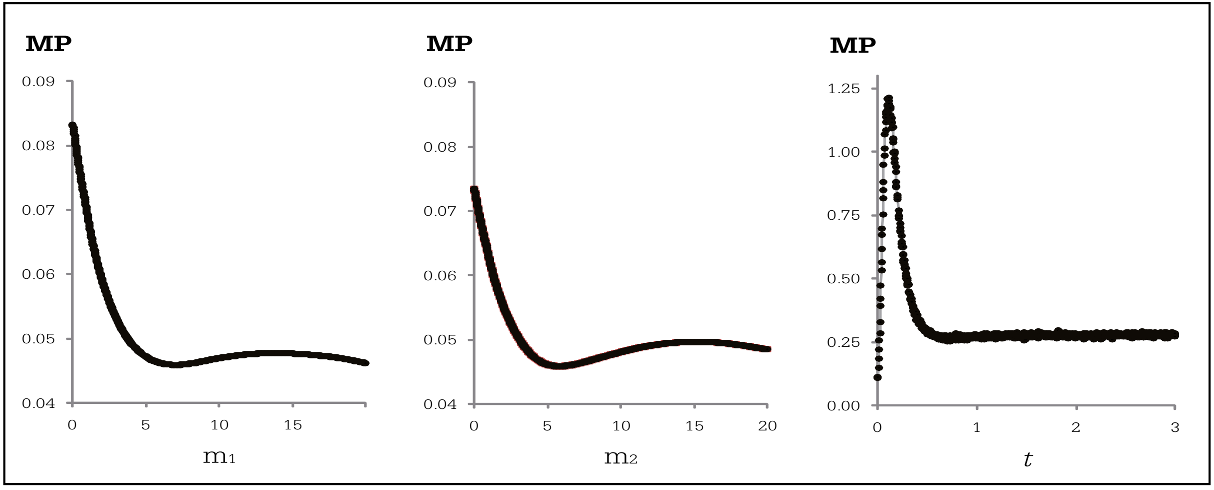
	T. rudis						*T. protogigas*				*T. protogigas*					
	Santiago						**Fogo**				**Brava**					
	Males (*n*=9)		Females (*n*=16)		All (*n*=25)		Males (*n*=1)	Females (*n*=1)	All (*n*=2)		Males (*n*=16)		Females (*n*=11)		All (*n*=27)	
	mean±SD	Range	mean±SD	Range	mean±SD	Range	mean±SD	mean±SD	mean±SD	Range	mean±SD	Range	mean±SD	Range	mean±SD	Range
SVL	71.78±9.49	56.00–83.00	66.91±5.19	60.00–76.00	68.66±7.25	56.00–83.00	83.00	77.00	80.00 ± 4.24	77.00 – 83.00	65.25 ± 6.49	56.00 – 77.00	61.73 ± 4.00	57.00 – 69.00	63.81 ± 5.79	56.00 – 77.00
TrL	30.18±4.65	23.05–36.12	28.64±4.16	21.32–37.70	29.19±4.31	21.32–37.70	28.39	34.84	31.62 ± 4.56	28.39 – 34.84	28.28 ± 3.28	24.64 – 34.77	27.07 ± 4.40	21.34 – 36.57	27.79 ± 3.74	21.34 – 36.57
TW	8.41±1.10	6.47–10.11	7.14±0.96	5.62–08.85	7.60±1.17	5.62–10.11	8.53	7.77	8.15 ± 0.54	7.77 – 8.53	6.70 ± 1.02	4.97 – 8.57	5.66 ± 0.41	5.18 – 6.48	6.28 ± 0.97	4.97 – 8.57
FLL	25.08±3.17	20.11–28.95	24.23±2.46	18.67–29.14	24.54±2.70	18.67–29.14	28.88	29.54	29.21 ± 0.47	28.88 – 29.54	23.92 ± 2.39	20.44 – 28.14	22.90 ± 2.28	20.74 – 26.54	23.51 ± 2.36	20.44 – 28.14
CFL	16.59±2.26	13.12–19.17	16.03±1.82	11.8–19.54	16.23±1.96	11.80–19.54	18.34	18.97	18.66 ± 0.45	18.34 – 18.97	15.31 ± 1.69	12.32 – 17.78	14.47 ± 2.2	10.54 – 17.85	14.97 ± 1.92	10.54 – 17.85
HLL	30.52±4.67	23.15–38.61	28.99±2.34	24.48–32.11	29.54±3.36	23.15–38.61	41.02	33.86	37.44 ± 5.06	33.86 – 41.02	30.13 ± 2.60	26.6 – 35.73	29.17 ± 1.93	26.31 – 32.82	29.74 ± 2.36	26.31 – 35.73
FFL	17.58±2.36	13.63–21.24	16.59±1.46	13.66–18.69	16.94±1.85	13.63–21.24	22.93	20.54	21.74 ± 1.69	20.54 – 22.93	17.37 ± 1.67	14.68 – 19.99	16.95 ± 1.32	15.53 – 18.96	17.20 ± 1.52	14.68 – 19.99
HW	16.35±1.93	12.68–18.84	15.66±1.31	14.04–18.31	15.91±1.56	12.68–18.84	19.66	17.55	18.61 ± 1.49	17.55 – 19.66	14.98 ± 1.44	12.42 – 17.50	13.90 ± 0.90	12.65 – 15.47	14.54 ± 1.34	12.42 – 17.50
HH	10.14±1.47	7.57–12.35	9.43±0.83	7.90–11.23	9.69±1.13	7.57–12.35	12.52	10.46	11.49 ± 1.46	10.46 – 12.52	9.25 ± 0.87	7.45 – 10.51	8.55 ± 0.45	7.89 – 9.2	8.96 ± 0.8	7.45 – 10.51
OD	4.04±0.32	3.55–4.40	3.87±0.29	3.36–4.28	3.93±0.31	3.36–4.40	3.83	4.15	3.99 ± 0.23	3.83 – 4.15	3.68 ± 0.32	3.14 – 4.19	3.7 ± 0.34	3.23 – 4.12	3.69 ± 0.32	3.14 – 4.19
EL	2.20±0.31	1.91–2.80	2.01±0.22	1.65–2.42	2.08±0.27	1.65–2.80	2.97	2.75	2.86 ± 0.16	2.75 – 2.97	2.23 ± 0.29	1.85 – 2.84	2.12 ± 0.28	1.58 – 2.54	2.19 ± 0.29	1.58 – 2.84
NED	7.17±1.09	5.08–8.59	7.03±0.56	6.24–8.04	7.08±0.77	5.08–8.59	9.09	8.55	8.82 ± 0.38	8.55 – 9.09	6.62 ± 0.7	5.57 – 7.84	6.37 ± 0.44	5.75 – 7.27	6.52 ± 0.61	5.57 – 7.84
SED	8.97±1.33	6.17–10.53	8.85±0.72	7.81–9.98	8.89±0.96	6.17–10.53	11.14	10.77	10.96 ± 0.26	10.77 – 11.14	8.25 ± 0.74	6.81 – 9.51	7.99 ± 0.51	7.12 – 8.88	8.15 ± 0.66	6.81 – 9.51
EED	7.22±1.10	5.19–8.44	6.75±0.59	5.90–7.70	6.92±0.82	5.19–8.44	9.32	7.96	8.64 ± 0.96	7.96 – 9.32	6.23 ± 0.66	5.3 – 7.45	5.79 ± 0.7	4.43 – 7.26	6.05 ± 0.7	4.43 – 7.45
SLS	–	–	–	–	–	–	11	10	10.50 ± 0.71	10 – 11	10.06 ± 0.85	9 – 12	9.64 ± 0.92	8 – 11	9.89 ± 0.89	8 – 12
ILS	–	–	–	–	–	–	9	9	9.00 ± 0.00	9	8.19 ± 0.66	7 – 9	7.73 ± 0.65	7 – 9	8 ± 0.68	7 – 9
Lam	–	–	–	–	–	–	11	10	10.50 ± 0.71	10 – 11	11.86 ± 0.86	11 – 13	11.82 ± 0.87	11 – 13	11.84 ± 0.85	11 – 13
Trow	–	–	–	–	–	–	13	12	12.50 ± 0.71	12 – 13	14.38 ± 0.62	13 –15	14.00 ± 0.77	13 –15	14.22 ± 0.70	13 –15
Tline	–	–	–	–	–	–	18	18	18	18	20.06 ± 1.57	15 – 21	20.27 ± 0.65	19 – 21	20.15 ± 1.26	15 – 21
Srow	–	–	–	–	–	–	4	3.5	3.75 ± 0.35	3.50 – 4.00	3.78 ± 0.48	3.00 – 4.50	3.95 ± 0.27	3.50 – 4.50	3.85 ± 0.41	3.00 – 4.50
medS	–	–	–	–	–	–	2.5	2	2.25 ± 0.35	2.00 – 2.50	2.95 ± 0.44	2.25 – 3.75	2.86 ± 0.41	2.25 – 3.75	2.92 ± 0.42	2.00 – 3.75

Appendix IV.3 Descriptive statistics for all the linear measurements and meristic variables of adult specimens of the different *Tarentola* taxa included in the multivariate analysis. For each variable mean± standard deviation (SD), range, and sample size (*n*) is given.

	T. bocagei						***T. fogoensis***						***T. darwini***					
	São Nicolau						**Fogo**						**Santiago**					
	Males (*n*=19)		Females (*n*=14)		All (*n*=33)		Males (*n*=16)		Females (*n*=13)		All (*n*=29)		Males (*n*=15)		Females (*n*=15)		All (*n*=30)	
	mean±SD	Range	mean±SD	Range	mean±SD	Range	mean±SD	Range	mean±SD	Range	mean±SD	Range	mean±SD	Range	mean±SD	Range	mean±SD	Range
SVL	60.00±3.45	54.00–65.50	55.82±3.34	49.00–63.50	58.23±3.95	49.00–65.50	61.84±4.91	54.00–69.50	55.54±5.81	48.50–69.00	59.02±6.13	48.50–69.50	55.77±5.39	45.00–64.00	56.70±2.81	51.00–60.00	56.23±4.25	45.00–64.00
TrL	23.04±1.64	19.40–26.19	21.12±1.31	19.17–24.47	22.22±1.77	19.17–26.19	25.80±2.82	20.98–32.57	23.23±3.45	20.60–31.97	24.65±3.33	20.60–32.57	23.75±3.07	18.40–30.00	24.49±1.56	20.90–26.20	24.12±2.42	18.40–30.00
TW	7.23±0.65	5.86–8.06	6.25±0.70	5.08–7.40	6.82±0.83	5.08–8.06	6.48±1.09	4.80–8.64	5.07±0.83	3.64–6.60	5.85±1.20	3.64–8.64	6.25±1.04	4.30–7.60	5.92±0.65	4.80–7.10	6.09±0.87	4.30–7.60
FLL	20.64±1.37	18.27–24.13	18.89±1.61	15.94–21.09	19.90±1.70	15.94–24.13	22.78±1.69	19.81–26.37	21.03±1.68	19.22–24.66	22.00±1.88	19.22–26.37	19.71±1.83	15.80–23.10	19.42±1.06	18.00–21.30	19.56±1.47	15.80–23.10
CFL	13.06±0.98	11.16–15.06	11.98±1.09	10.08–13.76	12.60±1.15	10.08–15.06	14.55±1.23	12.10–16.36	13.52±1.41	12.05–17.07	14.08±1.39	12.05–17.07	12.86±1.52	10.40–15.00	13.06±1.14	9.90–14.50	12.96±1.32	9.90–15.00
HLL	25.18±1.44	22.52–27.97	23.86±1.70	20.6–26.34	24.62±1.67	20.60–27.97	29.11±1.74	25.40–31.78	26.05±2.28	21.77–31.07	27.74±2.50	21.77–31.78	24.03±2.15	20.50–28.60	24.24±1.59	21.90–26.90	24.13±1.86	20.50–28.60
FFL	14.61±0.95	12.97–16.45	13.81±1.10	12.18–15.58	14.27±1.08	12.18–16.45	16.84±1.15	14.61–18.58	14.86±1.13	12.93–16.60	15.96±1.50	12.93–18.58	13.90±1.69	11.20–16.60	14.12±0.73	13.20–15.40	14.01±1.28	11.20–16.60
HW	13.56±0.78	12.48–15.32	12.45±0.75	11.10–13.85	13.09±0.94	11.10–15.32	13.95±1.20	12.22–15.97	12.49±1.30	10.75–15.70	13.29±1.43	10.75–15.97	12.59±1.52	9.80–14.80	12.71±0.69	11.60–13.80	12.65±1.16	9.80–14.80
HH	8.28±0.48	7.17–9.17	7.43±0.47	6.67–8.19	7.94±0.63	6.67–9.17	8.41±0.70	7.67–10.16	7.44±0.74	6.64–8.87	7.98±0.86	6.64–10.16	7.67±1.04	5.70–9.00	7.76±0.45	7.00–8.50	7.72±0.79	5.70–9.00
OD	3.64±0.21	3.38–4.02	3.67±0.20	3.16–3.85	3.65±0.20	3.16–4.02	3.74±0.23	3.39–4.16	3.46±0.27	3.09–4.12	3.62±0.28	3.09–4.16	3.23±0.28	2.70–3.60	3.32±0.24	2.90–3.70	3.28±0.26	2.70–3.70
EL	2.73±0.26	2.05–3.20	2.68±0.26	2.22–3.20	2.71±0.26	2.05–3.20	2.64±0.30	2.07–3.05	2.33±0.25	1.87–2.70	2.50±0.31	1.87–3.05	2.31±0.32	1.90–2.80	2.20±0.24	1.90–2.70	2.26±0.28	1.90–2.80
NED	5.73±0.48	5.07–6.93	5.22±0.39	4.50–5.68	5.52±0.50	4.50–6.93	6.30±0.44	5.43–7.00	5.81±0.45	5.36–6.69	6.08±0.50	5.36–7.00	5.48±0.55	4.60–6.50	5.61±0.40	4.80–6.40	5.54±0.48	4.60–6.50
SED	6.99±0.71	5.93–8.30	6.41±0.51	5.55–7.80	6.74±0.69	5.55–8.30	7.96±0.57	6.69–8.67	7.23±0.50	6.60–8.01	7.63±0.65	6.60–8.67	6.99±0.67	6.00–8.20	7.10±0.47	6.40–8.10	7.04±0.57	6.00–8.20
EED	5.43±0.40	4.62–6.01	4.96±0.39	4.17–5.45	5.23±0.46	4.17–6.01	5.91±0.66	4.92–7.24	5.21±0.61	4.34–6.52	5.60±0.72	4.34–7.24	5.37±0.64	4.20–6.60	5.44±0.45	4.80–6.10	5.41±0.54	4.20–6.60
SLS	11.05±0.85	10–13	10.93±0.83	10–12	11.00±0.83	10–13	10.73±0.80	10–12	11.08±0.79	10–12	10.89±0.80	10–12	10.29±0.73	9–12	9.93±0.88	9–12	10.1±0.82	9–12
ILS	9.11±0.74	8–10	8.43±0.51	8–9	8.82±0.73	8–10	8.75±0.58	8–10	9.15±0.80	8–11	8.93±0.70	8–11	8.43±0.51	8–9	8.33±0.62	7–9	8.38±0.56	7–9
Lam	9.32±0.75	8–10	9.57±0.65	8–10	9.42±0.71	8–10	10.07±0.46	9–11	10.27±0.79	9–11	10.15±0.61	9–11	9.73±0.9	8–11	9.64±0.81	8–11	9.68±0.84	8–11
Trow	16.11±1.20	14–18	15.57±1.22	14–18	15.88±1.22	14–18	15.50±1.37	14–18	15.08±0.76	14–17	15.31±1.14	14–18	16.27±0.88	15–18	15.67±1.45	13–18	15.97±1.22	13–18
Tline	20.74±1.91	17–24	20.21±1.31	18–22	20.52±1.68	17–24	22.94±1.95	20–27	22.62±2.36	20–27	22.79±2.11	20–27	23.2±2.18	21–27	22±2.65	17–26	22.6±2.46	17–27
Srow	2.39±0.49	1.50–3.00	2.71±0.43	2.00–3.00	2.53±0.48	1.50–3.00	2.56±0.36	2.00–3.00	2.38±0.51	1.50–3.00	2.48±0.43	1.50–3.00	2.37±0.55	1.5–3.5	2.17±0.24	2–2.5	2.27±0.43	1.5–3.5
medS	2.00±0.24	1.50–2.50	2.13±0.42	1.25–2.75	2.05±0.33	1.25–2.75	1.59±0.40	1.00–2.50	1.69±0.47	1.00–2.50	1.64±0.43	1.00–2.50	1.53±0.3	1.0–2.0	1.58±0.42	1.0–2.5	1.56±0.36	1.0–2.5

Appendix IV.4 Networks corresponding to cytochrome *b* sequence variation in endemic Cape Verde *Tarentola* geckos (modified from Vasconcelos *et al.* 2010). Lines represent a mutational step, dots missing haplotypes and circles haplotypes. The circle area is proportional to the number of individuals. Dotted circles represent probable ancestral haplotypes. For correspondences of sample and location codes, see Vasconcelos *et al.* (2010).

Appendix IV.5 Marginal probabilities of migration rates (m1 and m2) and time of divergence (*t*) between *T. bocagei* and *T. nicolauensis*, present in S. Nicolau Islands, obtained by fitting the IM model to the three-locus (PDC, ACM4, MC1R) dataset.



Appendix IV.6 Estimates of genetic differentiation of the PDC, ACM4 and MC1R between ESUs using *Snn* test values. All results are based on 1000 permutation tests of 148, 146 and 136 sequences (homozygotes duplicated), respectively. Analyses were conducted in DNAsp. All positions containing missing data were eliminated from the dataset. There were a total of 392, 431 and 668 positions in each final dataset, respectively. (n.s., not significant; * *P* <0.05; ** *P* <0.01; * *P* <0.001).**

				PDC		**ACM4**		**MC1R**	
Taxa 1	**ESU 1**	**Taxa 2**	**ESU 2**	*Snn*	*P*-value	*Snn*	*P*-value	Snn	*P*-value
Tv	A1	*Tb*	A2	0.9375	0.0000 ***	0.9306	0.0000 ***	1.00000	0.0000 ***
Tv	A1	*Tf*	A3	0.9412	0.0000 ***	0.9524	0.0000 ***	1.00000	0.0000 ***
Tv	A1	*Td*	A4	0.6957	0.0000 ***	0.9635	0.0000 ***	1.00000	0.0000 ***
Tv	A1	*Ts*	B1	1.0000	0.0000 ***	0.9167	0.0010 **	1.00000	0.0000 ***
Tv	A1	*Tz*	B2	0.6683	0.0470 *	0.9167	0.0000 ***	1.00000	0.0000 ***
Tv	A1	*Tc*	B3	0.9643	0.0000 ***	0.9286	0.0000 ***	1.00000	0.0000 ***
Tv	A1	*Tn*	C	0.6487	0.0790 ns	0.9167	0.0000 ***	1.00000	0.0000 ***
Tv	A1	*Tgg*	D1	0.6487	0.2390 ns	0.9231	0.0000 ***	1.00000	0.0000 ***
Tv	A1	*Tr*	D2	0.5573	0.0630 ns	0.9333	0.0000 ***	1.00000	0.0000 ***
Tv	A1	*Tpp*	D3	1.0000	0.0000 ***	0.9167	0.0010 **	1.00000	0.0000 ***
Tv	A1	*Tph*	D4	0.9286	0.0000 ***	0.9286	0.0000 ***	1.00000	0.0000 ***
Tv	A1	*Tm*	D6	-	ns	0.9167	0.0010 **	1.00000	0.0000 ***
Tb	A2	*Tf*	A3	0.9412	0.0000 ***	0.6334	0.0070 **	0.93750	0.0000 ***
Tb	A2	*Td*	A4	0.9600	0.0000 ***	0.7082	0.0090 **	0.99605	0.0000 ***
Tb	A2	*Ts*	B1	0.9833	0.0000 ***	0.5947	0.5860 ns	1.00000	0.0000 ***
Tb	A2	*Tz*	B2	0.8667	0.0000 ***	0.6055	0.1410 ns	1.00000	0.0000 ***
Tb	A2	*Tc*	B3	0.9306	0.0000 ***	0.5233	0.5240 ns	1.00000	0.0000 ***
Tb	A2	*Tn*	C	0.7778	0.0030 **	0.5527	0.4360 ns	0.57792	0.4860 ns
Tb	A2	*Tgg*	D1	0.8796	0.0020 **	0.6397	0.1200 ns	0.57792	0.3950 ns
Tb	A2	*Tr*	D2	0.8990	0.0000 ***	0.5217	0.3480 ns	1.00000	0.0000 ***
Tb	A2	*Tpp*	D3	1.0000	0.0000 ***	0.5947	0.5730 ns	0.57792	0.5230 ns
Tb	A2	*Tph*	D4	0.9000	0.0000 ***	0.5233	0.5110 ns	0.47778	0.6940 ns
Tb	A2	*Tm*	D6	0.8750	0.0120 *	0.5947	0.5750 ns	1.00000	0.0000 ***
Tf	A3	*Td*	A4	0.7692	0.0000 ***	0.6590	0.0000 ***	1.00000	0.0000 ***
Tf	A3	*Ts*	B1	1.0000	0.0000 ***	0.7409	0.3660 ns	1.00000	0.0000 ***
Tf	A3	*Tz*	B2	0.7179	0.0110 *	0.7322	0.0160 *	1.00000	0.0000 ***
Tf	A3	*Tc*	B3	0.9667	0.0000 ***	0.6290	0.0860 ns	1.00000	0.0000 ***
Tf	A3	*Tn*	C	0.7069	0.0330 *	0.6871	0.0740 ns	1.00000	0.0000 ***
Tf	A3	*Tgg*	D1	0.7069	0.0240 *	0.7594	0.0120 *	1.00000	0.0000 ***
Tf	A3	*Tr*	D2	0.6467	0.0020 **	0.6000	0.1550 ns	1.00000	0.0000 ***
Tf	A3	*Tpp*	D3	1.0000	0.0000 ***	0.7409	0.3400 ns	1.00000	0.0000 ***
Tf	A3	*Tph*	D4	0.9333	0.0000 ***	0.6290	0.0680 ns	1.00000	0.0000 ***
Tf	A3	*Tm*	D6	0.7539	0.1230 ns	0.7409	0.3600 ns	1.00000	0.0000 ***
Td	A4	*Ts*	B1	1.0000	0.0000 ***	0.8194	0.4090 ns	1.00000	0.0000 ***
Td	A4	*Tz*	B2	0.8126	0.0010 **	0.8084	0.0300 *	1.00000	0.0000 ***
Td	A4	*Tc*	B3	0.9783	0.0000 ***	0.7154	0.1010 ns	1.00000	0.0000 ***
Td	A4	*Tn*	C	0.8035	0.0030 **	0.7734	0.1360 ns	1.00000	0.0000 ***
Td	A4	*Tgg*	D1	0.8035	0.0030 **	0.8280	0.0100 *	1.00000	0.0000 ***
Td	A4	*Tr*	D2	0.7456	0.0010 **	0.6809	0.1200 ns	1.00000	0.0000 ***
Td	A4	*Tpp*	D3	1.0000	0.0000 ***	0.8194	0.3700 ns	1.00000	0.0000 ***
Td	A4	*Tph*	D4	0.9565	0.0000 ***	0.7154	0.1170 ns	1.00000	0.0000 ***
Td	A4	*Tm*	D6	0.8413	0.0290 *	0.8194	0.3680 ns	1.00000	0.0000 ***

				PDC		**ACM4**		**MC1R**	
Taxa 1	**ESU 1**	**Taxa 2**	**ESU 2**	*Snn*	*P*-value	*Snn*	*P*-value	Snn	*P*-value
Ts	B1	*Tz*	B2	1.0000	0.0040 **	0.4984	0.3720 ns	1.00000	0.0000 ***
Ts	B1	*Tc*	B3	0.5887	0.1840 ns	-	ns	0.97893	0.0000 ***
Tz	B2	*Tc*	B3	0.9286	0.0000 ***	0.5405	0.1680 ns	0.99864	0.0000 ***
Ts	B1	*Tn*	C	1.0000	0.0050 **	0.4556	1.0000 ns	1.00000	0.0000 ***
Tz	B2	*Tn*	C	0.4537	1.0000 ns	0.5046	0.4410 ns	1.00000	0.0000 ***
Tc	B3	*Tn*	C	0.9286	0.0000 ***	0.4799	0.3970 ns	0.90346	0.0020 **
Ts	B1	*Tgg*	D1	1.0000	0.0050 **	0.5429	0.4270 ns	1.00000	0.0240 *
Ts	B1	*Tr*	D2	1.0000	0.0010 **	-	ns	1.00000	0.0010 **
Ts	B1	*Tpp*	D3	1.0000	0.0330 *	-	ns	1.00000	0.0220 *
Ts	B1	*Tph*	D4	0.9167	0.0010 **	-	ns	1.00000	0.0000 ***
Ts	B1	*Tm*	D6	1.0000	0.0230 *	-	ns	1.00000	0.0210 *
Tz	B2	*Tgg*	D1	0.4537	1.0000 ns	0.5820	0.2360 ns	1.00000	0.0270 *
Tz	B2	*Tr*	D2	0.5114	0.4510 ns	0.5737	0.1390 ns	1.00000	0.0000 ***
Tz	B2	*Tpp*	D3	1.0000	0.0040 **	0.4984	0.3770 ns	1.00000	0.0310 *
Tz	B2	*Tph*	D4	0.8286	0.0000 ***	0.5405	0.1730 ns	1.00000	0.0020 **
Tz	B2	*Tm*	D6	0.4429	1.0000 ns	0.4984	0.3510 ns	1.00000	0.0250 *
Tc	B3	*Tgg*	D1	0.9286	0.0010 **	0.5844	0.1640 ns	1.00000	0.0270 *
Tc	B3	*Tr*	D2	0.9383	0.0010 **	-	ns	1.00000	0.0020 **
Tc	B3	*Tpp*	D3	0.8333	0.0260 *	-	ns	1.00000	0.0370 *
Tc	B3	*Tph*	D4	0.8125	0.0000 ***	-	ns	1.00000	0.0020 **
Tc	B3	*Tm*	D6	0.9167	0.0110 *	-	ns	1.00000	0.0330 *
Tn	C	*Tgg*	D1	0.4537	1.0000 ns	0.5463	0.4680 ns	0.42500	1.0000 ns
Tn	C	*Tr*	D2	0.4968	0.8070 ns	0.5119	0.3720 ns	1.00000	0.0000 ***
Tn	C	*Tpp*	D3	1.0000	0.0070 **	0.4556	1.0000 ns	0.42500	1.0000 ns
Tn	C	*Tph*	D4	0.8452	0.0040 **	0.4799	0.4360 ns	0.52780	0.6000 ns
Tn	C	*Tm*	D6	0.4556	1.0000 ns	0.4556	1.0000 ns	1.00000	0.0300 *
Tgg	D1	*Tr*	D2	0.4968	0.7740 ns	0.6154	0.0420 *	1.00000	0.0000 ***
Tgg	D1	*Tpp*	D3	1.0000	0.0060 **	0.5429	0.4910 ns	0.42500	1.0000 ns
Tgg	D1	*Tph*	D4	0.8452	0.0080 **	0.5844	0.1440 ns	0.52780	0.5740 ns
Tgg	D1	*Tm*	D6	0.4556	1.0000 ns	0.5429	0.4310 ns	1.00000	0.0270 *
Tr	D2	*Tpp*	D3	0.9762	0.0010 **	-	ns	1.00000	0.0000 ***
Tr	D2	*Tph*	D4	0.8549	0.0010 **	-	ns	1.00000	0.0000 ***
Tr	D2	*Tm*	D6	0.5368	1.0000 ns	-	ns	0.57792	0.5400 ns
Tpp	D3	*Tph*	D4	0.5030	1.0000 ns	-	ns	0.44440	1.0000 ns
Tpp	D3	*Tm*	D6	1.0000	0.0260 *	-	ns	1.00000	0.0310 *
Tph	D4	*Tm*	D6	0.8333	0.0090 **	-	ns	1.00000	0.0010 **

Tv, T. boavistensis; *Tb, T. bocagei*; *Tf, T. fogoensis*; *Td, T. darwini*; *Ts, T. substituta*; *Tz, T. raziana*; *Tc, T. caboverdiana*; *Tn, T. nicolauensis*; *Tg, T. gigas*; *Tr, T. rudis*; *Tpp, T. protogigas protogigas*; *Tph, T. protogigas hartogi*; *Tm, T. maioensis.*

ARTICLE V

An integrative taxonomic revision of the Cape Verdean skinks (Squamata, Scincidae)

A. Miralles[1,*]; R. Vasconcelos [2,3,4],*; A. Perera[2]; D. J. Harris[2,3] & S. Carranza[4]

* These authors contributed equally to this work

[1] Department of Evolutionary Biology, Zoological Institute, Technical University of Braunschweig,
Spielmannstrasse 8, 38106 Braunschweig, Germany.

[2] CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, Campus Agrário de Vairão,
R. Padre Armando Quintas, 4485-661 Vairão, Portugal.

[3] Departamento de Biologia, Faculdade de Ciências da Universidade do Porto,
Rua Campo Alegre s/n, 4169-007 Porto, Portugal.

[4] Institute of Evolutionary Biology (CSIC-UPF),
Passeig Marítim de la Barceloneta, 37-49, E-08003 Barcelona, Spain.

ABSTRACT

A comprehensive taxonomic revision of the Cape Verdean skinks is proposed based on an integrative approach combining (i) a phylogenetic study pooling all the previously published molecular data, (ii) new population genetic analyses using mitochondrial and nuclear data resulting from additional sampling, together with (iii) a morphological study based on an extensive examination of the scalation and colour patterns of 516 live and museum specimens, including most of the types. All Cape Verdean species of skinks presently recognised, formerly regarded as members of the genera *Mabuya* Fitzinger, 1826 and *Macroscincus* Bocage, 1873 are considered as members of the Cape Verdean endemic genus *Chioninia* Gray, 1845. The new phylogeny and networks obtained are congruent with the previously published phylogenetic studies, although suggesting older colonization events (between 11.6 and 0.8 My old), and indicate the need for taxonomic changes. Intraspecific diversity has been analysed and points to a very recent expansion of *Chioninia delalandii* on the southern islands and its introduction on Maio, to a close connection between *Chioninia stangeri* island populations due to Pleistocene sea-level falls and to a generally low haplotypic diversity due to the ecological and geological characteristics of the archipelago. Three new consistent morphological synapomorphies supporting two of the four main clades of the genus have been identified. The complex taxonomic status of *Euprepes fogoensis* O'Shaughnessy, 1874 has been resolved and a lectotype has been designated for this species; *Chioninia fogoensis nicolauensis* (Schleich, 1987) is elevated to species rank, whereas *Chioninia fogoensis antaoensis* (Schleich, 1987) is now regarded as a junior subjective synonym of *C. fogoensis*. Additionally, one new subspecies of *Chioninia vaillanti* and two of *Chioninia spinalis* are described (*Chioninia vaillanti xanthotis* ssp. n., *Chioninia spinalis santiagoensis* ssp. n. *and Chioninia spinalis boavistensis* ssp. *n.*) and a lectotype has been designated for *Mabuia spinalis* Boulenger, 1906. Finally, an identification key for the *Chioninia* species is presented.

INTRODUCTION

Definition of species concepts is one of the most intensively debated subjects in evolutionary biology, but the issue of empirically testing species boundaries has been given little attention (Sites & Marshall 2003; De Queiroz 2007). The issue of species delimitation has long been confused with that of species conceptualization, leading to a half century of controversy concerning both the definition of the species category and methods for inferring the boundaries and numbers of species (Mayr 1970; Mayden 1997; Mishler & Theriot 2000; De Queiroz 2007). The practical issue of delimiting species boundaries is nevertheless of central importance to evolutionary biology, as it defines the limits within or across which evolutionary processes operate. Recently, intellectual progress in this field has been achieved in two ways: firstly, through the General Lineage Species Concept it is now widely understood that almost all species concepts agree in defining that species are population-level evolutionary lineages, and that refer to diagnostic characters of these lineages that become recognizable in a variable order and after different intervals of time; secondly, there is a vivid and fruitful discussion about the novel concept of integrative taxonomy (*sensu* Dayrat 2005). This concept rejects the superiority of any particular set of characters (morphological, behavioural, molecular, etc.) over others during the process of recognizing and diagnosing species, and advocates the combined and integrated use of various such methods. However, the development of this concept is ongoing, so there is still no clear and consensual definition of what 'integrative taxonomy' is (see Padial *et al.* 2010). Among the proposed work protocols there are those that seek for congruence among datasets as a main criterion for delimiting species boundaries (Cardoso *et al.* 2009) and those that argue that differences in a single marker are sufficient (Padial *et al.* 2009). Regrettably, papers dealing with integrative taxonomy have been until now theoretical, none of them having yet applied such protocols to achieve concrete taxonomic revisions. Therefore, in this article, a pragmatic, standardized and repeatable protocol of species boundaries delimitation has been defined, which integrates the results of phylogenetic, population genetic analyses, and morphological studies, putting it into practice to propose a comprehensive taxonomic revision of the Cape Verdean skinks of the genus *Chioninia*.

For a long time, the genus *Mabuya* Fitzinger, 1826 was regarded as a very large pantropical group of lizards, including more than 110 species occurring in tropical areas of Africa, Asia and the New World (Greer & Broadley 2000). Then, during the last decade, several phylogenetic analyses (Mausfeld *et al.* 2002; Carranza & Arnold 2003) identified distinct geographic monophyletic lineages supporting its breakup into four genera. As a consequence, *Mabuya sensu stricto* is now a term restricted to the Neotropics, whereas *Eutropis* Fitzinger, 1843 is applied to the Asian clade, *Trachylepis* Fitzinger, 1843 (see Bauer 2003) to the Afromalagasy clade [including *Trachylepis atlantica*, from Fernando de Noronha and the enigmatic *Trachylepis tschudii*, described from the Peruvian Amazonia (see Miralles *et al.* 2009)] and *Chioninia* Gray, 1845 exclusive to the Cape Verdean clade (Mausfeld *et al.* 2002; although see Jesus *et al.* 2005 and Whiting *et al.* 2006).

The Cape Verde Islands constitute one of the four oceanic archipelagos of the Macaronesian biogeographical region, situated approximately 500 km off the Senegal coast. It is a volcanic archipelago with 10 islands and various islets, ranging from 26 to 6 My old (Fig. V.1). Before this study, 13 extant native reptile species were recognised (see Joger 1993; Arnold *et al.* 2008), all endemic to the archipelago. These belong to three genera: the *Hemidactylus* and *Tarentola* geckos and the *Chioninia* skinks. Within the latter, six extant species were recognised by Joger (1993): *Chioninia delalandii* (Duméril & Bibron, 1839), *Chioninia vaillanti* (Boulenger, 1887), *Chioninia. fogoensis* (O'Shaughnessy, 1874), *Chioninia geisthardti* (Joger, 1993), *Chioninia stangeri* (Gray, 1845), *Chioninia spinalis* (Boulenger, 1906) and the extinct *Chioninia coctei* (Duméril & Bibron, 1839). Although the phylogenetic relationships within *Chioninia* have been investigated previously (Brehm *et al.* 2001; Brown *et al.* 2001; Carranza *et al.* 2001), all these studies stressed that a review of the systematics of the Cape Verdean skinks was needed. For instance, '*Mabuya*' *spinalis* formed a complex assemblage of distinct lineages, and '*Mabuya*' *fogoensis* was paraphyletic. Therefore the last revisions published (Mertens 1955; Schleich 1987) are now largely obsolete. Given the new data about the phylogenetic relationships of the group, its evolutionary history needs to be recounted. Also, as effective conservation

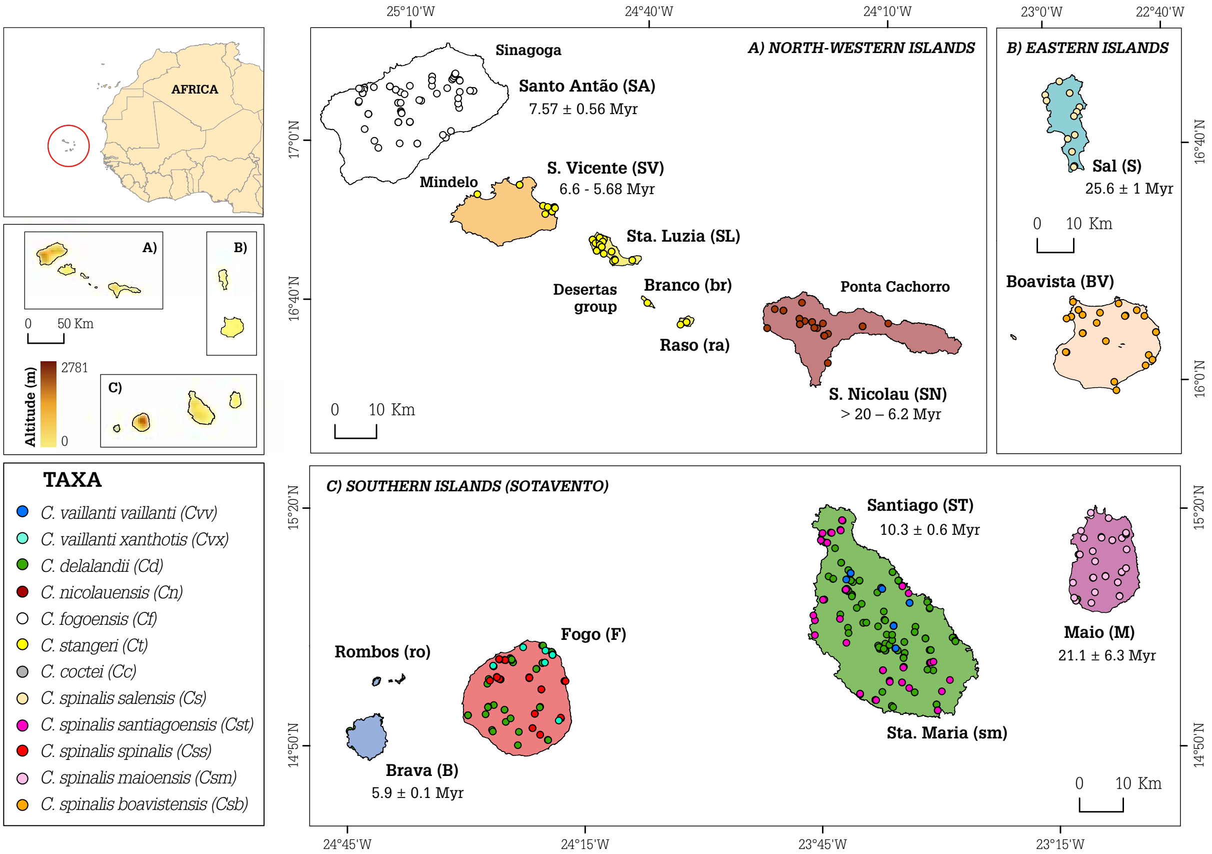


Figure V.1 Map of the Cape Verde Islands showing the geographic location (latitude and longitude in decimal degrees) and altitudes of the archipelago islands and the origins of the new *Chioninia* samples included in the molecular analyses (Geographic Coordinate System, Datum WGS 84). Island colours match the colours used on the network analyses. The dashed line divides the *C. spinalis* southern and northern haplotypes in Santiago.

measures depend largely on a good knowledge of the taxonomy and phylogeny of the species (Mace 2004), this study is essential for the assessments and future management of the *Chioninia* skinks.

In this work, a comprehensive review of the Cape Verdean skinks is proposed based on an integrative taxonomic approach, combining (i) a new phylogenetic study pooling all the molecular data previously published for this genus to estimate divergence times and island colonization patterns; (ii) new population genetic analyses using mitochondrial (cyt *b*, cytochrome *b*) and nuclear data (RAG2, recombination activating gene), resulting from broad sampling to examine intraspecific diversity; (iii) an extensive examination of the morphology and colour patterns of live animals and specimens housed at museums (including most of the types) to reassess the systematics of the group.

MATERIALS AND METHODS

Origin of tissue samples and specimens

A total of 236 new samples of *Chioninia* were collected from the 10 islands of the Cape Verde archipelago (DGA License nr. 07/2008), prospected between 2006 and 2008, during mid-May to mid-July. Animals were identified in the field using diagnosable characters published by Schleich (1987), photographed, and a piece of tail was removed and stored in 96% ethanol. Sampled animals were released immediately afterwards. Identification codes, localities and GenBank accession numbers of the new samples used are listed in Appendix V.1.

The 272 voucher specimens examined for the morphological study (Appendix V.2; and Fig. V.2) are deposited at the British Natural History Museum, London (BMNH), the Museu de Ciències Naturals de Barcelona (MZB) and the Museum National d'Histoire Naturelle, Paris (MNHN). Additionally, several individuals photographed in the field were also studied, to enhance the data-set of morphological characters available, and to analyse qualitatively the colour pattern characteristics that may disappear in preserved specimens. Some of their photos were deposited on MorphoBank (http://www.morphobank.org/). Additional acronyms mentioned in the manuscript refer to the Hessisches Landesmuseum Wiesbaden (HLMW), Finnish Museum of Natural History, Helsinki (FMNHH), Museo Civico di Storia Naturale di Genova (MSNG), University of Madeira (UMa), National Museum of Natural History, Smithsonian Institution, Washington (USNM), Museum für Naturkunde der Humboldt-Universität zu Berlin (ZMB), Zoologische Staatssammlung München (ZSM).

Molecular studies

Phylogenetic trees were inferred using sequences from GenBank only. The new samples together with some available sequences from GenBank were used to infer phylogenetic networks and to carry out population genetics analyses.

Phylogenetic analysis

All the mitochondrial DNA (mtDNA) sequences from cyt *b*, cytochrome oxidase I (COI) and 12S rRNA of *Chioninia* published by Brehm *et al.* (2001), Brown *et al.* (2001), Carranza *et al.* (2001) and Mausfeld *et al.* (2002) were downloaded from GenBank and incorporated in this study. This final data set included 125 individual skinks. Of these, 122 were members of the endemic Cape Verdean genus *Chioninia* from 12 different taxa and three specimens were used as outgroups – two representatives of the genus *Trachylepis* and one *Plestiodon egregius* (Appendix V.3).

DNA sequences were aligned using ClustalX (Thompson *et al.* 1997) with default parameters. The two coding genes (cyt *b* and COI) did not present gaps or stop codons and although some gaps were postulated to resolve length differences in the 12S rRNA fragment, all positions could be unambiguously aligned and were therefore included in the analyses.

Two methods of phylogenetic analysis, namely maximum likelihood (ML) and Bayesian inference (BI), were employed for each one of the three mitochondrial regions (cyt *b*, COI and 12S rRNA) and for the combined data set, respectively, and their results compared. ModelTest v.0.1.1 (Posada 2008) was used to select the most appropriate model of sequence evolution for the ML and BI of the independent partitions and the combined data sets, under the Akaike Information Criterion. The models selected were: GTR+G for cyt *b* and COI partitions and for the combined data set and HKY+G for the 12S rRNA partition. BI were performed with MrBayes v.3.0b4 (Huelsenbeck & Ronquist 2001) using the selected model for each partition. The analyses were run for $2x10^6$ generations, with sampling intervals of 100 generations, to produce 20,000 trees. After verifying that stationarity had been reached, the first 4000 trees in the cyt *b*+COI+12S data set were discarded and independent majority rule consensus trees were generated from the remaining (post-'burn-in') trees. ML analyses were performed with phyml (Guindon & Gascuel 2003), with model parameters fitted to the data by likelihood maximization. The reliability of the ML trees was assessed by bootstrap analysis (Felstenstein 1985), with 1000 replications.

Any topological incongruence between partitions was tested using the incongruence length difference (ILD) test (Michkevich & Farris 1981; Farris *et al.* 1994), with 10 000 heuristic searches performed after removing all invariable characters (Cunningham 1997). A reciprocal 70% bootstrap proportion (Mason-Gamer & Kellogg 1996)

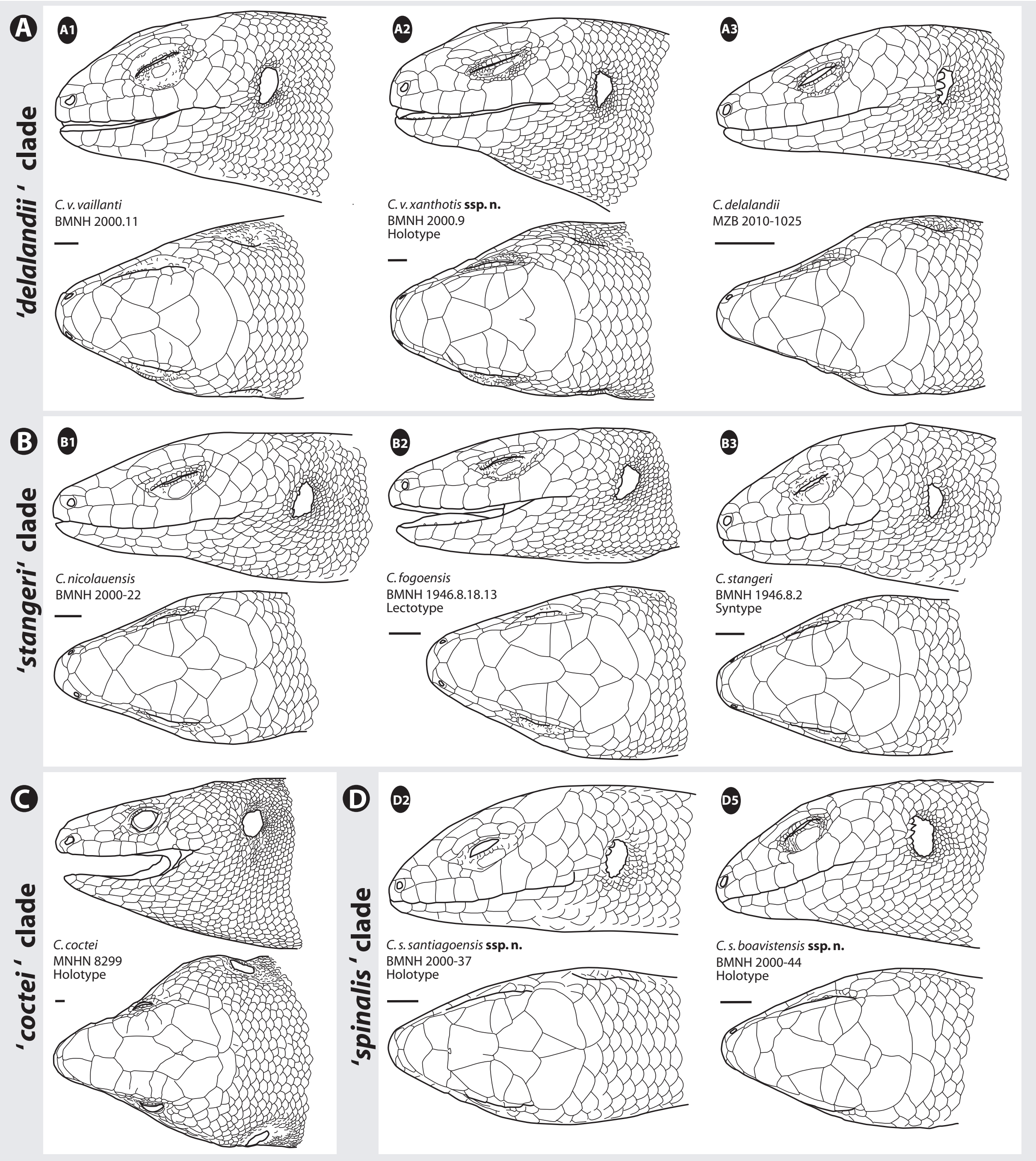


Figure V.2 Drawings of the lateral and dorsal view of the head for all *Chioninia* species, including the holotype of the new subspecies presently described. Scale bar = 2 mm. Head lateral views in A1-3, C and D5 have been symetrically reversed, and thus represent the right side.

or a 95% posterior probability threshold was also used to test for incongruence between data sets. Topological constraints to test alternative topologies were constructed using MacClade v.4.0 (Maddison & Maddison 2000) and compared to optimal topologies using the approximately unbiased test (Shimodaira 2002) implemented in consel (Shimodaira & Hasegawa 2001).

Estimation of divergence times

Unfortunately, there are no internal calibration points available for the genus *Chioninia* or for *Mabuya*, *Eutropis*, or *Trachylepis*. As a result, and in order to have an idea of the approximate time of the different cladogenetic events of our phylogeny, we had to apply the substitution rates calculated for other lizard groups. As calibrations of the substitution rates for other taxa were only available for the cyt *b*+12S rRNA, a phylogenetic tree of *Chioninia* was inferred for calibration purposes including only these two genes (1415 bp). The topology of this tree was identical to the tree inferred using all three genes and only varied in the support values of some clades. The substitution rates per lineage for the combination of these two mitochondrial genes ranged from 1.15% per lineage per My in the *Hemidactylus* geckos (Arnold *et al.* 2008) to 1.35% per lineage per My in the lacertid lizards of the tribe Lacertini (Carranza *et al.* 2004; Arnold *et al.* 2007) and the *Chalcides*, *Scincus*, and *Plestiodon* skinks (Carranza *et al.* 2008).

Those evolutionary rates were applied to a linearized tree using the nonparametric rate smoothing (NPRS) algorithm implemented in r8s v1.6.4 (Sanderson 1997, 2002) with the ML tree estimated from the concatenated data set (cyt *b*+12S) and the GTR+G model of sequence evolution calculated in jModelTest (reference tree), assigning an arbitrary value of 1 to the root node. This transformed the reference tree into a linearized tree with arbitrary scale. To re-establish the genetic distance scale, we calculated the K scaling factor that approximates the linearized tree to the reference tree as much as possible, using the method developed by Soria-Carrasco *et al.* (2007) and implemented in the computer program Ktreedist (available at http://molevol.cmima.csic.es/castresana/Ktreedist.html). In our case, K=0.25296. Upon scaling the NPRS tree with an arbitrary scale with this factor, we obtained a linearized tree with the most appropriate genetic distance scale (NPRS tree with genetic distance scale). The calculated evolutionary rates for other lizard groups (1.15% and 1.35% per My) were applied to the NPRS tree with genetic distance scale using TreeEdit v 1.0 (available at: http://tree.bio.ed.ac.uk/software/treeedit).

Network and population analyses

Total genomic DNA was extracted from small pieces of tail of 236 specimens (see Appendix V.1) using standard methods. Polymerase Chain Reaction primers used in amplification and sequencing were cyt *b*1 and cyt *b*2 (modified from Kocher *et al.* 1989; Palumbi 1996) for the mtDNA cyt *b* fragment and 31 FN venk and Lung 460R (Chiari *et al.* 2004) combined with RAG2 Lung 35F and RAG2 Lung 320R (Hoegg *et al.* 2004) for the nuclear DNA (nDNA) RAG2. Thermocycling for cyt *b* was performed using standard conditions described by Carranza *et al.* (1999) and for RAG2 following Chiari *et al.* (2004). Amplified mitochondrial fragments were sequenced from both strands on a 3100 Applied Biosystems DNA Sequencing Apparatus, Foster City, CA, USA.

Uncorrected genetic distances (*p*-dist) between specimens used for the network analyses were calculated with Mega4 (Tamura *et al.* 2007).

Network analyses. The application of DNA to taxonomy is complicated when the total variation within the lineages of interest is unknown (Monaghan *et al.* 2009). Therefore, after all major lineages had been identified through the phylogenetic analysis, the genealogical relationships among and within lineages were assessed with haplotype networks constructed using statistical parsimony (Templeton *et al.* 1992), as implemented in the program TCS v1.21 (Clement *et al.* 2000) with a connection limit of 95%. For these analyses, two independent markers were used: a mtDNA fragment of the cyt *b* gene (307 bp) from 354 samples (236 new samples, plus 118 from GenBank) and a nDNA fragment of RAG2 (834 bp) from 51 new samples. PHASE v2.1.1 (Stephens & Donnelly 2003), a software package for haplotype reconstruction, was used to estimate haplotype pairs from RAG2 genotyped data. The localities and GenBank accession codes of the new samples are given in Appendix V.1.

Population analyses. Genetic differentiation between island populations belonging to the same network was calculated through the *Snn* statistics (Hudson 2000) using the DnaSP v.5 program (Librado & Rozas 2009), as well as various population genetics parameters and statistical tests. Independent networks and those island populations which were part of a network but presented significant *Snn* values were considered distinct Evolutionarily Significant Units (ESUs), following Fraser & Bernatchez (2001). Parameters such as haplotype (*Hd*) and nucleotide diversity (π), number of haplotypes (*h*) and segregation sites (*S*) were calculated for each diagnosable ESU.

To test for the hypothesis of a rapid demographic expansion and to estimate the time since its occurrence, a series of analyses were carried out. Firstly, to test for deviations from the neutral Wright-Fisher model consistent with a population expansion under a neutrality hypothesis, Fu's F_s statistic (Fu 1997) was calculated using coalescent simulations (based on the segregating sites and assuming no recombination, with 10,000 replicates and 0.95 as a confidence interval) with DnaSP v.5 (Librado & Rozas 2009). Secondly, to characterize expansion, Arlequin version 3.1 (Excoffier *et al*. 2005) was used to determine the historical demography of the populations using mismatch distributions with the models of Rogers & Harpending (1992) and Rogers (1995).

Morphological studies

The meristic, mensural and qualitative characters examined here, such as scale counts, presence or absence of homologous scale fusions and variability in colour patterns, are routinely used in taxonomic studies of Scincidae. Scale nomenclature, scale counts, and measurements used in the morphological analyses followed Ávila-Pires (1995), including the additional characters proposed by Greer & Broadley (2000), Greer & Nussbaum (2000), Miralles (2006) and this study (see Appendix V.4) for the taxonomic study of the genus *Mabuya sensu lato*. Measurements of specimens were recorded to the nearest 0.5 mm with dial callipers. Animals were not sexed since it was needed to open some of them for that purpose and permission from museums for that was sometimes denied.

Integrative approach

The phylogenetic tree inferred has been used as a preliminary framework to investigate the taxonomy of the genus *Chioninia*. Three lines of evidence have been defined on the basis of the alledged independence of their respective data sets (mtDNA, nDNA and morphology) to decide the taxonomic status of each ESU (see Fig. V.3). Each of these lines represents equivalent, independent and combinable indicators able to detect splits between different species: (i) mtDNA: presence of independent cyt *b* parsimony networks with a connection limit of 95% (see Hart & Sunday 2007); (ii) nDNA: absence of shared haplotypes in RAG2 (see Monaghan *et al*. 2009); and (iii) morphology: detection of at least one fixed diagnostic character state (e.g. presence or absence for qualitative characters, non-overlapping values for meristic or mensural characters) might be strong evidence of reduced or absence of gene flow (Wiens & Servedio 2000).

Different possible integration approaches are presented in Fig. V.3, ranging from the most conservative to the most inflationist. The integration by total congruence (ITC) was achieved by retaining only the candidate species that are supported by all the three lines of evidence, whereas the integration by cumulation (IC) was performed considering that one line of evidence was sufficient for splitting taxa. However, both methods have relevant limitations: the ITC is a highly stringent approach that might under-estimate the number of species by being unable to detect cryptic or young species (false negative), whereas the IC is likely to over-estimate it by identifying distinct species where there is intraspecific character variation only (false positive; see Padial *et al*. 2010). Considering this, a third approach was defined, coined as integration by partial congruence (IPC), which is intermediate between the two previous ones, by retaining only candidate species that are supported by at least two independent lines of evidence. This approach represents a balanced and pragmatic trade-off between the higher resolving power of the IC and the higher confidence given by the ITC.

Additionally, the weakly divergent infraspecific allopatric ESUs (split supported by only one of these three lines of evidence) have been considered as different subspecies in this study.

RESULTS

The IPC protocol recognises the existence of seven species within the genus *Chioninia* (Fig. V.3). The distinctiveness of four species is supported by three lines of evidence, whereas the remaining three species are supported by only two lines of evidence. A total of eight subspecies (taxa supported by a single line of evidence according to the same protocol) have been identified in two different species. Based on these results, a new taxonomy for the genus *Chioninia* is proposed below:

Taxonomic review of the genus *Chioninia* (Gray, 1845)

Chioninia (Gray, 1845: 116). Type species: *Euprepes Delalandii* Duméril & Bibron, 1839, presently fixed by subsequent designation (Art. 69, ICZN 1999).

Macroscincus Bocage, 1873b. Type species: *E. Coctei* Duméril & Bibron, 1839.
Charactodon Troschel 1874: 225. Type species: *E. Coctei* Duméril & Bibron, 1839.

Diagnosis. The genus *Chioninia* represents the only lineage of skinks from the Cape Verde archipelago, from which it is endemic. It differs from other African, Asian and American genera formerly included in the genus *Mabuya sensu lato* by the following combination of characters: palatine bones in contact in the median; palatal notch separating the pterygoids, extending forwards to between the centre of the eyes; pterygoid teeth absent or present; 26-27 presacral vertebrae; reproduction either viviparous or ovoviviparous; the most posterior supraocular contacted by the frontal is always the third (Mausfeld *et al*. 2002); and supranasals are always in contact (this study).

Chioninia vaillanti (Boulenger, 1887) Figs. V.2.A1-2, V.3.A1-2, V.4.A, V.5.A1-2 and V.6.A1-2)

Diagnosis. *Chioninia vaillanti* is a relatively large species (adults between 87.5 and 123 mm Snout-vent length, SVL; Table V.1), with paired supranasals in contact, paired prefrontals in contact, fused frontoparietals, both parietals and interparietal fused into a single plate, and a single pair of nuchals. Seven supralabials, the fifth being the subocular one; and the posteriormost not horizontally divided. Four (rarely three) supraoculars; four to seven (most often five or six) supraciliaries. A high number of temporal scales: more than two secondary and three tertiary (Figs. V.2.A1-2 and V.4.A). Number of transverse rows of dorsal scales from 77 to 95 (Table V.1). Presence of a light vertebral stripe.

Remarks on the status of *Chioninia vaillanti*. Based on the present molecular studies, Fogo and Santiago *C. vaillanti* populations split very recently, approximately between 1.1 and 0.9 Mya (see below molecular studies section and also Figs. V.3.A1-2, V.5.A1-2, V.6.A1-2, Table V.2 and Appendix V.5). The morphology of both populations has however significantly diverged in the number of ventral and dorsal scale rows along the body (Table V.1). More interestingly, the examination of live specimens (six from each island) reveals very distinctive non-melanic chromatic characters on the head not visible in fixed specimens. The population from Santiago is characterised by a bright orange-coloured chin and snout whereas the one from Fogo has a bright yellow-coloured margin of the ear-openings (Fig. V.4.A). Both these different characteristics are present in all live specimens examined and do not seem to reflect any sexual dimorphism, as specimens from both sexes have been examined.

In many lizard species, such brightly coloured patches on the head, highly contrasting with a faded background, are known to play an essential role of visual species-recognition signal (Pianka & Vitt 2003; Losos 2009). In the present case, the significant divergence observed between island populations – both in term of colouration (orange vs. yellow) and localisation (ears vs. snout and chin) – lead us to hypothesize that this divergence may reduce the interpopulational degree of recognition, thus constituting a particularily relevant ‘taxonomic character’.

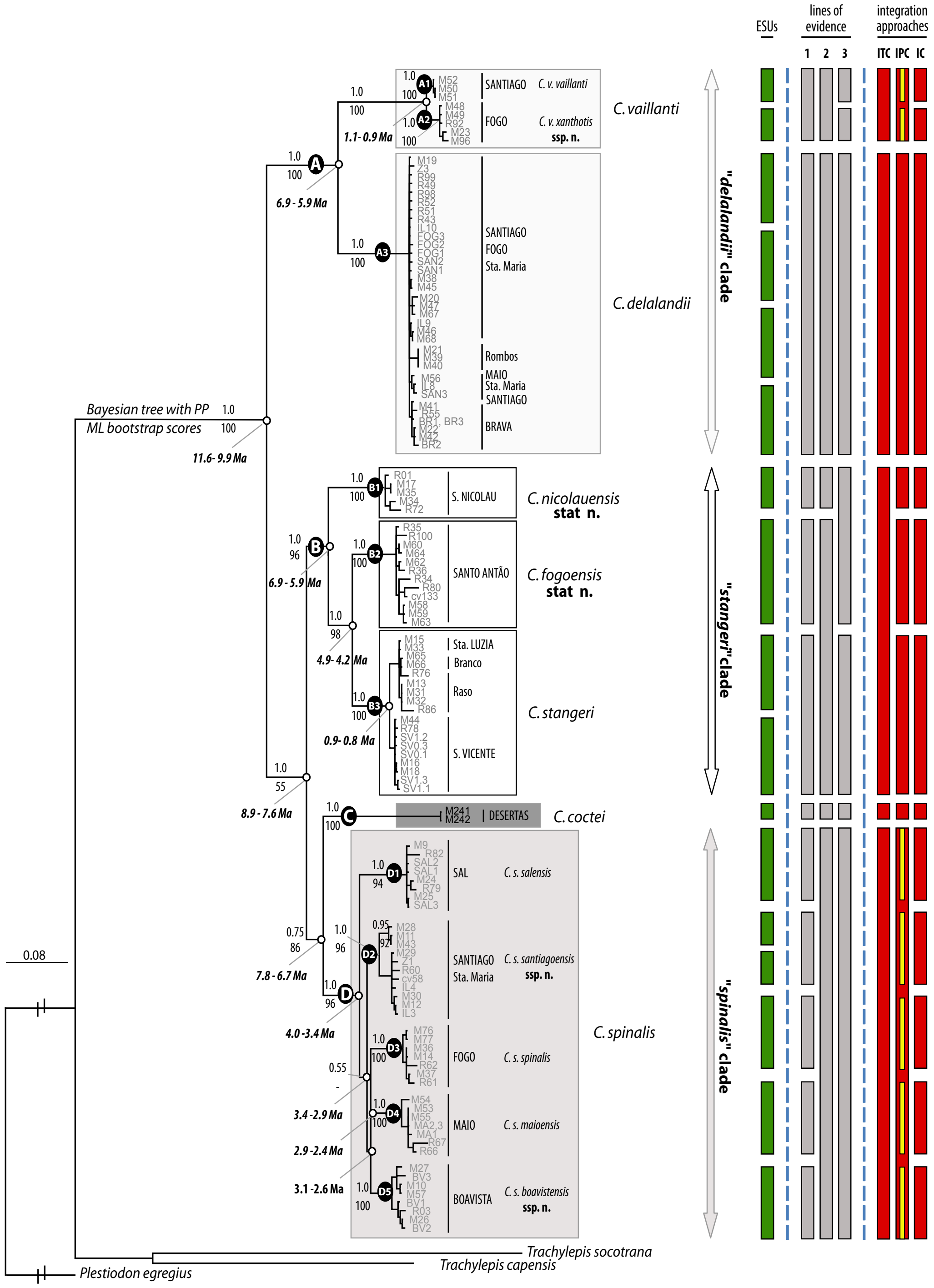


Figure V.3 Maximum Likelihood (ML) tree showing relationships and estimated times of divergence of endemic Cape Verde *Chioninia* skinks. The tree is rooted using *Plestiodon egregius*. Posterior probability values (PP) for the Bayesian analysis and bootstrap support values above 60% for the ML analysis are shown above and below nodes, respectively. Italic numbers in some selected nodes (highlighted with a blank circle) indicate the estimated age intervals of the speciation event of that node in millions of years (see Materials and methods). For locality data of the GenBank sequences see Appendix V.3. Letters immediately to the right of support values correspond to the clades recognised in the present work and shown in detail on the networks (Figs. V.5 and V.6). Lines of evidence (in light grey): (1) Mitochondrial DNA (independent cyt *b* parsimony networks with a connection limit of 95%); (2) Nuclear DNA (absence of shared haplotypes in RAG2); and (3) Morphology (detection of any diagnostic morphological character). Integration approaches (in red) from the most conservative to the most inflationist: ITC stands for an integration by total congruence (all lines of evidence should be congruent), IPC stands for integration by partial congruence which have been presently retained in this study to revise the taxonomy of the genus *Chioninia* (at least two lines of evidence are necessary); IC stands for an integration by cumulation (one line of evidence is sufficient). ESUs are represented in split green bars; species in red bars, and for the IPC protocol, subspecies are represented within those bars in yellow.

		A) '*delalandii*' clade			B) '*stangeri*' clade				C)	D) '*spinalis*' clade				
	Species	***C. vaillanti***		***C. delalandii***	***C.nicolauensis***	***C. fogoensis***		***C. stangeri***	***C. coctei***^{1,2}	***C. spinalis***				
	Clades	**A1**	**A2**	**A3**	**B1**	**B2**		**B3**	**C**	**D1**	**D2**	**D3**	**D4**	**D5**
		Cvv	***Cvx***	***(Sotavento***				***(Desertas,***		***Csl***	***Cst***	***Css***	***Csm***	***Csb***
Scales	**Variation**	**(Santiago)**	**(Fogo)**	**Islands)**	**(S. Nicolau)**	**(Sto. Antão)**	**'Fogo' types**	**S. Vicente)**	**(Desertas)**	**(Sal)**	**(Santiago)**	**(Fogo)**	**(Maio)**	**(Boavista)**
Divided SL	% (n sides)	16.7 (18^a)	0 (10^a)	0 (164)	100 (18)	100 (22)	93.8 (16)	94.6 (112)	–	0 (38)	0 (44)	0 (36)	0 (16)	0 (24)
Polyparietal	% (n)	100 (12^a)	100 (8^a)	100 (82)	0 (9)	0 (11)	0 (8)	0 (56)	0 (10)	0 (19)	0 (22)	0 (18)	0 (8)	0 (12)
FP fused	% (n)	100 (12^a)	100 (8^a)	100 (82)	0 (9)	0 (11)	0 (8)	0 (56)	0 (10)	0 (19)	0 (22)	0 (18)	0 (8)	0 (12)
O/F3	C				73.7 %	8.3 %	25.0 %	8.7 %						
	S/P	–	–	–	26.3 %	91.7 %	75.0 %	91.3 %	–	–	–	–	–	–
	n sides				(19)	(24)	(16)	(46)						
Supra-ciliaries	2	–	–	–	–	–	–	–	–	–	–	2.8 %	–	8.3 %
	3	–	–	–	–	–	–	–	–	88.9 %	15.2 %	38.9 %	75.0 %	70.8 %
	4	5.5%	–	5.8%	44.4 %	–	12.5 %	6.4 %	–	11.1 %	82.6 %	55.5 %	25.0 %	8.3 %
	5	44.4%	16.7%	91.0%	50.0 %	100 %	75.0 %	85.4 %	10.0%	–	2.2	2.8 %	–	12.5
	6	44.4%	66.6%	3.2%	5.6 %	–	12.5 %	8.2 %	45.0%	–	–	–	–	–
	7	5.5%	16.7%	–	–	–	–	–	45.0%	–	–	–	–	–
	n sides	(18^a)	(12^a)	(156)	(18)	(22)	(16)	(110)	(20)	(27)	(46)	(36)	(16)	(24)
Lamellae under 4th finger	Range	15 – 17	14 – 16	10 – 15	13 – 17	13 – 17	13 – 17	10 – 15	19 – 21	13 – 18	11 – 15	12 – 14	11 – 17	13 – 16
	mean ± SD	16.55 ± 0.82	15 ± 0.81	13.38 ± 1.07	14.71 ± 1.26	14.52 ± 0.98	14.71 ± 1.07	13.18 ± 0.75	19.76 ± 0.66	14.34 ± 1.06	13.26 ± 0.79	12.89 ± 0.51	14.94 ± 1.39	14.22 ± 0.80
	n sides	(11)	(4)	(122)	(17)	(21)	(14)	(106)	(17)	(35)	(43)	(27)	(16)	(23)
Lamellae under 4th toe	Range	21 – 25	20 – 24	17 – 23	20 – 24	19 – 24	19 – 22	16 – 22	24 – 28	18 – 25	18 – 22	19 – 22	20 – 24	19 – 23
	mean ± SD	23.58 ± 1.0	21.75 ± 1.70	19.50 ± 1.20	21.47 ± 1.06	21.18 ± 1.26	20.06 ± 0.92	19.20 ± 1.13	25.47 ± 1.01	21.84 ± 1.37	19.56 ± 1.24	20.25 ± 1.07	21.81 ± 1.05	20.87 ± 1.10
	n sides	(12)	(4)	(123)	(15)	(22)	(16)	(101)	(17)	(38)	(43)	(24)	(16)	(23)
Ventrals	Range	47 – 52	53 – 58	43 – 60	57 – 64	56 – 65	53 – 66	39 – 50	91 – 103	37 – 50	33 – 44	36 – 50	37 – 47	38 – 47
	mean ± SD	49.75 ± 1.42	54.75 ± 1.58	49.57 ± 3.72	59.25 ± 2.38	61.20 ± 3.08	58.25 ± 5.00	43.45 ± 2.26	94.33 ± 3.74	42.23 ± 3.29	37.42 ± 2.41	42.34 ± 3.10	41.18 ± 2.94	42.49 ± 4.48
	n	(12^a)	(8^a)	(46)	(8)	(10)	(8)	(47)	(9)	(22^a)	(38^a)	(29^a)	(27^a)	(35^a)
Dorsals	Range	77 – 87	84 – 95	68 – 91	84 – 93	87 – 95	87 – 95	52 – 69	134 – 152	60 – 73	52 – 63	57 – 71	56 – 67	59 – 72
	mean ± SD	81.73 ± 3.55	87.75 ± 3.69	78.40 ± 6.27	88.63 ± 3.25	89.90 ± 2.28	91.25 ± 2.91	62.94 ± 2.69	140.1 ± 6.37	67.55 ± 2.94	57.25 ± 2.22	64.03 ± 3.17	61.07 ± 3.10	65.17 ± 3.07
	n	(11^a)	(8^a)	(53)	(8)	(10)	(8)	(54)	(10^a)	(29^a)	(48^a)	(33^a)	(26^a)	(46^a)
Midbody	Range	52 – 56	53	40 – 54	54 – 59	56 – 65	60 – 61	40 – 45	102 – 110	34 – 44	33 – 36	37 – 41	36 – 40	40 – 46
	mean ± SD	53.50 ± 1.38	53.0 ± 0.0	47.55 ± 3.30	56.88 ± 1.96	59.80 ± 3.16	60.33 ± 0.51	42.60 ± 1.28	106.11 ± 2.76	40.54 ± 3.18	35.0 ± .89	38.5 ± 1.34	38.0 ± 1.15	43.0 ± 2.41
	n	(6)	(2)	(44)	(8)	(10)	(6)	(43)	(9)	(13)	(21)	(14)	(7)	(12)
SVL (mm)	Range	92 – 123	87.5 – 105	52 – 92	53 – 68.5	57 – 70.5	58 – 79	48 – 74	225 – 320	55 – 82.5	55 – 65	54 – 79	55 – 81	52 – 81
	mean ± SD	110.4 ± 8.72	99.4 ± 7.01	69.46 ± 7.88	58.38 ± 6.94	60.5 ± 5.47	68.75 ± 7.39	63.63 ± 6.2	267.7 ± 24.9	69.17 ± 9.83	62.17 ± 3.42	61.19 ± 6.18	67.95 ± 7.25	69.17 ± 9.87
	n	(10^a)	(5^a)	(178^a)	(4)	(7)	(6)	(16)	(35)	(6)	(11)	(29^a)	(21^a)	(9^b)

(1) The very high number of small scales in the temporal region of *Chioninia coctei* (probably correlated to the gigantism of this derived species) prevented us to reliably identify homologies for scales from the lateral sides of the head; (2) Snout-vent length statistics based on the data published by Andreone & Gavetti (1998); (3) Character examined only within the '*stangeri*' clade; [a] Data from both museum and live specimens; [b] Larger body sizes (maximum 91 mm SVL) have been recorded from live specimens (R. Vasconcelos & A. Perera, pers. obs).

Table V.1 (previous page) Comparisons of some characteristics distinguishing the different *Chioninia* taxa belonging to the different clades. For each meristic and mensural character, range, mean ± standard deviation (SD) and sample size (*n*; inside parentheses) are given. For some bilateral characters, the sample size has been noted as the number of sides rather than specimens. SL, Posteriormost supralabial scale; FP, Frontoparietal scale; O, Supraocular; F, Frontal scale; C, 'scales in contact'; S/), 'scales separated or barely in point contact'; SVL, snout-vent length; *Cvv, Chioninia v. vaillanti; Cvx, C. vaillanti xanthotis; Csl, C. spinalis salensis; Cst, C. s. santiagoensis; Css, C. s. spinalis; Csm, C. s. maioensis; Csb, C. s. boavistensis.*

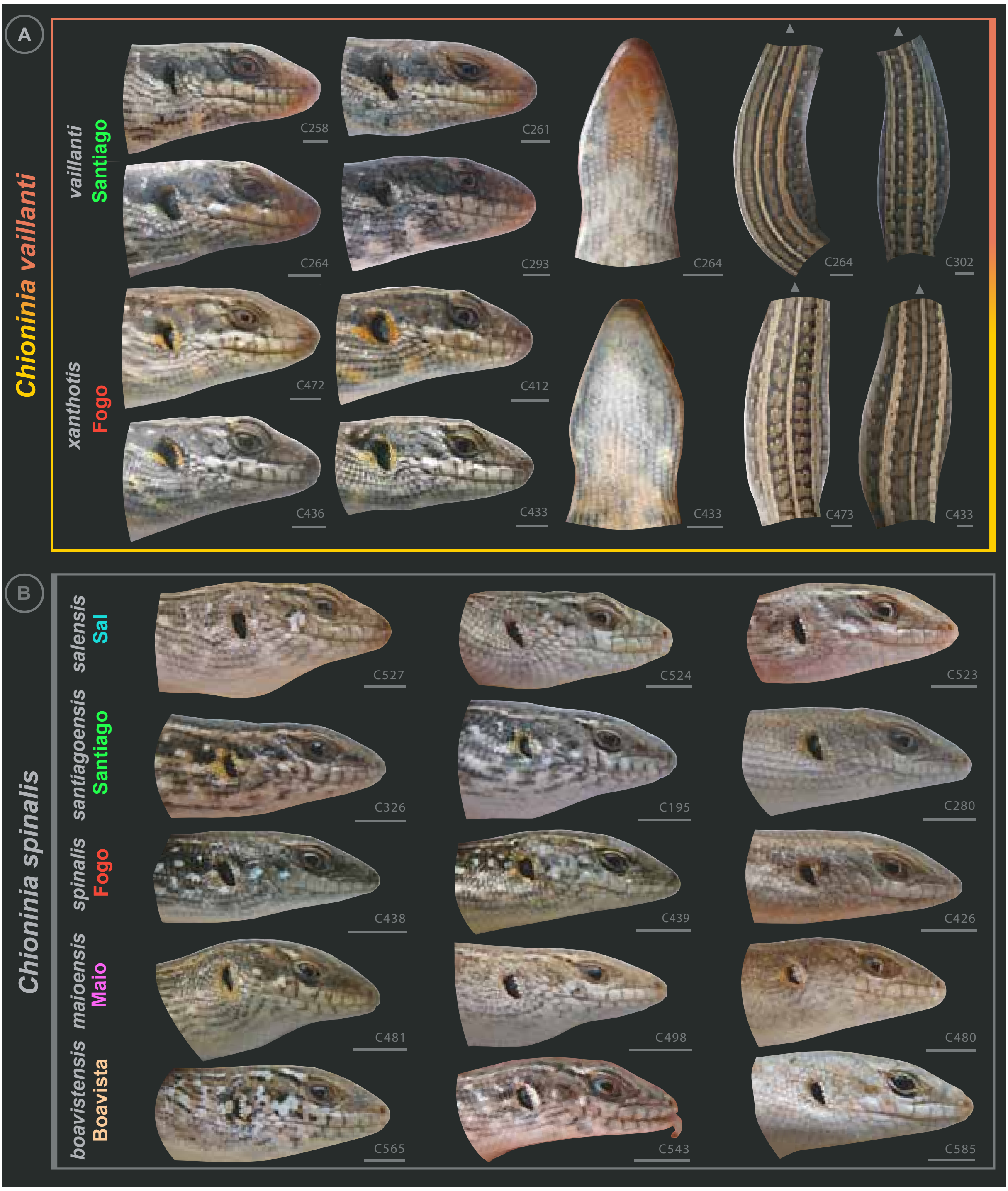


Figure V.4 Inter- and intra-subspecific phenotypic variation in (**A**) *Chioninia vaillanti* (lateral and ventral side of the head, and dorsal side of the body) and (**B**) *C. spinalis* (lateral side of the head) illustrated by a selection of photographs of live specimens. See Appendix V.1 for exact localities.

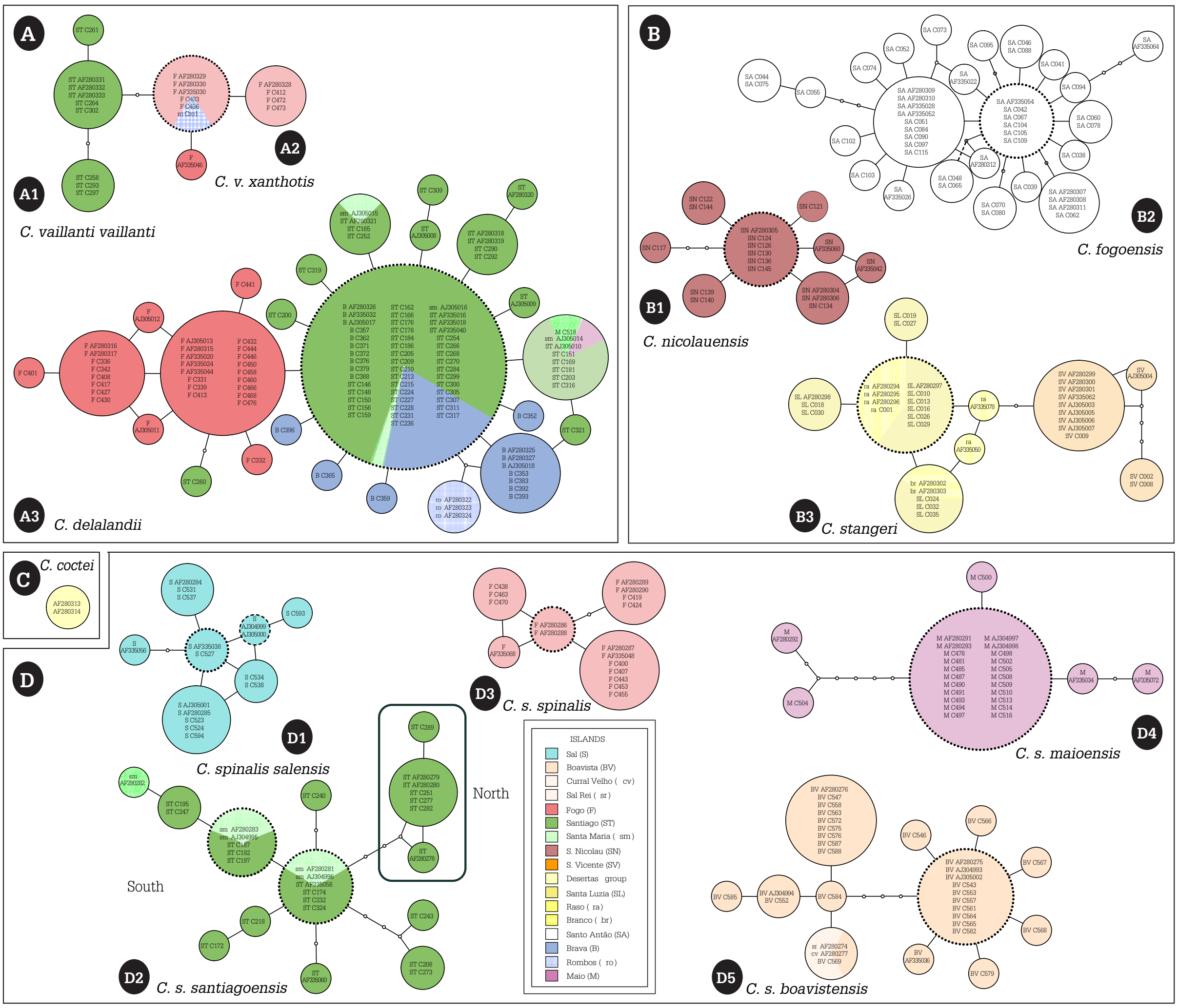


Figure V.5 Parsimony networks corresponding to cyt *b* sequence variation calculated with TCS with a connection limit of 95%. Lines represent a mutational step, dots missing haplotypes and circles haplotypes. The circle area is proportional to the number of individuals. Dashed lines represent probable ancestral haplotypes. For correspondences of sample locations and GenBank codes see Appendix V.1 and 3. **A**) '*delalandii*' clade; **B**) '*stangeri*' clade; **C**) *C. coctei* and **D**) '*spinalis*' clade.

Nevertheless, according to the presently selected protocol of integration (IPC), none of the two molecular lines of evidence (mtDNA and nDNA) clearly support the differentiation of both island populations (see Figs. V.3, V.5.A1-2 and V.6.A1-2), which is only based on morphological characters. Consequently these taxa have to be considered only as distinct subspecies. As *C. vaillanti* was initially described from Santiago, this population maintains the restrictive subspecific name. The taxonomic description of the new subspecies from Fogo is given below.

Distribution (Fig. V.1). Fogo, Santiago and Rombos Islets (Boulenger 1887; Angel 1937; Schleich 1982, 1987, 1996; Joger 1993; Andreone 2000; Brehm *et al.* 2001; Carranza *et al.* 2001; Carranza & Arnold 2003; López-Jurado *et al.* 2005; this study).

Conservation status. Listed as Indeterminate and so in need of urgent protection on the archipelago and also on Santiago and Fogo Islands, being considered Data Deficient in Rombos islets under the criteria of the First Red List of Cape Verde (Schleich 1996). Later, the Cape Verde authorities confirmed the status of this species as Indeterminate on all populations (Anonymous 2002).

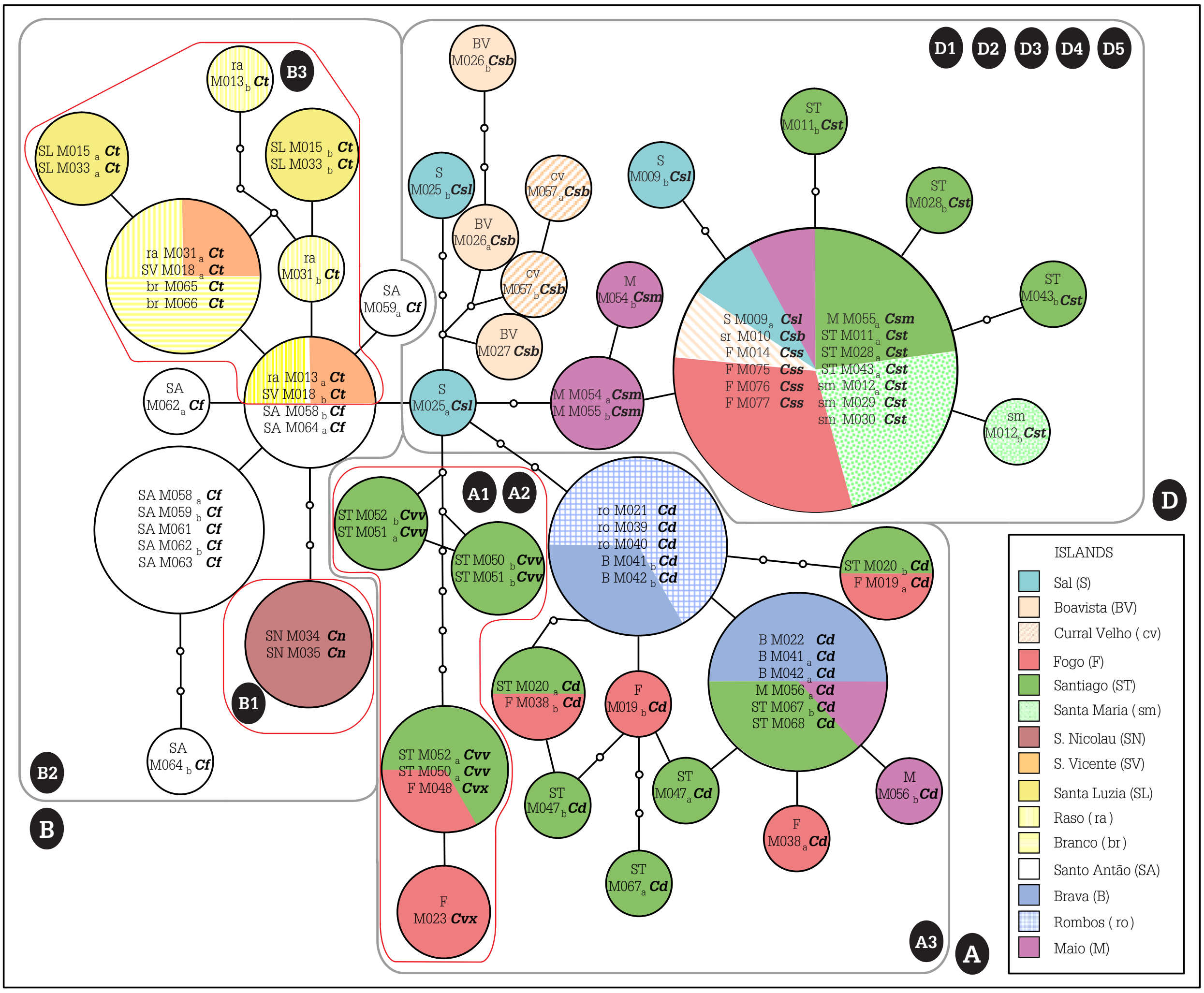


Figure V.6 Parsimony networks corresponding to RAG2 sequence variation calculated with TCS with a connection limit of 95%. Lines represent a mutational step, dots missing haplotypes and circles haplotypes. The circle area is proportional to the number of haplotypes. For correspondences of sample locations and GenBank codes see Appendix V.1. **A**) '*delalandii*' clade: A1) *Chioninia v. vaillanti* (Cvv), A2) *C. vaillanti xanthotis* (Cvx) and A3) *C. delalandii* (Cd); **B**) '*stangeri*' clade: B1) *C. nicolauensis* (Cn), B2) *C. fogoensis* (Cf), B3) *C. stangeri* (Ct); **C**) *C. coctei* (Cc); **D**) '*spinalis*' clade *C. spinalis salensis* (Csl), *C. s. santiagoensis* (Cst), *C. s. spinalis* (Css), *C. s. maioensis* (Csm), and *C. s. boavistensis* (Csb).

Chioninia vaillanti vaillanti (Boulenger, 1887) (Figs. V.2.A1, V.3.A1, V.4.A, V.5.A1 and V.6.A1)

Mabuia vaillantii Boulenger, 1887: 159. Five syntypes: BMNH 1948.8.18.25 to 1948.8.18.29. Type locality '*St. Jago, Cape Verde Islands*'.

Mabuia Vaillantii: Bocage 1896, 1902.

Mabuya vaillanti: Angel 1937 (*part.*); Schleich 1982 (*part.*), 1987, 1996 (*part.*); Joger 1993 (*part.*); Brehm *et al.* 2001 (*part.*); Carranza *et al.* 2001(*part.*); López-Jurado *et al.* 2005 (*part.*).

Other chresonyms

Mabuya delalandii: Mertens 1955 (*part.*).

Diagnosis. *Chioninia vaillanti vaillanti* are large-sized skinks (adults between 92 and 123 mm SVL; Table V.1) that differ from the *Chioninia vaillanti* population from Fogo by the following characters: anterior and posterior margin of the ear-openings grey or whitish in living specimens; bright orange-reddish colouration of the chin and snout (Fig. V.4.A); a lower number of transversal scale rows along the body (47 to 52 and 77 to 87 rows of ventrals/ dorsals, respectively; Table V.1).

Table V.2 Genetic differentiation between populations belonging to the same network: *Snn* values for mitochondrial (cyt *b*) and nuclear DNA (RAG2) calculated using DnaSP. Statistical significant *P*-values (**P* <0.05, ***P* <0.01). Taxa and island abbreviations as in Figs. V.1 and V.6.

Population 1		**Population 2**		**cyt *b***	**RAG2**
Clade	**Taxa/Island**	**Clade**	**Taxa/Island**	***Snn***	***Snn***
A1	*Cvv* ST	A2	*Cvx* F	1.000***	0.733
A3	*Cd* sm	A3	*Cd* ST	0.894	-
A3	*Cd* B	A3	*Cd* ro	1.000***	0.714
A3	*Cd* ST + sm	A3	*Cd* F	0.989***	0.317
A3	*Cd* ST + sm	A3	*Cd* B	0.741***	0.531
A3	*Cd* ST + sm	A3	*Cd* ro	1.000***	0.857**
A3	*Cd* F	A3	*Cd* B	1.000***	0.500
A3	*Cd* F	A3	*Cd* ro	1.000***	0.600**
B1	*Cn* SN	B2	*Cf* SA		1.000**
B2	*Cf* SA	B3	*Ct* SV		0.762
B2	*Cf* SA	B3	*Ct* Desertas		0.938**
B1	*Cn* SN	B3	*Ct* SV		1.000**
B1	*Cn* SN	B3	*Ct* Desertas		1.000**
B3	*Ct* SL	B3	*Ct* ra	0.692	-
B3	*Ct* SL	B3	*Ct* br	0.813	-
B3	*Ct* ra	B3	*Ct* br	0.905*	0.500
B3	*Ct* Desertas	B3	*Ct* SV	1.000***	0.689
D1	*Csl* S	D2	*Cst* ST + sm		0.736*
D1	*Csl* S	D3	*Css* F		0.685*
D1	*Csl* S	D4	*Csm* M		0.563
D1	*Csl* S	D5	*Csb* BV		0.639
D2	*Cst* STNorth	D2	*Cst* STSouth	1.000***	0.455
D2	*Cst* sm	D2	*Cst* ST	0.709	-
D2	*Cst* ST + sm	D3	*Css* F		0.473
D2	*Cst* ST + sm	D4	*Csm* M		0.847**
D2	*Cst* ST + sm	D5	*Csb* BV		0.782**
D3	*Css* F	D4	*Csm* M		0.833*
D3	*Css* F	D5	*Csb* BV		0.778**
D4	*Csm* M	D5	*Csb* BV		0.833
A1+A2	*Cv* TOTAL	A3	*Cd* TOTAL		1.000**
A1+A2	*Cv* TOTAL	B1	*Cn*		1.000**
A1+A2	*Cv* TOTAL	B2	*Cf*		1.000**
A1+A2	*Cv* TOTAL	B3	*Ct* TOTAL		1.000**
A1+A2	*Cv* TOTAL	D	*Cs* TOTAL		1.000**
A3	*Cd* TOTAL	B1	*Cn*		1.000**
A3	*Cd* TOTAL	B2	*Cf*		1.000**
A3	*Cd* TOTAL	B3	*Ct* TOTAL		1.000**
A3	*Cd* TOTAL	D	*Cs* TOTAL		1.000**
B1	*Cn* SN	B3	*Ct* TOTAL		1.000**
B1	*Cn* SN	D	*Cs* TOTAL		1.000**
B2	*Cf* SA	B3	*Ct* TOTAL		0.856**
B2	*Cf* SA	D	*Cs* TOTAL		1.000**
B3	*Ct* TOTAL	D	*Cs* TOTAL		1.000**

Distribution (Fig. V.1). Santiago Island (Boulenger 1887; Bocage 1896, 1902; Angel 1937; Schleich 1982, 1987, 1996; Joger 1993; Brehm *et al.* 2001; Carranza *et al.* 2001; López-Jurado *et al.* 2005 and this study).

Chioninia vaillanti xanthotis ssp. n. (Fig. V.2.A2, V.3A2, V.4A, V.5A2 and V.6A2)
Holotype. Unsexed adult, CAPE VERDE, Near Mosteiros, Fogo, 1999, Carranza, (BMNH 2000.9).
Paratype. Cova Figueira, Fogo, 1997, Mateo & Geniez, (BMNH 2000.8).

Mabuia vaillanti: Boulenger 1906.

Mabuya vaillanti: Angel 1937 (*part.*); Schleich 1982 (*part.*), 1987 (*part.*), 1996 (*part.*); Joger 1993 (*part.*); Andreone 2000; Brehm *et al.* 2001 (*part.*); Carranza *et al.* 2001 (*part.*); Carranza & Arnold 2003; López-Jurado *et al.* 2005 (*part.*).

Other chresonyms

Mabuya delalandii: Mertens 1955 (*part.*).

Etymology. The subspecific epithet refers to the yellow colour of the ear-openings and is derived from the Greek 'xanthos' (yellow) and 'otis' (ear).

Diagnosis. *Chioninia vaillanti xanthotis* are large-sized skinks (adults between 87.5 and 105 mm SVL; Table V.1) that differ from *Chioninia vaillanti vaillanti* by the following characters: anterior and posterior margin of the ear-openings brightly yellow-coloured on living specimens; a faded greyish colouration of the chin and a brownish colouration of the snout (Fig. V.4.A); a higher number of transversal scale rows along the body, (53 to 58 and 84 to 95 rows of ventrals/ dorsals, respectively; Table V.1 and MorphoBank M52245–M52252).

Description (holotype). SVL 103.5 mm. Rostral slightly wider than high, contacting first supralabials, nasals and supranasals. Paired supranasals in median contact, contacting anteriormost loreal. Frontonasal approximately hexagonal, wider than long, laterally contacting anterior loreal. Paired prefrontals roughly pentagonal, as wide as long, in broad contact medially, contacting frontonasal, both anterior and posterior loreals, first and second supraoculars, and frontal. Frontal roughly trapezoidal/pentagonal, longer than wide, wider anteriorly, in contact with prefrontal, first, second and third supraoculars and frontoparietal. Four supraoculars; the first the smallest, the second the longest, the third the widest. Posteriormost supraocular in contact with the frontal is the third. Six supraciliaries, the second the longest. Frontoparietals fused into a single scale, in contact with frontal, the third and the fourth supraoculars and the polyparietal scale. The polyparietal scale, which results from the fusion of both parietals and the interparietal, is twice wider than long, anteriorly convex and posteriorly concave, overlapping the upper temporal scales. A single pair of transversely enlarged nuchals, as wide as three rows of dorsals, no secondary enlarged nuchals. Nostril located in the middle of the nasal. Lower eyelid undivided with a transparent disk, a single row of small scales across its dorsal edge. Seven supralabials, the fifth being the enlarged subocular, and the posteriormost not horizontally divided. Six infralabials. Three pretemporal scales between the primary temporal and the fourth supraocular. On the right side, one primary temporal, four secondary temporals in contact and four tertiary temporals. Ear-opening lacking auricular lobules. Palms and soles covered with small tubercles, subequal in size. Subdigital lamellae smooth, single, 15 under right fourth finger, and 16 under left fourth finger, 20 under right fourth toe, and 21 under left fourth toe. Fifty-three scale rows around midbody, 90 transverse rows of dorsal scales, 53 transverse rows of ventral scales (Table V.1).

Colouration in preservative. Background colour of upper side of the head, neck, back, and lateral sides of the body, limbs and tail brown/dark bronze. Black transversal marblings formed by a succession of more-or-less aligned dark dots on the back (approximately 20, from the neck to the hindlimbs), flanks and temporal region; black dots on the limbs and tail, and white dots on the lateral sides of the anterior half of the body. Peripheral area of the venter, lower side of head, throat, lower side of limbs and tail grey. Median part of the venter, palms, and soles cream coloured, fingers and toes slightly darker. Not distinct limits between the peripheral areas of the venter and the bronze lateral sides of the body. Three well-contrasted golden longitudinal stripes on the back, lighter than the background colouration: a vertebral stripe, from the mid-length of the neck to shortly after the tail; two dorsolateral stripes, from the posteriormost supraciliaries roughly to the tip of the tail. Anterior margin of the ear-openings whitish (discoloured) and well contrasted.

Variation. See Table V.1 and also Fig. V.4.A for an overview of the intraspecific variability of meristic and mensural characters and colour patterns, respectively.

Phylogenetic remarks (Figs. V.3.A2, V.5.A2, V.6.A2, Table V.2 and Appendix V.5). This monophyletic group presents a relatively low genetic divergence from *C. v. vaillanti* (*p*-dist=1.25 ± 0.50% and 0.62 ± 0.20% for cyt *b* and RAG2, respectively). However, it presents significant *Snn* values for cyt *b*.

Distribution. Fogo Island and Rombos Islets, more precisely in Ilhéu de Cima (Boulenger 1906; Angel 1937; Schleich 1982, 1987, 1996; Joger 1993; Andreone 2000; Brehm *et al.* 2001; Carranza *et al.* 2001; Carranza & Arnold 2003; López-Jurado *et al.* 2005; this study).

Chioninia delalandii (Duméril & Bibron, 1839) (Figs. V.2A.3, V.3.A3, V.5.A3 and V.6.A3)

Euprepes Delalandii Duméril & Bibron, 1839: 690. Holotype: MNHN 263, collected by Delalande. Original type locality: '*cap de Bonne-Espérance*', erroneous locality corrected by Bocage 1875: 289-290 into '*ile Santiago*' and Mertens (1955:10); Bocage 1875.

Euprepis Delalandii: Gray 1845.

Mabuia delalandii: Boulenger 1887; Angel 1935.

Mabuia delalandi: Boulenger 1906.

Mabuia Delalandii: Bocage 1896, 1902.

Mabuya delalandei: Dekeyser & Villiers 1951.

Mabuya delalandi: Greer 1976.

Gongylus Delalandii: Brygoo 1985.

Mabuya delalandii: Angel 1937; Mertens 1955 (*part.*); Schleich 1982, 1987, 1996; Joger 1993; Andreone 2000; Greer *et al.* 2000; Greer & Nussbaum 2000; Brehm *et al.* 2001; Brown *et al.* 2001; Carranza *et al.* 2001; Mausfeld *et al.* 2002; Carranza & Arnold 2003; López-Jurado *et al.* 2005.

Chioninia delalandii: Mausfeld *et al.* 2002; Köhler *et al.* 2007.

Euprepis venustus Girard, 1857: 195 (synonym according to Bocage 1875 and Peters 1869). Holotype: USNM 12205. Type locality: '*Cape de Verde islands*' (the most accurate locality of '*San Jago*' is mentioned in the USNM herpetological collection database, what is in accordance with the presence of *C. delalandii* on Santiago Island).

Euprepes venustus: Bocage 1875.

Euprepis Belcheri Gray, 1845: 116. Two syntypes: BMNH 1946.8.19.55, 1946.8.19.56. Type locality: '*Borneo*' (erroneous).

Diagnosis. *Chioninia delalandii* is a medium-sized species (adults between 52 and 92 mm SVL, Table V.1), with paired supranasals in contact, paired prefrontals in contact, fused frontoparietals, both parietals and interparietal fused into a single plate, and a single pair of nuchals. Seven supralabials, the fifth being the subocular one and the posteriormost not horizontally divided. Four supraoculars; four to six (most often five) supraciliaries (Fig. V.2.A3). Number of transverse rows of dorsal scales from 68 to 91 (Table V.1). Presence of black dot on the axilla; live specimens with yellow eyelids (MorphoBank M42109–M42114, please consult http://www.morphobank.org/).

Phylogenetic remarks (Figs. V.2.A3, V.3.A3, V.5.A3, V.6.A3, Table V.2 and Appendix V.5). *Chioninia delalandii*, despite being a monophyletic group, is separated in allopatric non-reciprocally monophyletic populations. These populations present very low levels of divergence in the molecular markers and do not show any sign of divergence in morphology either (see lines of evidence in Fig. V.3). However, they are isolated, with significant *Snn* values for cyt *b* and hence considered as ESUs.

Distribution (Fig. V.1). Brava, Fogo, Santiago, including Santa Maria islet, and Rombos islets, namely Ilhéu Grande, Ilhéu Luiz Carneiro ('Ilheu Rombos Luiza' *sensu* Mertens 1955) and Ilhéu de Cima (Bocage 1875, 1896, 1902; Boulenger 1887, 1906; Angel 1935, 1937; Dekeyser & Villiers 1951; Mertens 1955; Schleich 1982, 1987, 1996; Joger 1993; Brehm *et al.* 2001; Brown *et al.* 2001, Carranza *et al.* 2001; Mausfeld *et al.* 2002; Carranza & Arnold

2003; López-Jurado *et al.* 2005; Köhler *et al.* 2007 and this study). *Chioninia delalandii* was recently introduced in Maio, Vila do Maio and possibly also in Boavista, Vila de Sal Rei (Schleich 1987, 1996; Carranza *et al.* 2001; López-Jurado *et al.* 2005; Chadwick & Slater 2005; this study), although some authors claim that it went extinct or that is presently absent in Boavista (López-Jurado *et al.* 1999; Brown *et al.* 2001). Andreone (2000) reports the existence of two specimens (MSNG 50001) from São Nicolau, collected by Leonardo Fea in 1898, but the author admits that it is likely due to a mislabelling.

Conservation status. Listed as Low Risk on the archipelago and all islands of its range except Rombos Islets, where it is considered as Data Deficient under the criteria of the First Red List of Cape Verde (Schleich 1996).

Chioninia nicolauensis (Schleich, 1987) (Figs. V.2B.1, V.3.B1, V.5.B1 and V.6.B1)
Mabuya fogoensis nicolauensis Schleich, 1987: 20. Holotype: ZSM 1.82.1; six paratypes: ZSM 1.82.2 to 1.82.7. Type locality: '*S. Nicolau*'; Joger 1993; Schleich 1996; Andreone 2000; Carranza *et al.* 2001; Carranza & Arnold 2003
Chioninia fogoensis nicolauensis: Frazen & Glaw 2007; Köhler *et al.* 2007.
Other chresonyms.
Mabuia fogoensis: Boulenger 1906;
Mabuya fogoensis: Angel 1937 (*part.*); Dekeyser & Villiers 1951 *(part.)*; Mertens 1955 (*part.*); Schleich 1982; Brehm *et al.* 2001 (*part.*); López-Jurado *et al.* 2005 (*part.*).

Diagnosis. *Chioninia nicolauensis* is a medium-sized species (adults between 53 and 68 mm SVL, Table V.1), with paired supranasals in contact, paired prefrontals in contact, paired frontoparietals in contact, paired parietals in contact, and a single pair of nuchals. Seven (sometimes eight) supralabials, the fifth being the subocular one and the posteriormost horizontally divided. Four supraoculars; four or five (sometimes six) supraciliaries. Most often, first supraoculars and frontal in broad contact (Fig. V.2.B1). Number of transverse rows of dorsal scales from 84 to 93 (Table V.1). Throat without grey marblings, or very faded when present. In living specimens, throat covered by a bright red brick colour patch extending to the lateral side of the chin shields, and ventrum whitish, always with two ventrolateral well contrasted bright orange trails extending from forelimbs to hindlimbs (MorphoBank M42115–M42136).

Distribution (Fig. V.1). São Nicolau Island (Boulenger 1906; Angel 1937; Dekeyser & Villiers 1951; Mertens 1955; Schleich 1982, 1987, 1996; Joger 1993; Andreone 2000; Brehm *et al.* 2001; Carranza *et al.* 2001; Carranza & Arnold 2003; López-Jurado *et al.* 2005; Frazen & Glaw 2007; Köhler *et al.* 2007; this study).

Conservation status. Listed as Low Risk on S. Nicolau under the criteria of the First Red List of Cape Verde (Schleich 1996).

Chioninia fogoensis (O'Shaughnessy, 1874) (Figs. V.2.B2, 3.B2 and 5.B2)
Euprepes fogoensis O'Shaughnessy, 1874. Lectotype: BMNH 1946.8.18.13, from '*Fogo'*. Eight paralectotypes: BMNH 1946.8.18.8, 9, 10, 11, 12, 14, and 16, from '*Fogo*', and BMNH 1946.8.19.53, from '*St. Vincente*', Reverend R. T. Lowe; Bocage 1875.
Mabuia fogoensis: Boulenger 1887; Bocage 1896, 1902; Angel 1935.
Mabuya fogoensis: Angel 1937 (*part.*); Dekeyser & Villiers 1951 *(part.)*; Mertens 1955 (*part.*); Greer 1976; Schleich 1982 (*part.*); Brehm *et al.* 2001 (*part.*); López-Jurado *et al.* 2005 (*part.*).
Mabuya fogoensis fogoensis: Schleich 1987, 1996; Joger 1993; Andreone 2000.
Mabuya fogoensis antaoensis Schleich, 1987: 22. Holotype: ZSM 23.1982.1; eight paratypes: ZSM 23.1982.2 to 23.1982.9. Type locality: '*St. Antão*'; Joger 1993; Schleich 1996; Carranza *et al.* 2001; Carranza & Arnold 2003.

Mabuya antaoensis: López-Jurado *et al.* 2005.

Chioninia fogoensis antaoensis: Frazen & Glaw 2007.

Mabuya geisthardti Joger, 1993: 442. Holotype: HLMW 3274, collected by M. Geisthardt. Type locality: '*Grande da Lagoa, NW of the Cova plateau, 10 km from the east coast of Sto. Antão, at 1200 m elevation*'; Schleich 1996; Greer *et al.* 2000; Carranza *et al.* 2001.

Chioninia geisthardti: Köhler & Güsten 2007.

Diagnosis. *Chioninia fogoensis* is a medium-sized species (adults between 57 and 79 mm SVL; Table V.1), with paired supranasals in contact, paired prefrontals in contact, paired frontoparietals in contact, paired parietals in contact, and a single pair of nuchals. Seven supralabials, the fifth being the subocular one and the posterior-most being horizontally divided. Most often, first supraoculars and frontal separated or barely in point contact. Four supraoculars; four to six (most often five) supraciliaries (Fig. V.2.B2). Number of transverse rows of dorsal scales from 87 to 95 (Table V.1). Throat with grey marblings, sometimes very dark. In living specimens, chin shields with a dark grey patch (less frequently with an orange/brown background colouration), and ventrum yellowish, sometimes with two ventrolateral light orange trails extending from forelimbs to hindlimbs (MorphoBank M42137–M42202 and M52253–M52287).

Remarks on the status of *Chioninia fogoensis sensu lato*. *Euprepis fogoensis* was described by O'Shaughnessy in 1874, and was considered a monotypic species until Schleich (1987) described two additional subspecies. After this, up to three intraspecific taxa have been recognised in several recent studies (Joger 1993; Andreone 2000; Carranza *et al.* 2001): (i) *Mabuya fogoensis fogoensis* (O'Shaughnessy, 1874) from Fogo and São Vicente; (ii) *M. f. antaoensis* Schleich, 1987 from Santo Antão; and (iii) *M. f. nicolauensis* Schleich, 1987 from São Nicolau. The molecular phylogenies published on the Cape Verdean skinks (Brehm *et al.* 2001; Carranza *et al.* 2001; this study) clearly demonstrate the existence only of the last two subspecies as distinct clades in *Chioninia fogoensis*. The Santo Antão lineage was shown to be more closely related to *C. stangeri* than to the S. Nicolau lineage, both island lineages not forming a monophyletic assemblage (Fig. V.3.B). As a result, these two subspecies of *C. fogoensis* are considered different phylogenetic species (Mishler & Theriot 2000; Wheeler & Platnick 2000).

Both in the original description (O'Shaughnessy 1874: 301) and in the collection catalogue of the BMNH, the type localities mentioned for *Euprepes fogoensis* are '*Fogo*' and '*St. Vincent's*' (BMNH 1946.8.18.8-14, 16, and BMNH 1946.8.19.53, respectively). Paradoxically, this species had never been collected, nor observed in Fogo subsequently (Angel 1935; Mertens 1955; Schleich 1987; Joger 1993; Brehm *et al.* 2001; Carranza *et al.* 2001; this study). The only two exceptions being Angel (1937: 1695) who mentioned the existence of specimens of *Mabuya fogoensis* in Fogo probably based on old reference data and Andreone (2000: 26) who also mentions specimens collected by L. Fea in 1898 (MSNG 28464 and 49255). However, this latter author recognised that some geographic attributions of these old specimens could be mislabelled. Moreover, Fogo is located on the southern part of the archipelago (Sotavento Islands), and no other species of the '*stangeri'* clade have ever been collected on this region (Fig. V.1). All these facts support the theory that *C. fogoensis* is not present on Fogo, and that this type-locality is probably erroneous. São Vicente constitutes a more reliable type locality as it is located just 15 Km East of Santo Antão and inside the distribution range of the *C. fogoensis* clade. However, despite the many visits by several different herpetological expeditions and intensive searches across the whole island, Mertens (1954) is the only one to mention the existence of *C. fogoensis* in São Vicente (eight specimens; FMNHH 9./20.3.1954). Only two distinct taxonomic units could in fact be recognised in *C. fogoensis sensu lato*: one from Santo Antão, and another one from São Nicolau. It is now needed to determine to which of these two taxa the *C. fogoensis* types belong to.

Some of the best-preserved types 'from Fogo' present the same subtle colouration pattern as the individuals from Santo Antão. They also share a low rate of broad contact between first supraoculars and the frontal (25% and 8.3% respectively, vs. 73.7% in São Nicolau specimens; Table V.1) and a robust shape of head (the head of São

Nicolau specimens being slightly more elongated and flattened in the supraocular region). Finally, Santo Antão is much closer from S. Vicente than S. Nicolau, so it is more probable that a labelling error may have occurred after visiting both Santo Antão and S. Vicente on the same day, as these errors frequently happened in the past. These observations have multiple taxonomic consequences: first, the *C. f. fogoensis* types must be considered conspecific with the population from Santo Antão (previously regarded as a distinct subspecies). However, it is impossible to guarantee that all the syntypes belong to this species due to the existence of some discoloured and poorly preserved specimens. Therefore, it was decided to designate the syntype specimen BMNH 1946.8.18.13 (Fig. V.2.B2) as the lectotype of *E. fogoensis*. Indeed, it is not only the best-preserved syntype of *E. fogoensis*, but also the specimen with the most similar colouration to the individuals of Santo Antão (particularly on the dorsum and with the characteristic grey marblings on the throat). All other syntypes therefore lose their status and become paralectotypes. As a consequence, *C. f. antaoensis* (Schleich, 1987) becomes a junior subjective synonym of *C. fogoensis* (O'Shaughnessy, 1874). Secondly, the subspecies from S. Nicolau is elevated to species rank, *C. nicolauensis* (see above), as its distinctiveness is clearly supported by at least two independent lines of evidence (Figs. V.3, V.5 and V.6).

To confirm if *C. geisthardti* (Joger, 1993) is a valid synonym of *C. fogoensis*, as proposed by Carranza *et al.* (2001), 11 animals were sampled in several different localities around the type locality of this species, of which five were genetically analysed (M051, M052, M055, M060), and no morphological or genetical differences were noticed. The *C. geisthardti* holotype was also studied and its morphological characters fell within *C. fogoensis* variation (Joger 1993).

Distribution (Fig. V.1). Santo Antão Island (Bocage 1896, 1902; Angel 1935, 1937; Dekeyser & Villiers 1951; Mertens 1955; Schleich 1982, 1987, 1996; Joger 1993; Brehm *et al.* 2001, Carranza *et al.* 2001; Carranza & Arnold 2003; López-Jurado *et al.* 2005; Frazen & Glaw 2007; Köhler & Güsten 2007; this study).

Conservation status. Listed as Low Risk on Santo Antão under the criteria of the First Red List of Cape Verde (Schleich 1996).

Chioninia stangeri (Gray, 1845) (Figs. V.2.B3, V.3.B3, V.5.B3 and V.6.B3)
Euprepis Stangeri Gray, 1845: 112. Four syntypes: BMNH 1946.8.1 to 1946.8.4, collected during the Niger Expedition. Type localities: '*W. Africa*'.

Mabuia stangeri: Boulenger 1887 (*part.*), 1906 (*part.*).

Mabuia Stangeri: Bocage 1896, 1902 (*part.*).

Mabuya stangeri stangeri: Mertens 1955; Schleich 1982, 1987.

Mabuya stangeri: Angel 1937 (*part.*); Dekeyser & Villiers 1951 (*part.*); Mertens 1955 (*part.*); Greer 1976; Schleich 1980, 1982, 1987, 1996; Joger 1993; Mateo *et al.* 1997; Andreone 2000; Greer *et al.* 2000; Greer & Nussbaum 2000; Brehm *et al.* 2001; Brown *et al.* 2001; Carranza *et al.* 2001; Carranza & Arnold 2003; López-Jurado *et al.* 2005.

Chioninia stangeri: Köhler et al. 2007.

Euprepes polylepis Peters, 1870 (1869): 660. Syntypes: ZMB 6154, 6154A. Type locality '*Africa occidentali (Damara)*'.
Euprepes Hopfferi Bocage, 1875: 287. At least two syntypes: BMNH 1946.8.18.43, ZMB 8999. Type locality: '*Ilheo Raso*'.

Diagnosis. *Chioninia stangeri* is a medium-sized species (adults between 48 and 74 mm SVL; Table V.1), with paired supranasals in contact, paired prefrontals in contact, paired frontoparietals in contact, paired parietals in contact, and a single pair of nuchals. Seven supralabials, the fifth being the subocular one and the posteriormost horizontally divided. Four supraoculars; four to six (most often five) supraciliaries. Most often, first supraoculars and frontal separated or barely in point contact (Fig. V.2.B3). Number of transverse rows of dorsal scales from 52 to 69 (Table V.1).

Phylogenetic remarks (Figs. V.2.B3, V.3.B3, V.5.B3, V.6.B3, Table V.2 and Appendix V.5). It is a monophyletic species which presents a low genetic divergence between the reciprocally monophyletic Desertas and S. Vicente populations (p-dist=1.13 ± 1.80% and 0.17 ± 0.08% for cyt *b* and RAG2, respectively). Following the IPC protocol, no line of evidence supports the distinctiveness of these two populations. However, they present significant *Snn* values for cyt *b*, being thus considered two ESUs.

Distribution (Fig. V.1). São Vicente, Santa Luzia and Branco and Raso Islets (Bocage 1875, 1896, 1902; Boulenger 1887, 1906; Angel 1937; Dekeyser & Villiers 1951; Mertens 1955; Schleich 1980, 1982, 1987, 1996; Schleich & Wuttke 1983; Joger 1993; Mateo *et al.* 1997; Andreone 2000; Brehm *et al.* 2001; Brown *et al.* 2001; Carranza *et al.* 2001; Carranza & Arnold 2003; López-Jurado *et al.* 2005; Köhler *et al.* 2007; this study). Additionally, Bocage (1902) cited the past presence of this species on S. Nicolau, probably based on Fea who cited it as *C. spinalis* erroneously (Andreone 2000). Later, Dekeyser & Villiers (1951) and Schleich (1982) cited it also on Brava, Boavista, and Sal, based on old references from Angel (1937) and Bannerman & Bannerman (1968) and others, but the latter author considered them doubtful.

Conservation status. Listed as Low Risk on the archipelago and on Santa Luzia Island, however it is considered Rare in Branco and Raso islets and Data Deficient in S. Vicente under the criteria of the First Red List of Cape Verde (Schleich 1996). Despite this, no conservation status was assigned on the national legislation (Anonymous 2002).

Chioninia coctei (Duméril & Bibron, 1839) (Figs. V.2.C, V.3.C and V.5.C)

Euprepes Coctei Duméril & Bibron, 1839: 666. Holotype: MNHN 8299. Type locality: *'côtes d'Afrique'*.

Euprepis Coctei: Gray 1845.

Euprepes coctei: Bocage 1873a, 1873b.

Charactodon coctei: Troschel 1874.

Macroscincus Coctei: Bocage 1873b; O'Shaughnessy 1874; Vaillant 1882; Bocage 1896, 1897, 1902.

Macroscincus Cocteaui: Bocage 1875.

Macroscincus coctaei: Peracca 1891; Boulenger 1887, 1906.

Macroscincus coctei: Orlandi 1894; Angel 1937; Mertens 1955; Greer 1976; Schleich 1982, 1987, 1996; Hutchinson 1989; Andreone & Gavetti 1998; Andreone 2000; Greer *et al.* 2000; Brehm *et al.* 2001; Carranza *et al.* 2001; Andreone & Guarino 2003; López-Jurado *et al.* 2005; Mateo *et al.* 2005; Köhler *et al.* 2007.

Gongylus Coctei: Brygoo 1985.

Macroscincus cocteaui: Joger 1993.

Diagnosis. *Chioninia coctei* is a 'giant' species (adults SVL > 200mm, maximum 320 mm, Andreone & Gavetti 1998), with paired supranasals in contact, paired prefrontals in contact, paired frontoparietals in contact, paired parietals separated by the interparietal, and a single pair of nuchals (Fig. V.2.C). Seven supralabials, the fifth being the subocular one. Four supraoculars; five to seven supraciliaries. A high number of transverse rows of dorsal scales (134 –152; Table V.1). Teeth with five cuspids (see figure in Bocage 1873b; Greer 1976; Mateo *et al.* 2005 and MorphoBank 52288).

Distribution (Fig. V.1). Branco and Raso Islet. According to Greer (1976) and Andreone (2000), this species might have been also present on Santa Luzia and São Vicente, as shown by subfossil records (*in* Carranza *et al.* 2001; Mateo *et al.* 2005). This distribution may have been facilitated by the Pleistocene sea level falls that allowed land bridges between all these islands. Its past presence in S. Nicolau is also supported by fisherman reports (Greer 1976; Schleich 1982) but solid proof for this is still lacking. Nevertheless, *Chioninia coctei* has not been observed alive after 1912 despite the effort invested by several expeditions, although, Mateo *et al.* (2005) claimed to have found a maxilla of a juvenile of that species in the faeces of a cat in Santa Luzia (for details see Bocage 1873a, b, 1896, 1897, 1902; Vaillant 1882; Peracca 1891; Angel 1937; Mertens 1955; Greer 1976; Schleich 1982, 1987, 1996;

Hutchinson 1989; Andreone & Gavetti 1998; Andreone 2000; Andreone & Guarino 2003; Carranza *et al.* 2001; Mateo *et al.* 2005; Köhler *et al.* 2007). For the present work, searches for the presence of *C. coctei* were conducted in 2006 by three observers on Santa Luzia Island during five days with no results (R. Vasconcelos. pers. obs.).

Conservation status. Considered as an Extinct species under the criteria of IUCN and the First Red List of Cape Verde (Schleich 1996; IUCN 2009).

Chioninia spinalis (Boulenger, 1906) (Figs. V.2.D, V.3.D, V.4.B, V.5.D and V.6.D)

Diagnosis. *Chioninia spinalis* is a medium-sized species (adults between 52 and 82.5 mm SVL; Table V.1), with paired supranasals in contact, paired prefrontals in contact, paired frontoparietals in contact, paired parietals in contact, and a single pair of nuchals. Seven (rarely eight) supralabials, the fifth being the subocular one; posteriormost supralabial not divided. Four supraoculars; most frequently three or four supraciliaries (Fig. V.2.D). Number of transverse rows of dorsal scales from 52 to 73 (Table V.1).

Remarks on the status of *Chioninia spinalis sensu lato*. *Chioninia spinalis sensu lato* is present in many islands of the south and eastern part of the Cape Verdean archipelago (Fogo, Santiago, Maio, Boavista, and Sal) (Fig. V.1). The systematics of this species was confusing during a long time, with Mertens (1955) and Schleich (1987) considering it as a subspecies of *C. stangeri*, namely *Mabuya stangeri salensis*, *M. s. spinalis*, and *M. s. maioensis*. Molecular phylogenetic and network analyses clearly demonstrated that *C. spinalis* is not affiliated to *C. stangeri*, being the latter more closely related to *C. nicolauensis* and *C. fogoensis* (see molecular studies section below and Figs. V.3, V.5, V.6 and Table V.2). In the past, a subgroup from Sal had been sometimes considered as a distinct species and described by Angel (1935) as *Mabuia salensis*. More recently, some of these subgroups have been recognised as distinct *C. spinalis* subspecies: *Mabuya spinalis* maioensis on Maio, *M. s. salensis* on Sal and Boavista, and *M. s. spinalis* on Fogo and Santiago (Joger 1993; Andreone 2000; Brehm *et al.* 2001; Carranza *et al.* 2001; Mausfeld *et al.* 2002). It is also evident from the tree presented in Fig. V.3.D that *C. spinalis sensu lato* forms a strongly supported clade, including all populations from Fogo, Santiago, Maio, Boavista, and Sal, that could be subdivided into five island subgroups. Each of these five subgroups is strongly supported and well differentiated from the others in the phylogenetic tree, mtDNA network and populational analyses. In the present paper, *C. spinalis* is regarded as a single species and each of its five subclades as distinct subspecies extremely similar in terms of morphology and ecology. Their divergence is supported by a single line of evidence (Figs. V.3 and V.6.D) which indicates that they do not deserve to be considered as full species. Even if most of them could be differentiated from the others morphologically, some pairs of subspecies could not (Table V.1). Each subspecies is endemic to its own island and, as a result of that, gene flow between them should be limited or non-existent. Consequently, the island of origin of a given specimen could be used as an indirect criterion for identification. Based on the support of the mitochondrial line of evidence, it appears necessary to describe below two of the five subspecies, which are currently unnamed (corresponding to Boavista and Santiago populations). Additionally, it is necessary to designate BMNH 1906.03.30.40 as the lectotype of *Mabuia spinalis* Boulenger, 1906 (restricted type locality: '*Fogo, Cape Verde Islands (…) Igreya*') among the nine available syntypes. All the other syntypes therefore lose their status and become paralectotypes.

Distribution (Fig. V.1). Fogo, Santiago (including Santa Maria islet), Maio, Boavista (including Curral Velho and Sal Rei islets) and Sal. Additionally, Andreone (2000) reports the existence of one specimen (MSNG 50000) from São Nicolau, collected by Leonardo Fea in 1898, but admits that it is likely a mislabelling. Two specimens (MNHN 1965-249 and 250) are labelled from Ilhéu dos Pássaros (off Mindelo, São Vicente).

Conservation status. Listed as Low Risk on the whole archipelago under the criteria of the First Red List of Cape Verde and also on each of the islands of occurrence (Schleich 1996).

Chioninia spinalis salensis (Angel, 1935) (Figs. V.3.D1, V.4.B, V.5.D1 and V.6.D)
Mabuia salensis Angel, 1935: 168. Holotype: MNHN 1935-197; one paratype: MNHN 1935-198. Type locality: '*Ile Sal*'; Angel 1937.
Mabuya stangeri salensis: Mertens 1955 (*part.*); Schleich 1982, 1987 (*part.*).
Mabuya spinalis salensis: Joger 1993 (*part.*); Schleich 1996; Brown *et al.* 2001 (*part.*); Carranza *et al.* 2001 (*part.*); Mausfeld *et al.* 2002; López-Jurado *et al.* 2005 (*part.*).
Mabuia salensis: Brygoo 1985.
Mabuya salensis: Brehm *et al.* 2001 (*part.*).
Chioninia spinalis salensis: Köhler *et al.* 2007.
Other chresonyms
Mabuya spinalis: Angel 1935 (*part.*), 1937 (*part.*);
Mabuia Stangeri: Bocage 1902 (*part.*);
Mabuya stangeri: Dekeyser & Villiers 1951 *(part.)*.

Distribution (Fig. V.1). Sal Island (Bocage 1902; Angel 1935, 1937; Dekeyser & Villiers 1951; Mertens 1955; Schleich 1982, 1987, 1996; Brygoo 1985; Joger 1993; Brehm *et al.* 2001; Brown *et al.* 2001; Carranza *et al.* 2001; Mausfeld *et al.* 2002; López-Jurado *et al.* 2005; Köhler *et al.* 2007 and this study).

Chioninia spinalis santiagoensis ssp. n. (Figs. V.2.D2, V.3.D2, V.4.B, V.5.D2 and V.6.D)
Holotype. Adult female, CAPE VERDE, Ilhéu Santa Maria, off Praia, Santiago, 1997, Mateo & Geniez, (BMNH 2000-37).
Paratypes. Same data as for holotype, Ilhéu Santa Maria, off Praia, Santiago (BMNH 2000-35, 36, 38; DBULPGC115; MZB 2010-0979); Santiago island, (from MZB 2010-0962 to MZB 2010-0977); Tarrafal, Santiago, (MZB 2010-0978); Chão Bom, Santiago, (DBULPGC114).
Other chresonyms
Mabuia Stangeri: Bocage 1902 (*part.*);
Mabuya stangeri spinalis: Schleich 1987 (*part*);
Mabuya spinalis: Brehm *et al.* 2001 (*part*);
Mabuya spinalis spinalis: Joger 1993 (*part.*); Schleich 1996 (*part.*); Brown *et al.* 2001 (*part.*); Carranza *et al.* 2001 (*part.*); Mausfeld *et al.* 2002; López-Jurado *et al.* 2005 *(part.)*.

Etymology. The subspecific epithet refers to the island where the taxon is found.

Diagnosis. *Chioninia spinalis santiagoensis* appears to be the *C. spinalis* subspecies that is morphologically most differentiated from the others by the combination of the following characters (Figs. V.2.D2, V.4.B and Table V.1): most often four supraciliaries (82.6%) with the second the longest [(vs. most often three, the first the longest in *C. spinalis* from Boavista (70.8%), *C. s. maioensis* (75.0%), and *C. s. salensis* (88.9%)] and a relatively low number of scales around midbody (33 to 36 vs. ≥ 36 in *C. spinalis* from Boavista, *C. s. maioensis* and *C. s. spinalis*).

Description (holotype). 64.5 mm SVL. Rostral wider than high, contacting first supralabials, nasals and supranasals. Paired supranasals in median contact, contacting anteriormost loreal. Frontonasal approximately hexagonal, wider than long, laterally contacting anterior loreal. Paired prefrontals roughly pentagonal, wider than long, in broad contact medially, contacting frontonasal, both anterior and posterior loreals, first supraoculars, and frontal. Frontal roughly trapezoidal, longer than wide, wider anteriorly, in contact with prefrontal, first, second and third supraoculars and frontoparietals. Four supraoculars; the first the smallest, the second the longest, the third the widest. Posteriormost supraocular in contact with the frontal is the third. Four supraciliaries, the second the longest. Paired frontoparietals, longer than wide, in broad contact at midline, in contact with frontal, the third and the fourth supraoculars, parietal and interparietal. Interparietal triangular, longer than wide, wider anteriorly, separated from nuchals by parietals. Parietals larger than interparietal, wider than long, overlapping the upper temporal scales. A single transversely enlarged nuchals on the right side, as wide as three rows of dorsals, no secondary enlarged nuchals. Nostril located posteriorly to the nasal. Lower eyelid undivided with a transparent disk, two rows of small scales across its dorsal edge. Seven supralabials, the fifth being the enlarged subocular. Seven infralabials. One pretemporal. One primary temporal, two secondary temporals in contact and three tertiary temporals. Ear-opening small, with three auricular lobules. Palms and soles covered with small tubercles, subequal in size. Subdigital lamellae smooth, single, 13 under left and right fourth fingers, 18 under right fourth toe, 20 under left fourth toe. Thirty-five scale rows around midbody, 59 transverse rows of dorsal scales, 37 transverse rows of ventral scales.

Colouration in preservative. Background colour of upper side of the head, neck, back, limbs and tail greyish/ bronze. Venter, lower side of head, throat, lower side of limbs and tail, palms, and soles immaculate whitish coloured. Three dorsolongitudinal rows of black dots: a thin vertebral one composed by succession of black longitudinal dashes, and two dorsolateral ones composed by a succession of black dots as wide as one/ two scales. Four thin whitish stripes run along body: two whitish dorsolateral stripes from the fourth supraoculars to hindlimbs, and two whitish lateral stripes from the insertions of forelimbs to those of hindlimbs. The stripes between dorsolateral and lateral whitish stripes same colour than the back, but with many transversal thin black stripes. Presence of white dots on the lateral side of the neck.

Variation. See Table V.1 and also Fig. V.4.B for an overview of the high intraspecific variability of meristic and mensural characters and colour patterns, respectively.

Phylogenetic remarks (Figs. V.3.D2, V.5.D2, V.6.D, Table V.2 and Appendix V.5). It is a monophyletic group which presents a moderate genetic divergence from other *C. spinalis* populations (*p*-dist=4.26 ± 1.00%/ 0.46 ± 0.13% from *C. s. salensis*, 4.98 ± 1.12%/ 0.07 ± 0.03% from *C. s. spinalis*, 6.10 ± 1.28%/ 0.19 ± 0.10% from *C. s. maioensis*, and 4.46 ± 1.02%/ 0.69 ± 0.21% from *C. spinalis* from Boavista for cyt *b* and RAG2, respectively). However, it presents significant *Snn* values for cyt *b* with all other *C. spinalis* populations except *C. s. spinalis*.

Distribution (Fig. V.1). Santiago Island, including Santa Maria islet (Bocage 1902; Schleich 1987, 1996; Joger 1993; Brehm *et al.* 2001; Brown *et al.* 2001; Carranza *et al.* 2001; Mausfeld *et al.* 2002; López-Jurado *et al.* 2005 and this study)

Chioninia spinalis spinalis (Boulenger, 1906) (Figs. V.3.D3, V.4.B, V.5.D3, V.6.D and Appendix V.4)
Mabuia spinalis Boulenger, 1906: 204. Lectotype: BMNH 1906.03.30.40 (Igreja); paralectotypes: BMNH 1906.03.30.41 (Igreja); MSNG 28168 (6 specimens, Igreja), MSNG 49252 ('*S. Filippe*'). Restricted type locality: '*Fogo, Cape Verde Islands (…) Igreya*'.

Mabuia spinalis: Angel 1935, 1937 (*part.*).

Mabuya stangeri spinalis: Mertens 1955; Schleich 1982, 1987 (*part.*).

Mabuya spinalis spinalis: Joger 1993 (*part.*); Schleich 1996 (*part.*); Andreone 2000; Carranza *et al.* 2001 (*part.*); López-Jurado *et al.* 2005 (*part.*).

Mabuya spinalis: Brehm *et al.* 2001 (*part.*); Brown *et al.* 2001 (*part.*)

Distribution (Fig. V.1). Fogo Island (Boulenger 1906; Angel 1935, 1937; Mertens 1955; Schleich 1982, 1987, 1996; Joger 1993; Andreone 2000; Brehm *et al.* 2001; Brown *et al.* 2001; Carranza *et al.* 2001; López-Jurado *et al.* 2005; this study).

Chioninia spinalis maioensis (Mertens, 1955) (Figs. V.3.D4, V.4.B, V.5.D4 and V.6.D)

Mabuya stangeri maioensis Mertens, 1955: 11. Holotype: FMNH 3.2.1954. Type locality: '*Maio, Kapverden*'; Schleich 1982, 1987.

Mabuya spinalis maioensis: Joger 1993; Schleich 1996, Greer *et al.* 2000; Brehm *et al.* 2001; Brown *et al.* 2001; Carranza *et al.* 2001; Carranza & Arnold 2003; López-Jurado *et al.* 2005.

Distribution (Fig. V.1). Maio Island (Mertens 1955; Schleich 1982, 1987, 1996; Joger 1993; Brehm *et al.* 2001; Brown *et al.* 2001; Carranza *et al.* 2001; Carranza & Arnold 2003; López-Jurado *et al.* 2005; this study).

Chioninia spinalis boavistensis ssp. n., (Figs. V.2.D5, V.3.D5, V.4.B, V.5.D5 and V.6.D)

Holotype. Unsexed adult, CAPE VERDE, Sal Rei, Boavista, 1997, Mateo & Geniez, (BMNH 2000-44).

Paratypes. Same data as for holotype, east side of Boavista (MNHN 1965-251); Sal Rei, Boavista, (from MZB 2010-0980 to MZB 2010-0983); Ilhéu de Sal Rei (DBULPGC118); Curral Velho, Boavista (BMNH 2000-45; MZB 2010-0984, 0985); 2.5 km E Sal Rei, Boavista (MZB 2010-0986).

Other chresonyms

Mabuia Stangeri: Bocage 1902 (*part.*);

Mabuia stangeri: Boulenger 1906 *(part.)*; Angel 1937 *(part.)*;

Mabuya stangeri: Dekeyser & Villiers 1951 *(part.)*;

Mabuya stangeri salensis: Mertens 1955 (*part.*); Schleich 1982 (*part.*), 1987 (*part.*);

Mabuya spinalis salensis: Joger 1993 (*part.*); Schleich 1996 (*part.*); López-Jurado *et al.* 1999 (*part.*), 2005 (*part.*); Andreone 2000 (*part.*); Brown *et al.* 2001 (*part.*); Carranza *et al.* 2001 (*part.*);

Mabuya salensis: Brehm *et al.* 2001 (*part.*).

Etymology. The subspecific epithet refers to the island where the taxon is found.

Diagnosis. *Chioninia s. boavistensis* is characterised by the combination of the following characters: most often three supraciliaries (70.8 %) with the first the longest (vs. most often four (82.6%) with the second the longest in *C. s. santiagoensis*); a relatively high number of scales around midbody (40 to 46 vs. ≤ 40 in *C. s. maioensis* and *C. s. santiagoensis*) (Figs. V.2.D5, V.4.B, Table V.1 and MorphoBank M52289–M52294). Despite the relatively high mtDNA genetic divergences (Appendix V.5) and subtle differences of colouration (Fig. V.4.B), we were not able to find reliable morphological diagnostic characters to differentiate it from the remaining subspecies.

Description (holotype). 73.6 mm SVL, tail 70 mm, missing the tip. Rostral wider than high, contacting first supralabials, nasals and supranasals. Paired supranasals in median contact, contacting anteriormost loreal. Frontonasal approximately hexagonal, wider than long, laterally contacting anterior loreal. Paired prefrontals roughly pentagonal, as wide as long, in broad contact medially, contacting frontonasal, both anterior and posterior loreals, first supraoculars, and frontal. Frontal roughly lanceolate and hexagonal, longer than wide, wider anteriorly, in contact with prefrontal, first, second and third supraoculars and frontoparietals. Four supraoculars; the first the smallest, the second the widest. Posteriormost supraocular in contact with the frontal is the third. Three supraciliaries, the first the longest. Paired frontoparietals in broad contact at midline, in contact with frontal, the third and the fourth supraoculars, parietal and interparietal. Interparietal roughly triangular, as long as wide, wider anteriorly, separated from nuchals by parietals. Parietals larger than interparietal, wider than long, overlapping the upper temporal scales. A single pair of transversely enlarged nuchals, as wide as three rows of dorsals, no secondary enlarged nuchals. Nostril located posteriorly to the nasal. Lower eyelid undivided with a transparent disk, two rows of small scales across its dorsal edge. Seven supralabials, the fifth being the enlarged subocular. Six infralabials. Two pretemporals. One primary temporal (divided on the right side), two secondary temporals in contact and three tertiary temporals. Ear-opening small, with four auricular lobules on each side. Palms and soles covered with small tubercles, subequal in size. Subdigital lamellae smooth, single, 13 both under left and right fourth fingers, 22 under right fourth toe, 22 under left fourth toe. Forty-five scale rows around midbody, 68 transverse rows of dorsal scales, 43 transverse rows of ventral scales.

Colouration in preservative. Although this specimen is well preserved, its colour is naturally poorly contrasted. Background colour of upper side of the head, neck, tail and an eight-scale-wide-large-dorsal-stripe bronze. Lateral side and limbs ocher. Venter, lower side of head, throat, lower side of limbs and tail, palms, and soles immaculate whitish colour. A very thin and faded darker vertebral stripe. Dark dots wider than long, along the margin of the wide bronze dorsal stripe. Lateral side of the body covered with white dots as wide as one scale.

Variation. See Table V.1 and also Fig. V.4.B for an overview of the high intraspecific variability of meristic and mensural characters and colour patterns, respectively.

Phylogenetic remarks (Figs. V.3.D2, V.5.D2, V.6.D, Table V.2 and Appendix V.5). It is a monophyletic group which presents a moderate genetic divergence from other *C. spinalis* subspecies (*p*-dist= 4.46 ± 1.06%/ 0. 62 ± 0.15% from *C. s. salensis*, 4.46 ± 1.02%/ 0.69 ± 0.21% from *C. s. santiagoensis*, 4.53 ± 1.08%/ 0.54 ± 0.18% from *C. s. spinalis* and 6.14 ± 1.23%/ 0.53 ± 0.16% from *C. s. maioensis*, for cyt *b* and RAG2, respectively). It also presents significant *Snn* values for cyt *b* with *C. s. santiagoensis* and *C. s. spinalis*.

Distribution (Fig. V.1). Boavista Island including Curral Velho Islet and Sal Rei Islet (Bocage 1902; Boulenger 1906; Angel 1937; Dekeyser & Villiers 1951; Mertens 1955; Schleich 1982, 1987, 1996; Joger 1993; López-Jurado *et al.* 1999, 2005; Andreone 2000; Brehm *et al.* 2001; Brown *et al.* 2001; Carranza *et al.* 2001; this study).

Molecular studies

Phylogenetic analysis

Independent ML and BI analyses of the three genes (cyt *b*, COI and 12S) produced trees that differed in some minor arrangements of taxa or individual samples. These differences had low bootstrap and posterior-probability support in all cases (< 70% and 95%, respectively). It was therefore considered that there were no major topological conflicts between the three gene-partitions (Mason-Gamer & Kellogg 1996). The ILD test ($P > 0.66$) similarly showed that the three independent data sets were not incongruent. All three partitions were therefore combined for further analyses. In total, the combined data set included 1915 bp (1041 bp of cyt *b*, 499 bp of COI and 375 bp of 12S), of which 721 bp were variable (425 bp of cyt *b*, 169 bp of COI and 127 bp of 12S) and 534 bp were parsimony-informative (318 bp of cyt *b*, 139 bp of COI and 77 bp of 12S).

The results of the ML and BI gave almost identical topologies and were very similar to other analyses previously published (see Fig. V.3 and Brehm *et al.* 2001; Carranza *et al.* 2001), the only difference being the species that occupied the most basal position within the '*spinalis*' clade (*C. s. salensis* in this study and *C. s. santiagoensis* in Brehm *et al.* 2001 and Carranza *et al.* 2001). As in the previous studies, the majority of the clades were highly supported, with the exception of the group formed by '*spinalis*' clade + *C. coctei*, which despite being recovered in all the analyses (and also by Carranza *et al.* 2001) received very low support in both ML and BI. The analyses also show that the skinks from S. Nicolau and Santo Antão, previously regarded as the same species, *C. fogoensis*, are paraphyletic, with the populations from Santo Antão more closely related to *C. stangeri*. The results of the topological constraint test, in which the populations from S. Nicolau and Santo Antão were forced to be monophyletic, rejected the null hypothesis (that the best tree and the constrained tree were not significantly different; $P < 0.05$). This indicates that from a strictly topological point of view, the mtDNA data set from Fig. V.3 supports the new taxonomic arrangement presented here, according to which the skinks from S. Nicolau and Santo Antão are two different species. All the other species and subspecies considered valid up to date are all reciprocally monophyletic.

Network and population analyses

Network analyses. Over the whole mitochondrial data set, 94 sites were polymorphic (corresponding to 18 aminoacid changes) and 118 haplotypes were identified. Based on the connection limit of 95%, 10 independent haplotype networks could be inferred: one for *C. vaillanti*, one for *C. delalandii*, one for *C. nicolauensis*, one for *C. fogoensis*, one for *C. stangeri*, and five for *C. spinalis* (Fig. V.5). As indicated by the phylogenetic analysis, *C. vaillanti*, *C. delalandii* and *C. stangeri,* are coherent linked groups, some of them with well-differentiated island population subgroups. In the network of *C. vaillanti* (Fig. V.5.A1-2) two subunits are visible, one including the population from Fogo and another one from Santiago, two mutational steps apart. In *C. stangeri* (Fig. V.5.B3), also two subunits are differentiated by two mutational steps: the S. Vicente Island and Desertas Island group (Sta. Luzia Island, Raso and Branco Islets). None of the subunits of these two taxa share haplotypes. However, in the network of *C. delalandii* (Fig. V.5.A3), most of the populations from different islands are closely connected or share haplotypes between them, namely Santiago, Sta. Maria Islet and Brava, even though there are several unique haplotypes for each island population and some substructuring, for example, in Fogo and Rombos Islets.

As previously noted, the networks of *C. nicolauensis*, with individuals from S. Nicolau Island, and *C. fogoensis*, with individuals from Santo Antão, are not associated (Fig. V.5.B1-2, respectively). The network of *C. fogoensis* includes a very high number of haplotypes. The same happens with *C. spinalis*, with each island population, of Sal, Santiago, Fogo, Maio and Boavista, represented as an independent network (Fig. V.5.D1-5, respectively).

Over the whole nuclear data set, 57 sites were polymorphic (corresponding to 27 aminoacid changes) and 40 haplotypes were identified. Based on the connection limit of 95%, a single haplotype network was inferred with some substructuring corresponding to the '*delalandii*', '*stangeri*' and '*spinalis*' clades (Fig. V.6). This network shows two different bifurcations corresponding to the *C. vaillanti* and *C. delalandii* samples (Fig. V.6.A1-2 and A3, respectively). Within these, although there are some unique haplotypes for each island population, there is also some haplotype sharing between them, for example between Fogo and Santiago in *C. vaillanti* and between Santiago and Brava in *C. delalandii*. Another bifurcation matches the '*stangeri*' clade from which two subgroups can be distinguished corresponding to *C. nicolauensis* (Fig. V.6.B1) and *C. stangeri* samples (Fig. V.6.B3), although in this last case, the central haplotype is shared also with some *C. fogoensis* samples (Fig. V.6.B2). Substructuring is less clear on the bifurcations regarding the '*spinalis*' clade, as the most frequent haplotype is shared by samples from all *C. spinalis* populations (Fig. V.6.D). However, various haplotypes were unique to specific islands, including Maio, Sal and Boavista.

Population analyses. The significant *Snn* comparisons tests (Table V.2) indicate that all populations with mtDNA independent networks, plus *C. vaillanti* subspecies from Santiago and Fogo, *C. delalandii* populations from each island where it occurs (including Rombos Islets), *C. stangeri* populations from Desertas and S. Vicente, and northern and southern *C. spinalis* populations from Santiago, should be considered as distinct ESUs for conservation issues (see Table V.2). Therefore, these 17 ESUs were regarded as independent units in the demographic analyses (Table V.3). As expected, genetic differentiation in the nDNA data revealed by the *Snn* tests was lower than in mtDNA, although significant when comparing all the different network-connected species (Fig. V.3) and some *C. spinalis* subspecies.

As expected from the star-like topologies of some of the mtDNA networks, seven out of the 17 ESUs cases identified in Fig. V.5, presented significantly negative Fu's F_s values that is an indicator that these populations could have experienced a demographic expansion event. To characterize the expansion pattern further, a model of sudden demographic growth was fitted to the pairwise sequence mismatch distribution of the seven populations. In six of these cases, the mismatch distributions were not significantly different from the sudden expansion model of Rogers and Harpending (1992). The results of Fu's test (F_s), the sum of squared deviation statistic (SSD) and other relevant demographic parameters are given in Table V.3.

Table V.3 Mitochondrial cyt *b* diversity, neutrality tests and demographic parameters in the 17 Evolutionarily Significant Units (ESUs) of *Chioninia* from Cape Verde Islands. (*n*), sample size; (π), nucleotide diversity; (*Hd*), haplotype diversity; (*h*), number of haplotypes; (*S*), segregation sites; (F_s) Fu's statistics; r, Harpending's raggedness index; (SSD), Sum of Squared deviation statistics; (τ), Tau; (θ_0), initial Theta; (θ_1), final Theta. Statistical significant *P*-values (**P* <0.05, ***P* <0.01). Island and taxa abbreviation as in Fig. V.1 and V.6.

Clade	**ESU (taxa/island)**	***n***	π	***h***	**Hd**	***S***	F_s	***r***	**SSD**	τ	θ_0	θ_1
A1	*Cvx* F	10	0.0024	3	0.6445	2	-0.1006	0.265679	0.043703	0.947	0.000	99999
A2	*Cvv* ST	11	0.0086	5	0.7636	9	0.2666	0.095537	0.035207	1.932	1.594	4.375
A3	*Cd* B	21	0.0028	6	0.6857	5	-2.6974*	0.201088*	0.026595	1.070	0.000	99999
A3	*Cd* ro	3	0.0000	1	0.0000	0						
A3	*Cd* ST+sm	59	0.0029	12	0.6125	13	-8.6551**	0.080158	0.002424	0.906	0.000	99999
A3	*Cd* F	30	0.0020	7	0.6230	6	-3.7452**	0.156269	0.018624	0.914	0.002	99999
B1	*Cn* SN	18	0.0063	9	0.8693	11	-3.8864**	0.110129	0.014411	1.625	0.000	99999
B2	*Cf* SA	44	0.0089	23	0.9345	26	-17.6764**	0.037295	0.001744	2.686	0.000	99999
B3	*Ct* Desertas	22	0.0033	6	0.7446	4	-1.3570	0.030160	0.008310	3.387	0.005	5.353
B3	*Ct* SV	12	0.0025	3	0.4394	3	0.1805	0.258264	0.286960**	0.000	0.000	427.2
C	*Cc* Desertas	2	0.0000	1	0.0000	0						
D1	*Csl* S	16	0.0050	7	0.8417	7	-2.6025*	0.086875	0.009499	1.699	0.000	99999
D2	Css F	17	0.0056	5	0.7721	5	0.0066	0.126027	0.030407	2.670	0.000	8.906
D3	*Cst* STNorth	7	0.0019	3	0.5238	2	-0.9218	0.185941	0.022031	0.732	0.000	99999
D3	*Cst* STSouth	21	0.0083	10	0.8714	13	-3.2814*	0.025329	0.124192*	0.934	0.000	99999
D4	*Csm* M	27	0.0042	6	0.3419	11	-1.0329	0.313252	0.022992	3.000	0.000	0.423
D5	*Csb* BV	32	0.0107	12	0.8286	14	-2.5575	0.130768	0.067319	6.098	0.004	6.656

Morphological studies

A synthetic table showing the quantitative results obtained in the morphological study is presented in Table V.1. Additionally, a qualitative analysis of the cephalic scales conformation revealed the existence of three consistent characteristics in the *Chioninia* genus. These usually present no intraspecific variability (see Fig. V.2 and Appendix V.4):

1. Division of the last supralabial. The posteriormost supralabial scale appears to be divided horizontally in some *Chioninia* species. Greer & Broadley (2000: 9) noticed this characteristic in three *C. stangeri* specimens, justly adding that this splitting gives the impression of the 2S configuration in the secondary temporal (=both secondary temporals separated). The this study reveals that this state of characters is not restricted to *C. stangeri* (94.6%), as it is also present in *C. fogoensis*, *C. nicolauensis* (both 100%) and *C. v. vaillanti* (16.7%), although absent in the other species of the genus.

2. Fusion of the frontoparietals. This state of characters is diagnostic for *C. delalandii* and *C. vaillanti* (both 100%) as it is always absent in all other *Chioninia* species.

3. Presence of a polyparietal plate. This new term is proposed here to designate the fusion of both parietals and the interparietal into a single large plate. This trait is diagnostic for *C. delalandii* and *C. vaillanti* (both 100%) as it is always absent in all other *Chioninia* species.

A list of diagnostic characters for newly described taxa and a description of their character variation is provided in the systematic account.

DISCUSSION

Molecular studies

Network and population analyses

Chioninia delalandii seems to have undergone a recent expansion in the Southern Islands as shown by the low level of mtDNA and nDNA differentiation between the island populations (Figs. V.5, V.6 and Appendix V.5), and population statistics (Table V.3). The *C. delalandii* individual found in Maio Island, in Vila do Maio, nearby the harbour, shares its mitochondrial and nuclear haplotypes with individuals from Santiago, indicating that it probably is a recent introduction from there. On the contrary to what was suggested by Brown *et al.* (2001), a taxonomic differentiation of the *C. delalandii* population from Fogo from the other island populations is not supported in either network or phylogenetic analyses, although it presents a lot of unique haplotypes and it is considered a distinct ESU based on the *Snn* values.

In *C. stangeri,* as expected, the Desertas group individuals share some mtDNA haplotypes between them and also nDNA haplotypes with S. Vicente, probably since these islands were connected during the sea level falls in the Pleistocene (*in* Carranza *et al.* 2001). However, the presumably near absence of gene flow after that event with S. Vicente Island allowed a low degree of differentiation to occur at the molecular level between these two populations, as shown in Fig. V.5.B3 and by *Snn* tests (Table V.2), nevertheless relevant to preserve in conservation terms. Hence, these two units were considered two distinct ESUs important to be taken into account in future management plans. Despite that, the two populations do not fulfil any of the criteria of the present integrative approach to be considered as different species or subspecies (see Fig. V.3).This taxon shares some nDNA haplotypes with *C. fogoensis* presumably due to incomplete lineage sorting.

Regarding *C. nicolauensis*, nDNA analysis points to an older separation of this taxon from the remaining taxa of the '*stangeri*' clade, supporting the phylogenetic analysis of mtDNA. Also *C. fogoensis* and *C. nicolauensis* seem to have suffered recent demographic expansions, probably posterior to the severe bottlenecks caused by the recent volcanic events which occurred on Santo Antão (0.09 Mya) and S. Nicolau (0.1 Mya) (Knudsen *et al.* 2003; Duprat *et al.* 2007).

As already suggested by Brown *et al.* (2001), the phylogenetic and the mitochondrial network analyses are new evidences of reciprocal monophyly within *C. spinalis* subspecies. Also there are substantial divergences between each island population based on the mtDNA *Snn* values (Table V.2), even though the substructuring of the nDNA marker, which is slow-evolving, is still less clear, with all *C. spinalis* subspecies sharing the most frequent haplotype.

As in *Tarentola darwini*, an endemic Cape Verdean gecko (Vasconcelos *et al.* 2010), *C. spinalis* presents northern and southern genetically differentiated mtDNA lineages in Santiago Island (Table V.2). However, in *C. spinalis* the northern lineage is restricted to the 'Tarrafal' basin that could constitute a physical barrier to limit the gene flow between the two ESUs (Fig. V.1). As in *Tarentola* geckos, the highest haplotypic diversity is present in mountainous islands such as Santo Antão, Fogo and S. Nicolau, which are also among the ones with the highest habitat diversity (Vasconcelos *et al.* 2010).

Biogeography

The results of the phylogenetic tree presented in Fig. V.3 suggest that the first speciation event of the genus *Chioninia* within the Cape Verde Islands may have been earlier than previously suggested by Carranza *et al.* (2001): between 11.6 and 9.9 Mya vs. 6.2 Mya, respectively. All the other presented dates for the colonization events within Cape Verde were also older than the ones inferred by Carranza *et al.* (2001), but in all cases younger than island ages. This difference in the age estimations may be the result of the different methods used to infer the dates of the cladogentic events: Kimura 2-parameter genetic distances in Carranza *et al.* (2001) and ML branch lengths and the NPRS algorithm implemented in the computer program r8s in this study. This situation highlights that since inference of divergence times is based on many assumptions, the present estimates are inevitably rough approximations. These are discussed in detail below and have to be taken very cautiously. In fact, these dates are more useful for giving a conception of the relative amount of time between different events indicated by branching points on the estimate of phylogeny than to precise dating of particular events.

According to the phylogeny presented in Fig. V.3, the direction of the main currents and trade winds and the age of the islands, it is probable that the first colonization event took place in some of the north-western islands. Radiometric age estimates of island ages based on potassium/argon (K/Ar) and on argon isotopes (^{40}Ar-^{39}Ar) indicate that the islands of the Cape Verde archipelago decrease in age from east to west. According to these analyses, Sal would be about 25.6 ± 1 My, Maio 21.1 ± 6.3 My, Santiago 10.3 ± 0.6 My, Santo Antão and Brava about 7.56 ± 0.56 and 5.9 ± 0.1 My, respectively, and S. Vicente about 6.6 to 5.68 My (see Mitchell-Thomé 1972; Stillman *et al.* 1982; Plesner *et al.* 2002; Torres *et al.* 2002; Duprat *et al.* 2007). Although there are no precise dates for S. Nicolau, it has been suggested that this island may be as old as 20 My, being the easternmost and thus the oldest island of the north-western group (see Fig. V.1; Bebiano 1932; Serralheiro & Urbaldo 1979). Thus, the present results rule out the possibility of Santo Antão or S. Vicente being the first islands of this group to be colonized, making S. Nicolau a very good candidate. According to this hypothesis, a propagule from S. Nicolau colonized the southern islands approximately 11.6–9.9 Mya, giving rise to the ancestor of the '*delalandii*' clade, which split about 6.9–5.9 Mya into the two sister taxa *C. vaillanti* and *C. delalandii*. Despite having originated in the Upper Miocene, diversification within *C. vaillanti* and *C. delalandii* did not occur until very recently (Fig. V.3), especially in *C. delalandii*, despite its large distribution range across all the southern islands (Fig. V.1) as suggested by its very recent population expansion (Table V.3). This pattern of large periods of stasis after a diversification event resulting in a pattern of long branches followed by a rapid population expansion could be explained by extinction as a result of the recurrent and intensive volcanic activity that occurred in some of the islands of this archipelago (see Carranza *et al.* 2001; Vasconcelos *et al.* 2010). Indeed, large quantities of recent subfossil material from a large lizard of the '*vaillanti'* type have been reported from Maio and Boavista (*in* Carranza *et al.* 2001). Approximately 8.9–7.6 Mya a speciation event separated the '*stangeri*' clade from the *C. coctei* + '*spinalis*' clade in the north-western islands. After this split, the members of the '*stangeri*' clade dispersed all across the north-western islands most probably following a stepping stone colonization pattern, starting with the colonization of the Desertas islands from S. Nicolau, some 6.9–5.9 Mya, and finishing with the colonization of Santo Antão approximately 4.9–4.2 Mya. It also shows that *C. spinalis salensis*, from the old eastern island of Sal, is sister to all the remaining members of the '*spinalis*' clade. Taking into account that both *C. coctei* and members of the '*stangeri*' clade are restricted to the north-western islands, it is suggested that diversification in the '*spinalis*' clade occurred from North to South. As in the case of *C. delalandii*, diversification in this clade was fast, although within the latter it occurred during the last 4 My and therefore there was enough time to produce monophyletic and relatively divergent mtDNA lineages that, with the connection limit of 95%, form independent networks (Fig. V.5).

As a result of the unknown historic distribution range of *C. coctei* it is not possible at the moment to infer its biogeography. The analysis of some subfossil material and other evidences suggests that this species may have been present in almost all the north-western islands in the past (Greer 1976; Andreone 2000; Carranza *et al.* 2001; Mateo *et al.* 2005; J.A. Mateo, pers. com.).

Due to the taxonomical and systematic reassessment and to the increase of knowledge regarding within-island distributions, the conservation status of some taxa and populations of *Chioninia* should be updated. These include, for example, the case of the population of S. Vicente of *C. stangeri*, the population of Rombos of *C. delalandii*, both considered as Data Deficient (Schleich 1996) and the new taxa presently described.

Morphological studies

Two of the main clades identified within the genus *Chioninia* by the molecular results are characterized by cephalic scalation characteristics previously described, which may constitute morphological synapomorphies in the light of the genetic results: (i) the division of the posteriormost supralabial for the '*stangeri*' clade B: *C. nicolauensis*, *C. fogoensis* and *C. stangeri* and (ii) the fusion of the frontoparietals as well as the presence of the polyparietal plate for the '*delalandii*' clade A: *C. delalandii* and *C. vaillanti*. The polyparietal plate also constitutes an absolute synapomorphy in the sense that this characteristic is absent from all other known Lygosomine skinks species, according to Greer (1976). Additionally, all the *C. spinalis* subspecies may present a very low number of supraciliaries (most frequently three or four, but ranging from two to five, apparently resulting from the fusion of the first two) in comparison with all other *Chioninia* species (ranging from four to seven). Nevertheless, this polymorphic character is not consistent within the *C. spinalis* subclades, and thus it does not constitute an unambiguous diagnostic character.

KEY TO THE CAPE VERDEAN SKINKS (GENUS *CHIONINIA*)

The present key is intended to identify species of the genus *Chioninia* (Scincidae), which can be easily distinguished from the other genera of Cape Verdean reptiles (*Hemidactylus* and *Tarentola,* Gekkonidae) by the presence of eyelids, of several big scales on the top of the head and of uniform bi- or tricarenated cycloid scales covering the body.

1. Frontoparietals fused into a single scale, both parietals and the interparietal fused together into a single polyparietal plate – '*delalandii*' clade **2**

1'. Two separated frontoparietal scales, two parietals separated by the median interparietal **3**

2. Presence of a vertebral light stripe, a relatively big sized skink with a robust morphology and a short snout (adults usually >90 mm SVL) brownish eyelids in live specimens .... *Chioninia vaillanti*

2'. Most frequently absence of a vertebral light stripe, a medium-sized skink with a long and pointed snout (adults usually <90 mm SVL), brightly yellow-coloured eyelids in live specimens .... *Chioninia delalandii*

3. A 'giant' skink (adults >200 mm SVL), >130 transverse rows of dorsal scales, parietals separated by the interparietal, five cuspid teeth ....*Chioninia coctei* (extinct)

3'. A small to medium-sized skink (adults <100 mm SVL), <100 transverse rows of dorsal scales, parietals in contact behind the interparietal **4**

4. Posteriormost supralabial divided – '*stangeri*' clade **5**

4'. Posteriormost supralabial not divided .... *Chioninia spinalis*

5. Less than 70 transverse rows of dorsal scales .... *Chioninia stangeri*

5'. More than 80 transverse rows of dorsal scales **6**

6. Most often, first supraoculars and frontal separated or barely in point contact; throat with grey marblings, sometimes very dark; in living specimens, chin shields with a dark grey patch (less frequently with an orange/brown background colouration), and ventrum yellowish, sometimes with two ventro lateral light orange trails extending from forelimbs to hindlimbs; only present on Santo Antão .... *Chioninia fogoensis*

6'. Most often, first supraoculars and frontal in broad contact; throat without grey marblings, or very faded when present; in living specimens only, throat covered by a bright red brick patch extending to the lateral side of the chin shields, and ventrum whitish, always with two ventrolateral well contrasted bright orange trails extending from forelimbs to hindlimbs; only present on São Nicolau ....*Chioninia nicolauensis*

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SUPPORTING INFORMATION

Appendix V.1 Details of material used in the network and population studies.

Code	Taxa	Island	Locality	Genbank
C001	*C. stangeri*	ra	Ponta de Casa	HQ316417
C002		SV	Salamansa	HQ316430
C008		SV	Calhau	HQ316429
C009		SV	Calhau	HQ316428
C010		SL	Água Doce	HQ316418
C013		SL	Água Doce	HQ316419
C016		SL	Água Doce	HQ316420
C018		SL	Água Doce	HQ316415
C019		SL	Água Doce	HQ316423
C024		SL	Ponta de Praia	HQ316425
C026		SL	Pr. de Palmo a Tostão	HQ316421
C027		SL	Monte Espia	HQ316424
C029		SL	Topinho de Nhô Lopes	HQ316422
C030		SL	Ribeira de Casa	HQ316416
C032		SL	Ribeira de Freira	HQ316426
C035		SL	Ribeira de Freira	HQ316427
C038	*C. fogoensis*	SA	Alto Mira	HQ316302
C039		SA	Alto Mira	HQ316303
C041		SA	Manta Velha-Endriano	HQ316304
C042		SA	Ladeirinha	HQ316305
C044		SA	Lombo de Diogo	HQ316306
C046		SA	Sabidela	HQ316307
C048		SA	Lagoa	HQ316308
C051		SA	Espongueiro cross	HQ316309
C052		SA	Chã do Mato – Losna	HQ316310
C055		SA	Losna	HQ316311
C060		SA	Rabo Curto	HQ316312
C062		SA	Cova de Urgeiro	HQ316313
C065		SA	Bordeira	HQ316314
C067		SA	Lombo Figueira	HQ316315
C070		SA	Os Lombos	HQ316316
C073		SA	Gudo do Salto Preto	HQ316317
C074		SA	Chã de Moroços	HQ316318
C075		SA	Chã de Norte	HQ316319
C078		SA	Chã de N – Aldeia	HQ316320
C080		SA	Aldeia	HQ316321
C084		SA	Chã de Norte	HQ316322
C088		SA	Chã de Cruz	HQ316323
C090		SA	Chã de Feijoal	HQ316324
C094		SA	Chã de Lagoinha	HQ316325
C095		SA	S.Tomé	HQ316326
C097		SA	Poio	HQ316327
C102		SA	Ribeira de Bodes	HQ316328
C103		SA	Ribeira de Bodes	HQ316329
C104		SA	Ribeira de Bodes	HQ316330
C105		SA	Chã de Banca	HQ316331
C109	*C. fogoensis*	SA	Chã de Nhã Nica	HQ316332
C115		SA	Tarrafal - Cpo. Redondo	HQ316333
C117	*C. nicolauensis*	SN	Praia Branca	HQ316301
C121		SN	Luís Afonso	HQ316300
C122		SN	Luís Afonso	HQ316298
C124		SN	Luís Afonso	HQ316290
C126		SN	Água das Patas	HQ316291
C130		SN	Cabeçalinho	HQ316292
C134		SN	Monte Gordo	HQ316295
C136		SN	Campo do Porto	HQ316293
C139		SN	Covoada	HQ316296
C140		SN	Hortelão	HQ316297
C144		SN	Ponta da Pr. do Garfo	HQ316299
C145		SN	Ponta Larga	HQ316294
C518	*C. delalandii*	M	Vila do Maio	HQ316207
C146		ST	S. Lourenço dos Órgãos	HQ316244
C148		ST	S. Lourenço dos Órgãos	HQ316245
C150		ST	S. Lourenço dos Órgãos	HQ316246
C151		ST	Cidade Velha	HQ316247
C156		ST	São Jorge	HQ316248
C159		ST	Serra Malagueta	HQ316249
C162		ST	Sta. Catarina	HQ316250
C165		ST	Sta. Catarina	HQ316251
C166		ST	Assomada	HQ316252
C169		ST	Ribeirão Chiqueiro	HQ316253
C176		ST	S. Nicolau Tolentino	HQ316254
C178		ST	S. Nicolau Tolentino	HQ316255
C181		ST	S. Nicolau Tolentino	HQ316256
C184		ST	Ribeira Seca	HQ316257
C186		ST	Pedra Badejo	HQ316258
C200		ST	Praia Baixo	HQ316259
C203		ST	Praia Baixo	HQ316260
C205		ST	Nossa Sra. da Luz	HQ316261
C209		ST	S. Lourenço dos Órgãos	HQ316262
C210		ST	Calheta São Miguel	HQ316263
C213		ST	Calheta São Miguel	HQ316264
C215		ST	S. Lourenço dos Órgãos	HQ316265
C224		ST	Pedra Barro	HQ316266
C227		ST	Ribeirão Galinha	HQ316267
C228		ST	Achada Além	HQ316268
C231		ST	Achada Além	HQ316269
C236		ST	Achada Além	HQ316270
C252		ST	Chão Bom	HQ316271
C254		ST	Montanhinha	HQ316272
C260		ST	Chão de Tanque	HQ316273
C266		ST	S. Lourenço dos Órgãos	HQ316274

Code	Taxa	Island	Locality	Genbank
C268	*C. delalandii*	ST	S. Lourenço dos Órgãos	HQ316275
C270		ST	S. Lourenço dos Órgãos	HQ316276
C284		ST	Trás os Montes	HQ316277
C290		ST	Tarrafal	HQ316278
C292		ST	Flamengos	HQ316279
C299		ST	Arribada	HQ316280
C300		ST	Tarrafal	HQ316281
C305		ST	Figueira das Naus	HQ316282
C307		ST	Jalalo Ramos	HQ316283
C309		ST	Achada Leitão	HQ316284
C311		ST	Serra Malagueta	HQ316285
C316		ST	Picos	HQ316286
C317		ST	Porto Madeira	HQ316287
C319		ST	Barragem	HQ316288
C321		ST	Barnabé	HQ316289
C352		B	Favatal	HQ316208
C353		B	Lima Doce	HQ316209
C357		B	Espradinha	HQ316210
C359		B	Fajã de Água	HQ316211
C362		B	Lomba Lomba	HQ316212
C365		B	Cova Rodela	HQ316213
C371		B	Palhal	HQ316214
C372		B	Chão de Sousa	HQ316215
C376		B	Campo Baixo	HQ316216
C379		B	Baleia	HQ316217
C383		B	Mato Grande	HQ316218
C388		B	Cachaço	HQ316220
C392		B	Morro Largo	HQ316221
C393		B	Campo da Porca	HQ316219
C396		B	Chão Queimado	HQ316222
C331		F	Lagariça	HQ316223
C332		F	Lagariça	HQ316224
C336		F	Campanas de Baixo	HQ316225
C339		F	Campanas de Cima	HQ316226
C342		F	Campanas de Baixo	HQ316227
C401		F	São Jorge	HQ316228
C408		F	Campanas de Baixo	HQ316229
C413		F	Galinheiro	HQ316230
C417		F	Velho Manuel	HQ316231
C427		F	Ledo	HQ316232
C430		F	Mosteiros	HQ316233
C432		F	Fonsaco	HQ316234
C441		F	Sta. Catarina do Fogo	HQ316235
C444		F	S. Filipe	HQ316236
C446		F	Monte Vermelho	HQ316237
C450		F	Cova Figueira	HQ316238
C458		F	Miguel Gonçalves	HQ316239
C460		F	Bordeira	HQ316240
C466		F	Bangueira	HQ316241
C468		F	Vulcão	HQ316242
C476	*C. delalandii*	F	Monte Velha	HQ316243
C258	*C. v. vaillanti*	ST	Montanhinha	HQ316198
C261		ST	S. Lourenço dos Órgãos	HQ316197
C264		ST	S. Lourenço dos Órgãos	HQ316196
C293		ST	Flamengos	HQ316199
C297		ST	Flamengos	HQ316200
C302		ST	Serra Malagueta	HQ316195
C412	*C. v. xanthotis*	F	Galinheiro	HQ316203
C433		F	Fonsaco	HQ316202
C436		F	Fonsaco	HQ316201
C472		F	Monte Velha	HQ316204
C473		F	Monte Velha	HQ316205
Cro1		ro	Cima Islet	HQ316206
C543	*C. s. boavistensis*	BV	Ponta do Sol	HQ316382
C546		BV	Lomba	HQ316383
C547		BV	Lomba	HQ316384
C552		BV	Lomba	HQ316385
C553		BV	Lomba	HQ316386
C557		BV	Rabil	HQ316387
C558		BV	Rabil	HQ316388
C561		BV	Alto de areia	HQ316389
C563		BV	Gata	HQ316390
C564		BV	Lomba de Curral	HQ316391
C565		BV	Lomba de Curral	HQ316392
C566		BV	Lomba de Curral	HQ316393
C567		BV	Lomba de Curral	HQ316394
C568		BV	Morrinho João Fitôr	HQ316395
C569		BV	Ervatão	HQ316396
C572		BV	Chão de Palhal	HQ316397
C575		BV	Porto Ferreira	HQ316398
C576		BV	Porto Ferreira	HQ316399
C579		BV	Espigueira	HQ316400
C582		BV	Bofareira	HQ316401
C584		BV	Morro de Areia	HQ316402
C585		BV	Morro de Areia	HQ316403
C587		BV	Chã de Calheta	HQ316404
C588		BV	João Gago	HQ316405
C523	*C. s. salensis*	S	Murdeira	HQ316406
C524		S	Curralona	HQ316407
C527		S	Pedra Lume	HQ316408
C531		S	Parda	HQ316409
C534		S	Monte Grade	HQ316410
C537		S	Ponta Palhona	HQ316411
C538		S	Buracona	HQ316412
C593		S	Morrinho Branco	HQ316413
C594		S	Santa Maria	HQ316414
C172	*C. s. santiagoensis*	ST	Ribeirão Chiqueiro	HQ316364
C174		ST	Ribeirão Chiqueiro	HQ316365
C187		ST	Porto Gouveia	HQ316366
C192		ST	Ponta Bombardeiro	HQ316367

Code	Taxa	Island	Locality	Genbank
C195	*C. s. santiagoensis*	ST	S. Martinho Pequeno	HQ316368
C197		ST	João Varela	HQ316369
C208		ST	Cancelo	HQ316370
C218		ST	Ribeira da Barca	HQ316371
C232		ST	Achada Além	HQ316372
C240		ST	Santa Ana	HQ316373
C243		ST	Santa Ana	HQ316374
C247		ST	Praia	HQ316375
C273		ST	Santa Catarina	HQ316376
C277		ST	Ponta do Lobrão	HQ316377
C289		ST	Tarrafal	HQ316378
C251		ST	Chão Bom	HQ316379
C282		ST	Trás os Montes	HQ316380
C324		ST	Barnabé	HQ316381
C400	*C. s. spinalis*	F	São Jorge	HQ316354
C407		F	Campanas de Baixo	HQ316355
C419		F	Velho Manuel	HQ316356
C424		F	Ledo	HQ316357
C438		F	Mosteiros	HQ316358
C443		F	S. Filipe	HQ316359
C453		F	Cova Figueira	HQ316361
C455		F	Fonte Aleixo	HQ316362
C463		F	Bangueira	HQ316360
C470		F	Vulcão	HQ316363
C478	*C. s. maioensis*	M	Calheta de Cima	HQ316334
C481		M	Monte Batalha	HQ316335
C485		M	Rocha Albarda	HQ316336
C487		M	Rocha Albarda	HQ316337
C490		M	Morro	HQ316338
C491		M	Terras Salgadas	HQ316339
C493		M	Casas Velhas	HQ316340
C494		M	Fig. Horta - Pilão Cão	HQ316341
C497		M	Ribeira D. João	HQ316342
C498		M	Cascabulho	HQ316343
C500		M	Monte Branco	HQ316344
C502		M	Pilão Cão de Cima	HQ316345
C504		M	Praia Vila do Maio	HQ316346
C505		M	Praia Vila do Maio	HQ316347
C508		M	Pêro Vaz	HQ316348
C509		M	Pêro Vaz	HQ316349
C510		M	Ponta Rabil	HQ316350
C513		M	Monte Batalha	HQ316351
C514		M	Monte Vermelho	HQ316352
C516		M	Figueira Lapa	HQ316353
M022	*C. delalandii*	B	Cachaço	HQ316443
M041		B	Furna	HQ316444
M042		B	Cachaço	HQ316445
M019		F	Mosteiros	HQ316441
M038	*C. delalandii*	F	Mosteiros	HQ316440
M056		M	Vila do Maio	HQ316442
M021		ro	Ilhéu Grande	HQ316447
M039		ro	Ilhéu Grande	HQ316448
M040		ro	Ilhéu Grande	HQ316446
M020		ST	Chão Bom	HQ316437
M047		ST	Tarrafal	HQ316436
M067		ST	Serra Malagueta	HQ316439
M068		ST	Picos	HQ316438
M023	*C. v. xanthotis*	F	Cova Figueira	HQ316435
M048		F	Atalaia	HQ316434
M050	*C. v. vaillanti*	ST	Santa Cruz	HQ316432
M051		ST	Santa Cruz	HQ316433
M052		ST	Santa Cruz	HQ316431
M034	*C. nicolauensis*	SN	Faro de Barril	HQ316462
M035		SN	Faro de Barril	HQ316463
M058	*C. fogoensis*	SA	Chã de Lagoa	HQ316457
M059		SA	Chã de Lagoa	HQ316458
M061		SA	Chã de Lagoa	HQ316461
M062		SA	Ponta do Brejo	HQ316456
M063		SA	Ribeira da Cruz	HQ316460
M064		SA	Dogoi	HQ316459
M065	*C. stangeri*	br	-	HQ316454
M066		br	-	HQ316455
M013		ra	-	HQ316452
M031		ra	-	HQ316451
M015		SL	Sta. Luzia	HQ316449
M033		SL	Sta. Luzia	HQ316450
M018		SV	Calhau	HQ316453
M009	*C. s. salensis*	S	Buracona	HQ316469
M025		S	Pedra Lume	HQ316468
M011	*C. s. santiagoensis*	ST	Chão Bom	HQ316472
M012		sm	Sta. Maria Islet	HQ316475
M028		ST	Chão Bom	HQ316473
M029		sm	Sta. Maria Islet	HQ316470
M030		sm	Sta. Maria Islet	HQ316471
M043		ST	Tarrafal	HQ316474
M014	*C. s. spinalis*	F	Achada Furna	HQ316479
M075		F	Cova Figueira	HQ316476
M076		F	Lomba	HQ316478
M077		F	Lomba	HQ316477
M026	*C. s. boavistensis*	BV	Sal Rei	HQ316465
M027		BV	Curral Velho	HQ316466
M010		sr	-	HQ316467
M057		cv	-	HQ316464
M054	*C. s. maioensis*	M	Praia Preta	HQ316481
M055		M	Praia Preta	HQ316480

br: Branco, B: Brava, BV: Boavista, F: Fogo, M: Maio, ra: Raso, ro: Rombos, SA: Santo Antão, SL: Santa Luzia, SN: São Nicolau, ST: Santiago, SV: São Vicente.

Appendix V.2 Voucher specimens used on the morphological study (*n*=275). See Materials and methods section for museum acronyms.

Chioninia vaillanti (*n*=9). *Chioninia v. vaillanti* (*n*=6). **Santiago**: BMNH 2000.11, Sta. Cruz; BMNH 1948.8.18.25, .26, .27, .28, .29 (previously 66.4.10.46, .47, .48, .49, .50, respectively) (syntypes of *Mabuia vaillanti*), no exact locality. *Chioninia v. xanthotis* (*n*=3). **Fogo**: BMNH 2000-8, Cova Figueira; BMNH 2000-9, near Mosteiros. **Rombos**: MNHN 1965-229, Ilhéu de Cima, coll. Père R. de Naurois in 1965.*Chioninia delalandii* (*n*=79). **Brava**: MZB 2010-0987, -0988, -0989, at 1km from Cachaço; MZB 2010-0990, Ribeira (Porto Ancião); MZB 2010-0991, -0992, at 3km from Furna; MZB 2010-0993, BMNH 2000-19, -20, DBULPGC105, no exact locality. **Fogo**: MNHN 1935-191,- 192, Curral Grande & Pico Peres (500-800m); MZB 2010-0994, -0995, Mosteiros airport; MZB 2010-0996, -0997, -0998 Atalaia; BMNH 2000-17, DBULPGC104, Mosteiros; BMNH 2000-18, MZB 2010-0999, Chã das Caldeiras; MZB 2010-1000, -1001, -1002, -1003, -1004, MNHN 1935-189, -190, no exact locality. **Maio**: MZB 2010-1005, Vila do Maio. **Rombos**: MZB 2010.1006, Ilhéu Grande; DBULPGC103, BMNH 2000-15, -16, no exact locality. **Santiago**: MNHN 1935-193, 1965-248; MZB 2010-1007, -1008, -1009, -1010, -1011, -1012, Arlinda; BMNH 2000-13, MZB 2010-1013, -1014, -1015, Tarrafal; MZB 2010-1016, Malagueta; BMNH 2000-12, Serra Malagueta; MZB 2010-1017, -1018, -1019, -1020, -1021, Rui Vaz; MZB 2010-1022, DBULPGC102, Chão Bom; MZB 2010-1023, -1024, ilhéu de Santa Maria; BMNH 2000-14, Picos; from MZB 2010-1025 to MZB 2010-1041 (17 specimens), no exact locality. **Unknown Island**: BMNH 1946.8.19.55, .56 (syntypes of *Euprepis Belcheri*), 'Borneo' (?); MNHN 263 (holotype of *Euprepes Delalandii*), 'Cap'; MNHN 1679, 1849.

Chioninia nicolauensis (*n*=10). **São Nicolau**: BMNH 2000-22, MZB 2010-1042, -1043, Faro (do Barril), 9km NW Tarrafal; BMNH 2000-21, Cachaço; MZB 2010-1044, -1045, -1046, viewpoint at 1km from Tarrafal; MZB 2010-1047, Queimada (?); DBULPGC106, no exact locality; ZSM 1.1982.1 (holotype of *Mabuya fogoensis nicolauensis*), 'S. Nicolau'.

Chioninia fogoensis (*n*=26). **Santo Antão**: MNHN 1935-194, Cova crater; BMNH 2000-25, DBLPGC107, MZB 2010-1048, -1049, -1050, road to Lagoa; BMNH 2000-24, MZB 2010-1051, Lagoa centre village; DBULPGC108, MZB 2010-1052, -1053, 5km Porto Novo; BMNH 2000-23, Ribeira da Cruz; BMNH 2000-26, Dogoi; ZSM 23.1982.2, .4, .6, .8 (paratypes of *Mabuya fogoensis antaoensis*), 'S. Antão'. Unknown Island: BMNH 1946.8.18.8, .9, .10, .11, .12, .13, .14, .16 (all syntypes *of Euprepes fogoensis*, previously labelled all together under the number BMNH 65.5.13.6) 'Fogo' (?); BMNH 1946.8.19.53 (syntypes *of Euprepes fogoensis*) 'St. Vincent' (?).

Chioninia stangeri (*n*=57). **Branco**: MNHN 1884-238, 1999-8249 (formerly 1884-238), 1884-153, -239, 1965-423, -424, -425, -246. **Raso**: MNHN 1965-247, -421, -422, 1962-955, -956, -957, -958, -959, BMNH 1946.8.18.43 (one of the types of *Euprepes hopfferi*; previously BMNH 75.4.26.9); MZB 2010-1054, -1055, -1056, -1057, DBULPGC112, BMNH 2000-31, -32. **Santa Luzia**: MNHN 1965-232 to -244, MZB 2010-1058, DBULPGC111, BMNH 2000-30. **São Vicente**: BMNH 2000-27, -28, MZB 2010-1059, -1060, -1061, Calhau; DBULPGC109, MZB 2010-1062, near Calhau; MZB 2010-1063, Topim; MNHN 1965-245, Ilhéu dos Pássaros; MNHN 5887, 1999-8248 (formerly 5887) no exact locality. Unknown Island: BMNH 1946.8.1 to .4 (all syntypes of *Euprepes stangeri*), 'W. Africa' (?); MNHN 5524; ZMB 6154 (photography only, available at www.biologie.uni-ulm.de/systax/), syntype of *Euprepis polylepis*, Peters 1870, 'Africa occidentali (Demara)' (?)

Chioninia coctei (*n*=13). **Branco**: MNHN 1884-148, -227, -228, -229, -231, -233, -236, -237. Unknown Island: MNHN 1906-295, 1987-941 (the later perhaps from Branco), MNHN 8299 (holotype of *Euprepes coctei*, 'Côte d'Afrique'); BMNH 91.9.24.1, .2 (from Branco or Raso).

Chioninia spinalis (*n*=81). *Chioninia s. salensis* (*n*=19). **Sal**: MZB 2010-1064, -1065, DBULPGC117, Buracona; MZB 2010-1066, -1067, -1068, -1069, -1070, 7 km S. airport; MZB 2010-1071, 9 km airport; BMNH 2000-43, Pedra Lume; MNHN 1923-166, 1935-197 (holotype of *Mabuia salensis*), MNHN 1935-195, -196, -198 (paratype of *Mabuia salensis*), MNHN 1965-417 to 420, no exact locality. Unknown Island: MNHN 1681. *Chioninia s. santiagoensis* (*n*=23).

Santiago: BMNH 2000-35, -36, -37, -38, DBULPGC115, MZB 2010-0979, Ilhéu Santa Maria; from MZB 2010-0962 to MZB 2010-0977 (16 specimens), unknown locality; MZB 2010-0978, Tarrafal; DBULPGC114, Chão Bom. *Chioninia s. spinalis* (*n*=19). **Fogo**: MZB 2010-1072, 3km from Cova Figueira; MZB 2010-1073, Ponta da Lagoa; MZB 2010-1074, -1075, -1076, -1077, -1078, 10 km North of Cova Figueira; MZB 2010-1079, Furna, Ilhéu de Contenda; MZB 2010-1080, -1081, -1082, DBLPGC116; BMNH 2000-41, -42, 7 km North of Achada; BMNH 2000-39, -40, Ilhéu de Contenda, BMNH 1906.3.30.40, .41 (lectotype of *Mabuia spinalis*), Igreja; BMNH 1906.3.30.41 (paralectotype of *Mabuia spinalis*), Igreja. *Chioninia s. maioensis* (*n*=8). Maio: MZB 2010-1083, near Pilão Cão; BMNH 2000-33, Praia Preta; MZB 2010-1084, -1085, Vila do Maio; MZB 2010-1086, Ponta Pedrenau; MZB 2010-1087, DBULPGC113, Morrinho; BMNH 2000-34, Santo António. *Chioninia s. boavistensis* (*n*=11). **Boavista**: MNHN 1965-251, East side; BMNH 2000-44, MZB 2010-0980, -0981, -0982, -0983, Sal Rei; DBULPGC118, Ilhéu de Sal Rei; BMNH 2000-45, MZB 2010-0984, -0985, Curral Velho; MZB 2010-0986, 2.5 km East of Sal Rei.

Appendix V.3 List of the taxa, specimen codes and origins, collection and GenBank accession numbers of the sequences used in this study published by Brehm *et al.* 2001(a), Brown *et al.* 2001(b), Carranza *et al.* 2001(c) and Mausfeld *et al.* 2002(d). Dashes represent missing data.

Taxa	Code	Island	Locality	Voucher	GenBank codes		
					12S	**cyt *b***	**CO1**
C. v.vaillanti	M51(c)	ST	Santa Cruz	DBULPGC-1001	AF280200	AF280332	AF280266
	M50(c)	ST	Santa Cruz	BMNH2000.10	AF280199	AF280331	AF280265
	M52(c)	ST	Santa Cruz	BMNH2000.11	AF280201	AF280333	AF280267
C. v. xanthotis	M23(c)	F	Cova Figueira	BMNH2000.8	AF280196	AF280328	AF280262
	M48(c)	F	Atalaia	DBULPGC-100	AF280197	AF280329	AF280263
	M49(c)	F	Feijoal	BMNH2000.9	AF280198	AF280330	AF280264
	R92(a)	F	-	UMa (2)	AF335031	AF335030	-
	R96(a)	F	-	UMa (2)	AF335047	AF335046	-
C. delalandii	M41(c)	B	Furna	BMNH2000.19	AF280194	AF280326	AF280260
	M22(c)	B	Cachaço	DBULPGC-105	AF280193	AF280325	AF280259
	M42(c)	B	Cachaço	BMNH2000.20	AF280195	AF280327	AF280261
	R55(a)	B	-	UMa (2)	AF335033	AF335032	-
	BR1(b, 1)	B	Vila Nova Sintra	-	-	AJ305017	-
	BR2(b)	B	Vila Nova Sintra	-	-	AJ305018	-
	BR3(b, 1)	B	Vila Nova Sintra	-	-	AJ305017	-
	M56	M	Vila do Maio				
	M67(c)	ST	Serra Malagueta	BMNH2000.12	AF280188	AF280320	AF280254
	M20(c)	ST	Chão Bom	DBULPGC-102	AF280186	AF280318	AF280252
	M46	ST	-				
	M47(c)	ST	Tarrafal	BMNH2000.13	AF280187	AF280319	AF280253
	M68(c)	ST	Picos	BMNH2000.14	AF280189	AF280321	AF280255
	R43(a)	ST	-	UMa (2)	AF335017	AF335016	-
	R49(a)	ST	-	UMa (2)	AF335041	AF335040	-
	R51(a)	ST	-	UMa (2)	AF335019	AF335018	-
	Z3(d)	ST	-	ZFMK 75064	AY070344	-	-
	SAN1(b)	ST	Praia	-	-	AJ305008	-
	SAN2(b)	ST	Praia	-	-	AJ305009	-
	SAN3(b)	ST	Praia	-	-	AJ305010	-
	IL8(b)	ST	Ilhéu Sta. Maria	-	-	AJ305014	-
	IL9(b)	ST	Ilhéu Sta. Maria	-	-	AJ305015	-
	IL10(b)	ST	Ilhéu Sta. Maria	-	-	AJ305016	-
	M19(c)	F	Mosteiros	BMNH2000.17	AF280183	AF280315	AF280249
	M38(c)	F	Mosteiros	DBULPGC-104	AF280184	AF280316	AF280250
	M45(c)	F	Chã das Caldeiras	BMNH2000.18	AF280185	AF280317	AF280251
	R52(a)	F	-	UMa (2)	AF335021	AF335020	-
	R98(a)	F	-	UMa (2)	AF335025	AF335024	-
	R99(a)	F	-	UMa (2)	AF335045	AF335044	-
	FOG1(b)	F	São Filipe	-	-	AJ305011	-
	FOG2(b)	F	São Filipe	-	-	AJ305012	-
	FOG3(b)	F	São Filipe	-	-	AJ305013	-
	M40(c)	ro	Ilhéu Grande	DBULPGC-103	AF280192	AF280324	AF280258
	M21(c)	ro	Ilhéu Grande	BMNH2000.15	AF280190	AF280322	AF280256
	M39(c)	ro	Ilhéu Grande	BMNH2000.16	AF280191	AF280323	AF280257
C. nicolauensis	M34(c)	SN	Cachaço	BMNH2000.21	AF280173	AF280305	AF280239
	M17(c)	SN	Faro de Barril	DBULPGC-106	AF280172	AF280304	AF280238
	M35(c)	SN	Faro de Barril	BMNH2000.22	AF280174	AF280306	AF280240
	R01(a)	SN	-	UMa (2)	AF335043	AF335042	-
	R72(a)	SN	-	UMa (2)	AF335061	AF335060	-
C. fogoensis	M63(c)	SA	Ribeira da Cruz	BMNH2000.23	AF280179	AF280311	AF280245

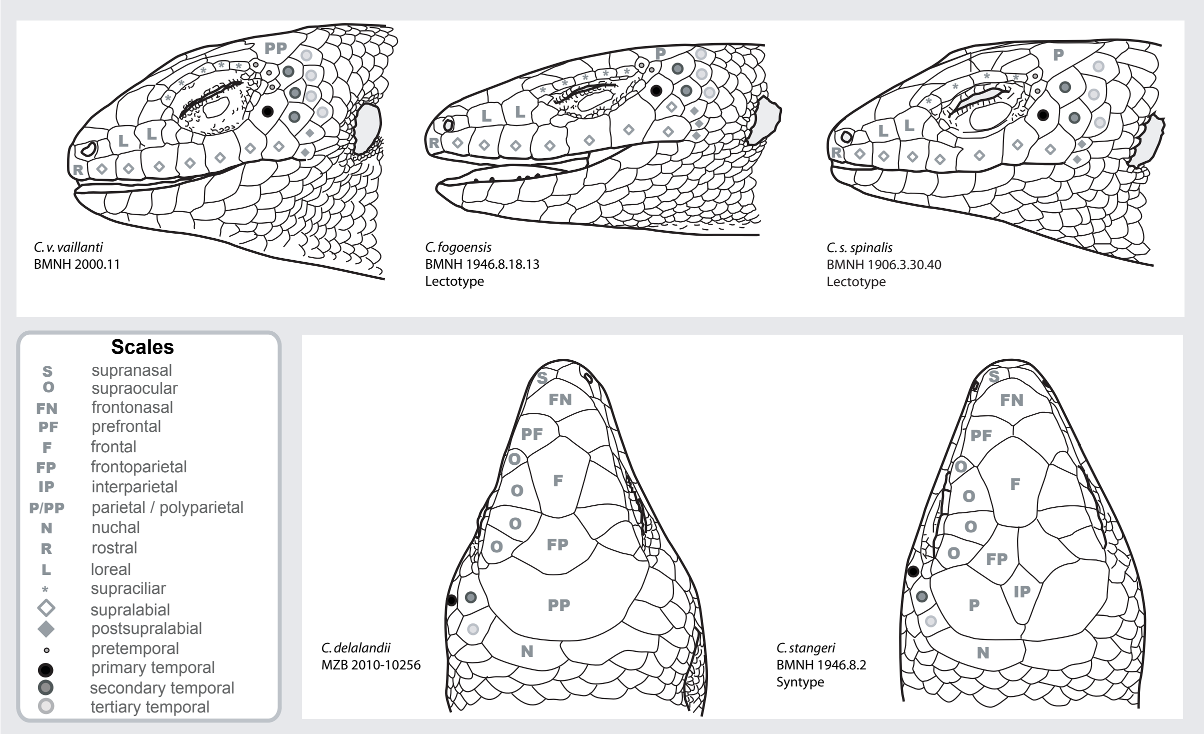
Taxa	**Code**	**Island**	**Locality**	**Voucher**	**GenBank codes**		
					12S	**cyt *b***	**CO1**
C. fogoensis	M58(c)	SA	Chã de Lagoa	DBULPGC-107	AF280175	AF280307	AF280241
	M59(c)	SA	Chã de Lagoa	BMNH2000.24	AF280176	AF280308	AF280242
	M62(c)	SA	Ponta do Brejo	DBULPGC-108	AF280178	AF280310	AF280244
	M60(c)	SA	Chã de Lagoa	BMNH2000.25	AF280177	AF280309	AF280243
	M64(c)	SA	Dogoi	BMNH2000.26	AF280180	AF280312	AF280246
	R34(a)	SA	-	UMa (2)	AF335023	AF335022	-
	R35(a)	SA	-	UMa (2)	AF335053	AF335052	-
	R36(a)	SA	-	UMa (2)	AF335029	AF335028	-
	R80(a)	SA	-	UMa (2)	AF335065	AF335064	-
	R100(a)	SA	-	UMa (2)	AF335027	AF335026	-
	Cv133(a)	SA	-	UMa (2)	AF335055	AF335054	-
C. stangeri	M65(c)	br	-	DBULPGC-110	AF280170	AF280302	AF280236
	M66(c)	br	-	BMNH2000.29	AF280171	AF280303	AF280237
	M32(c)	ra	-	DBULPGC-112	AF280164	AF280296	AF280230
	M13(c)	ra	-	BMNH2000.31	AF280162	AF280294	AF280228
	M31(c)	ra	-	BMNH2000.32	AF280163	AF280295	AF280229
	R76(a)	ra	-	UMa (2)	AF335051	AF335050	-
	R86(a)	ra	-	UMa (2)	AF335079	AF335078	-
	M15(c)	SL	-	DBULPGC-111	AF280165	AF280297	AF280231
	M33(c)	SL	-	BMNH2000.30	AF280166	AF280298	AF280232
	M18(c)	SV	Calhau	BMNH2000.27	AF280169	AF280301	AF280235
	M44(c)	SV	Calhau	DBULPGC-109	AF280167	AF280299	AF280233
	M16(c)	SV	Calhau	BMNH2000.28	AF280168	AF280300	AF280234
	SV1.1(b)	SV	Calhau	UMa-	-	AJ305005	-
	SV1.2(b)	SV	Calhau	UMa-	-	AJ305006	-
	SV1.3(b)	SV	Calhau	-	-	AJ305007	-
	R78(a)	SV	-	UMa (2)	AF335063	AF335062	-
	SV0.1(b)	SV	Morro Branco	-	-	AJ305003	-
	SV0.3(b)	SV	Morro Branco	-	-	AJ305004	-
C. coctei	M241	br or ra	-	BMNH91.9.24.1	AF280182	AF280314	AF280248
	M242 (c)	br or ra	-	BMNH91.9.24.2	AF280181	AF280313	AF280247
C. s. salensis	M9(c)	S	Buracona	DBULPGC-117	AF280152	AF280284	AF280218
	M25(c)	S	Pedra Lume	BMNH2000.43	AF280153	AF280285	AF280219
	R79(a)	S	-	UMa (2)	AF335057	AF335056	-
	R82(a)	S	-	UMa (2)	AF335039	AF335038	-
	SAL1(b)	S	Santa Maria	-	-	AJ304999	-
	SAL2(b)	S	Santa Maria	-	-	AJ305000	-
	SAL3(b)	S	Santa Maria	-	-	AJ305001	-
	Z2(d)	S	-	ZFMK75063	AY070327	-	-
C. s. santiagoensis	M28(c)	ST	Chão Bom	BMNH2000.35	AF280147	AF280279	AF280213
	M11(c)	ST	Chão Bom	DBULPGC-114	AF280146	AF280278	AF280212
	M43(c)	ST	Tarrafal	BMNH2000.36	AF280148	AF280280	AF280214
	M29(c)	ST	Ilhéu Sta. Maria	BMNH2000.37	AF280149	AF280281	AF280215
	M30(c)	ST	Ilhéu Sta. Maria	DBULPGC-115	AF280150	AF280282	AF280216
	M12(c)	ST	Ilhéu Sta. Maria	BMNH2000.38	AF280151	AF280283	AF280217
	IL3(b)	ST	Ilhéu Sta. Maria	-	-	AJ304995	-
	IL4(b)	ST	Ilhéu Sta. Maria	-	-	AJ304996	-
	R60(a)	ST	-	UMa (2)	AF335067	AF335066	-
	Cv58(a)	ST	-	UMa (2)	AF335059	AF335058	-
	Z1(d)	ST	-	ZFMK75065	AY070343	-	-
C spinalis spinalis	M76(c)	F	Lomba,	BMNH2000.39	AF280157	AF280289	AF280223
	M77(c)	F	Lomba,	BMNH2000.40	AF280158	AF280290	AF280224
	M37(c)	F	Achada Furna, 7 km N	DBULPGC-116	AF280155	AF280287	AF280221
	M36(c)	F	Achada Furna, 7 km N	BMNH2000.41	AF280154	AF280286	AF280220

Taxa	**Code**	**Island**	**Locality**	**Voucher**	**GenBank codes**		
					12S	**cyt *b***	**CO1**
C spinalis spinalis	M14(c)	F	Achada Furna, 7 km N	BMNH2000.42	AF280156	AF280288	AF280222
	R61(a)	F	-	UMa (2)	AF335049	AF335048	-
	R62(a)	F	-	UMa (2)	AF335069	AF335068	-
C s. maioensis	M54(c)	M	Praia Preta	BMNH2000.33	AF280160	AF280292	AF280226
	M53(c)	M	Morrinho	DBULPGC-113	AF280159	AF280291	AF280225
	M55(c)	M	Santo António	BMNH2000.34	AF280161	AF280293	AF280227
	R66(a)	M	-	UMa (2)	AF335035	AF335034	-
	R67(a)	M	-	UMa (2)	AF335073	AF335072	-
	MA1(b)	M	Vila do Maio	-	-	AJ304997	-
	MA2(b, 1)	M	Vila do Maio	-	-	AJ304998	-
	MA3(b, 1)	M	Vila do Maio	-	-	AJ304998	-
C. s. boavistensis	M27(c)	BV	Curral Velho	BMNH2000.45	AF280144	AF280276	AF280210
	M10(c)	BV	Ilhéu de Sal Rei	DBULPGC-118	AF280142	AF280274	AF280208
	M57(c)	BV	Ilhéu Curral Velho	BMNH2000.46	AF280145	AF280277	AF280211
	BV1(b)	BV	Sal Rei	-	-	AJ304993	-
	BV2(b)	BV	Sal Rei	-	-	AJ305002	-
	BV3(b)	BV	Sal Rei	-	-	AJ304994	-
	M26(c)	BV	Sal Rei	BMNH2000.44	AF280143	AF280275	AF280209
	R03(a)	BV	-	UMa (2)	AF335037	AF335036	-
Outgroups							
E. egregius(3)	-	-	Florida, USA	MVZ 150128	AB016606	AB016606	AB016606
T. socotrana	-	-	Socotra I., Yemen	-	AF280140	AF280272	AF280206
T.capensis	-	-	Kouga Mts., South Africa	-	AF280139	AF280271	AF280205

br: Branco, B: Brava, BV: Boavista, F: Fogo, M: Maio, ra: Raso, ro: Rombos, SA: Santo Antão, SL: Santa Luzia, SN: São Nicolau, ST: Santiago, SV: São Vicente.

The samples R59 of *C. spinalis maioensis* and R94 and R98 of *C. vaillanti* from Brehm *et al.* (2001) have not been included in the phylogenetic analyses because only the C-mos sequence was available on Genbank. (1) BR1 and BR3, and MA2 and MA3 have identical haplotypes respectively, with the same Genbank sequence (Brown *et al.* 2001); (2) According to Brehm *et al.* (2001), all the specimens belong to UMa but no collection number has been specified; (3) Complete mitochondrial genome (including 12S, cyt *b* and COI) sequenced by Kumazawa & Nishida (1999).

Appendix V.4 Terminology used for head scales.



Appendix V.5 Estimates of evolutionary divergence over sequence pairs between the ESUs for cyt *b* and RAG2 genes. The number of base differences per site from averaging over all sequence pairs between groups is shown (*p*-dist). Standard error estimates are shown in italic and were obtained by a bootstrap procedure (1000 replicates). All results are based on the pairwise analysis of 353 and 51 sequences for cyt *b* (307 base pairs) and RAG 2 (834 base pairs), respectively. The analyses were conducted in Mega4. Island and taxa codes as in Figs. V.1, V.5 and V.6.

cyt *b*

		Clade																	
		A1	**A2**	**A3**	**A3**	**A3**	**A3**	**B1**	**B2**	**B3**	**B3**	**C**	**D1**	**D2**	**D2**	**D2**	**D3**	**D4**	**D5**
	ESU	***Cvv***	***Cvx***	***Cd***	***Cd***	***Cd***	***Cd***	***Cn***	***Cf***	***Cst***	***Cst***	***Cc***	***Csl***	***Cst***	***Cst***	***Cst***	***Css***	***Csm***	***Csb***
Clade	(Taxa/Island)	ST	F	B	F	ro	ST	SN	SA	Desertas	SV	Desertas	S	total	ST$_{\text{North}}$	ST$_{\text{South}}$	F	M	BV
A1	*Cvv* ST		*0.50*	*1.65*	*1.66*	*1.68*	*1.66*	*2.04*	*1.89*	*1.96*	*1.89*	*1.93*	*1.78*	*1.74*	*1.88*	*1.84*	*1.78*	*1.76*	*1.79*
A2	*Cvx* F	1.25		*1.72*	*1.73*	*1.75*	*1.72*	*2.11*	*1.95*	*2.01*	*1.95*	*2.01*	*1.88*	*1.80*	*1.96*	*1.92*	*1.84*	*1.81*	*1.85*
A3	*Cd* B	10.15	10.74		*0.35*	*0.46*	*0.13*	*1.91*	*1.93*	*1.96*	*1.89*	*1.90*	*1.73*	*1.51*	*1.61*	*1.56*	*1.72*	*1.79*	*1.68*
A3	*Cd* F	10.04	10.63	0.66		*0.57*	*0.34*	*1.94*	*1.93*	*1.95*	*1.87*	*1.92*	*1.74*	*1.55*	*1.66*	*1.60*	*1.70*	*1.81*	*1.71*
A3	*Cd* ro	10.57	11.16	0.73	1.15		*0.46*	*1.90*	*1.92*	*1.95*	*1.88*	*1.89*	*1.72*	*1.50*	*1.63*	*1.57*	*1.72*	*1.77*	*1.67*
A3	*Cd* ST+sm	10.31	10.86	0.33	0.63	0.81		*1.91*	*1.93*	*1.96*	*1.88*	*1.90*	*1.72*	*1.50*	*1.61*	*1.56*	*1.72*	*1.78*	*1.67*
B1	*Cn* SN	16.09	17.04	12.26	12.70	12.26	12.24		*1.50*	*1.48*	*1.49*	*1.56*	*1.59*	*1.53*	*1.55*	*1.56*	*1.55*	*1.75*	*1.56*
B2	*Cf* SA	13.52	14.07	12.17	11.99	12.19	12.17	8.80		*1.48*	*1.42*	*1.70*	*1.51*	*1.58*	*1.64*	*1.60*	*1.57*	*1.69*	*1.57*
B3	*Cst* Desertas	15.54	16.16	13.52	13.32	13.54	13.51	7.85	7.97		*0.49*	*1.81*	*1.65*	*1.64*	*1.71*	*1.68*	*1.63*	*1.72*	*1.69*
B3	*Cst* SV	14.68	15.22	12.68	12.47	12.70	12.67	7.93	7.19	1.13		*1.80*	*1.57*	*1.55*	*1.64*	*1.59*	*1.59*	*1.67*	*1.63*
C	*Cc* Desertas	13.29	14.09	11.63	12.09	11.63	11.70	8.66	10.81	11.91	11.79		*1.51*	*1.55*	*1.50*	*1.63*	*1.66*	*1.66*	*1.60*
D1	*Csl* S	13.10	14.02	10.89	11.33	10.86	10.82	9.48	9.20	10.37	9.50	8.39		*1.00*	*1.14*	*1.00*	*1.21*	*1.30*	*1.06*
D2	*Cst* total ST	12.35	12.92	8.60	9.04	8.57	8.58	8.69	9.23	9.82	8.98	8.96	4.26		-	-	*1.12*	*1.28*	*1.02*
D2	*Cst* ST$_{\text{North}}$	12.56	13.16	8.67	9.10	8.64	8.67	8.70	9.58	10.00	9.16	7.64	4.78	-		*0.70*	*1.23*	*1.26*	*1.13*
D2	*Cst* ST$_{\text{South}}$	12.27	12.84	8.57	9.02	8.54	8.56	8.68	9.12	9.76	8.74	9.40	4.08	-	2.06		*1.18*	*1.28*	*1.05*
D3	*Css* F	12.47	13.16	10.84	10.59	10.81	10.88	9.25	9.08	9.64	9.28	9.30	5.70	4.98	4.94	5.00		*1.29*	*1.08*
D4	*Csm* M	12.13	12.50	11.28	11.67	11.25	11.23	11.46	11.17	11.10	10.60	9.33	6.23	6.10	5.74	6.21	6.16		*1.23*
D5	*Csb* BV	13.53	14.30	10.72	11.17	10.68	10.67	9.74	9.92	10.99	10.47	9.43	4.66	4.46	4.50	4.45	4.53	6.14	

RAG 2

		Clade																	
		A1	**A2**	**A3**	**A3**	**A3**	**A3**	**B1**	**B2**	**B3**	**B3**	**C**	**D1**	**D2**	**D2**	**D2**	**D3**	**D4**	**D5**
	ESU	***Cvv***	***Cvx***	***Cd***	***Cd***	***Cd***	***Cd***	***Cn***	***Cf***	***Cst***	***Cst***	***Cc***	***Csl***	***Cst***	***Cst***	***Cst***	***Css***	***Csm***	***Csb***
Clade	(Taxa/Island)	ST	F	B	F	ro	ST	SN	SA	Desertas	SV	Desertas	S	total	ST$_{North}$	ST$_{South}$	F	M	BV
A1	*Cvv* ST		*0.50*	*1.65*	*1.66*	*1.68*	*1.66*	*2.04*	*1.89*	*1.96*	*1.89*	*1.93*	*1.78*	*1.74*	*1.88*	*1.84*	*1.78*	*1.76*	*1.79*
A2	*Cvx* F	1.25		*1.72*	*1.73*	*1.75*	*1.72*	*2.11*	*1.95*	*2.01*	*1.95*	*2.01*	*1.88*	*1.80*	*1.96*	*1.92*	*1.84*	*1.81*	*1.85*
A3	*Cd* B	10.15	10.74		*0.35*	*0.46*	*0.13*	*1.91*	*1.93*	*1.96*	*1.89*	*1.90*	*1.73*	*1.51*	*1.61*	*1.56*	*1.72*	*1.79*	*1.68*
A3	*Cd* F	10.04	10.63	0.66		*0.57*	*0.34*	*1.94*	*1.93*	*1.95*	*1.87*	*1.92*	*1.74*	*1.55*	*1.66*	*1.60*	*1.70*	*1.81*	*1.71*
A3	*Cd* ro	10.57	11.16	0.73	1.15		*0.46*	*1.90*	*1.92*	*1.95*	*1.88*	*1.89*	*1.72*	*1.50*	*1.63*	*1.57*	*1.72*	*1.77*	*1.67*
A3	*Cd* ST+sm	10.31	10.86	0.33	0.63	0.81		*1.91*	*1.93*	*1.96*	*1.88*	*1.90*	*1.72*	*1.50*	*1.61*	*1.56*	*1.72*	*1.78*	*1.67*
B1	*Cn* SN	16.09	17.04	12.26	12.70	12.26	12.24		*1.50*	*1.48*	*1.49*	*1.56*	*1.59*	*1.53*	*1.55*	*1.56*	*1.55*	*1.75*	*1.56*
B2	*Cf* SA	13.52	14.07	12.17	11.99	12.19	12.17	8.80		*1.48*	*1.42*	*1.70*	*1.51*	*1.58*	*1.64*	*1.60*	*1.57*	*1.69*	*1.57*
B3	*Cst* Desertas	15.54	16.16	13.52	13.32	13.54	13.51	7.85	7.97		*0.49*	*1.81*	*1.65*	*1.64*	*1.71*	*1.68*	*1.63*	*1.72*	*1.69*
B3	*Cst* SV	14.68	15.22	12.68	12.47	12.70	12.67	7.93	7.19	1.13		*1.80*	*1.57*	*1.55*	*1.64*	*1.59*	*1.59*	*1.67*	*1.63*
C	*Cc* Desertas	13.29	14.09	11.63	12.09	11.63	11.70	8.66	10.81	11.91	11.79		*1.51*	*1.55*	*1.50*	*1.63*	*1.66*	*1.66*	*1.60*
D1	*Csl* S	13.10	14.02	10.89	11.33	10.86	10.82	9.48	9.20	10.37	9.50	8.39		*1.00*	*1.14*	*1.00*	*1.21*	*1.30*	*1.06*
D2	*Cst* total ST	12.35	12.92	8.60	9.04	8.57	8.58	8.69	9.23	9.82	8.98	8.96	4.26		-	-	*1.12*	*1.28*	*1.02*
D2	*Cst* ST$_{North}$	12.56	13.16	8.67	9.10	8.64	8.67	8.70	9.58	10.00	9.16	7.64	4.78	-		*0.70*	*1.23*	*1.26*	*1.13*
D2	*Cst* ST$_{South}$	12.27	12.84	8.57	9.02	8.54	8.56	8.68	9.12	9.76	8.74	9.40	4.08	-	2.06		*1.18*	*1.28*	*1.05*
D3	*Css* F	12.47	13.16	10.84	10.59	10.81	10.88	9.25	9.08	9.64	9.28	9.30	5.70	4.98	4.94	5.00		*1.29*	*1.08*
D4	*Csm* M	12.13	12.50	11.28	11.67	11.25	11.23	11.46	11.17	11.10	10.60	9.33	6.23	6.10	5.74	6.21	6.16		*1.23*
D5	*Csb* BV	13.53	14.30	10.72	11.17	10.68	10.67	9.74	9.92	10.99	10.47	9.43	4.66	4.46	4.50	4.45	4.53	6.14	

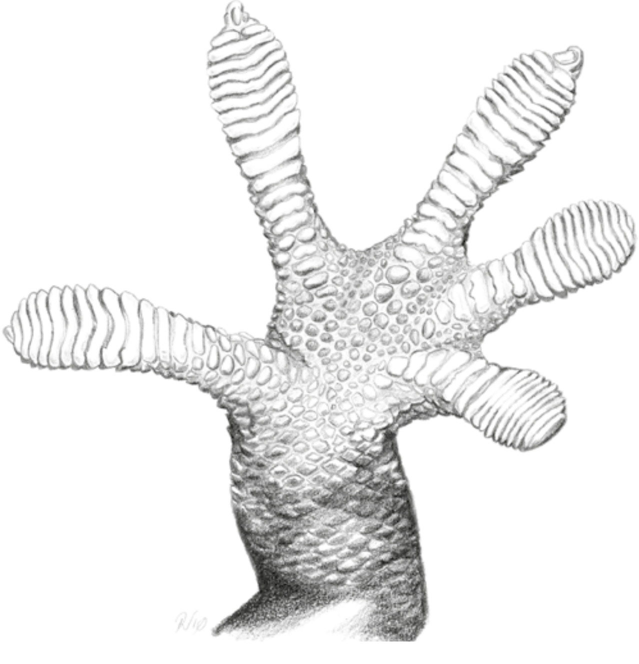
“A jug fills drop by drop.”

Buddha

CHAPTER 3

Reducing the Wallacean shortfall
Where are they?
How to conserve them?

Distribution atlas,
conservation status and priority areas
for the reptiles of Cape Verde



Article VI. Review of the distribution and conservation Status of the reptiles of the Cape Verde Islands.

R. Vasconcelos, J.C. Brito, D.J. Harris & S. Carranza
Oryx, submitted.

Article VII. Priority areas for island endemics using genetic diversity – the case of the reptiles of the Cape Verde Islands

R. Vasconcelos, J.C. Brito, S. Carvalho, D.J. Harris & S. Carranza
Biological Conservation, in preparation

ARTICLE VI
Review of the distribution and conservation status of the terrestrial reptiles of the Cape Verde Islands

R. Vasconcelos[1,2,3*], J.C. Brito[1,2], S. Carranza[3] & D.J. Harris[1,2]

[1] CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos da Universidade do Porto,
Campus Agrário de Vairão, R. Padre Armando Quintas, 4485-661 Vairão, Portugal;

[2] Departamento de Biologia, Faculdade de Ciências da Universidade do Porto,
Pr. Gomes Teixeira, 4099-002 Porto, Portugal;

[3] Institute of Evolutionary Biology (CSIC-UPF),
Passeig Marítim de la Barceloneta, 37-49, E-08003 Barcelona, Spain.

*Corresponding author

ABSTRACT

Cape Verde is the Macaronesian oceanic archipelago with the highest number of reptile taxa and endemics. Mapping the precise distributions and assessing the conservation status of reptiles is the first step towards effective conservation. Presence / absence and abundance data were gathered from extensive fieldwork and post-1980 references. A bibliographic revision was accomplished to deal with uncertainties and clarify reptile distributions. Evaluation of conservation status was considered at specific and subspecific levels, following IUCN Red List criteria and using RAMAS®. Fieldwork confirmed the occurrence of 34 of the 37 cited taxa (31 native, three exotic). One taxon was not refuted as Extinct. Three broad distribution and rareness patterns were identified: widespread and abundant taxa occurring on ≥2 islands / islets; widespread or abundant taxa restricted to one island; and rare or limited range taxa occurring on small island portions or islets. More than a third of taxa presented area of occupancy <20 km^2 and extent of occurrence <100 Km^2, geckos more than skinks due to their high habitat specialisation, and 58% occurred in only one island / islet. About half of all taxa were considered threatened, twice the proportion of the Canaries, what might be explained by the smaller area of the Cape Verdes and by the increased aridity. The most frequent classifying criterion was B (geographic range) and the most pervasive threats were natural disasters, intrinsic factors and introduced species. The importance of applying conservation status at subspecific level on island endemics is emphasised. Several conservation measures are proposed, including optimised design of protected areas.

KEY WORDS
Atlas, *Chioninia*, endemics, *Hemidactylus*, introductions, Macaronesia, Red List, *Tarentola*.

INTRODUCTION

Biodiversity loss is one of the top issues of the current century. Species with small range size and low gene flow are of particular concern as they have increased probability of extinction by chance alone (Pullin 2002). For this reason, island populations have higher risk of extinction than mainland populations (Frankman 1997). Moreover, even though islands usually present a low number of species, the number of endemic ones is generally high, as is the vulnerability to the introduction of exotic species (Whittaker & Fernández-Palacios 2007). Thus, it is crucial to increase the knowledge about the natural patrimony in remote and prone-to-extinction areas, such as oceanic islands. One way of fulfilling this goal begins with the completing of distribution atlases and updated red lists, since these are framework data for assisting conservation planning.

The Cape Verde Islands are an oceanic archipelago that lacks detailed information about biodiversity distribution. Although there are preliminary inventories of the flora (Paiva 1995), avian (Naurois 1994; Hazevoet 1995; Clarke 2006) and herpetofauna taxa (Schleich 1987), atlases of the distribution for terrestrial groups are unavailable. There are no endemic mammals or amphibians, and for birds there is intra-island distribution data in preparation (Hazevoet 1995), but accurate distribution data for reptiles is lacking. The archipelago has the highest number of endemic reptile taxa of the Macaronesia (Schleich 1987; López-Jurado *et al.* 1999; Pleguezuelos *et al.* 2002; Oliveira *et al.* 2005; Arnold *et al.* 2008; Miralles *et al.* 2010; Vasconcelos *et al.* submitted) that are distributed in three genera: the *Hemidactylus* (Gekkonidae) and *Tarentola* (Phyllodactylidae) geckos and the *Chioninia* (Scincidae) skinks (= *Mabuya* and *Macroscincus*; see Miralles *et al.* 2010). Thus, mapping the precise distributions of these taxa is an essential first step for conservation of Cape Verdean biodiversity.

After the discovery of this oceanic archipelago by the Portuguese in 1460, several anecdotal collections on the fauna of the Cape Verde Islands were conducted. Those data led to the firsts studies on the taxonomy, systematic and morphology of the Cape Verdean herpetofauna throughout the 19th century. In the late 20th century, a preliminary assessment of the reptiles listed 10 endemic terrestrial species (including 23 taxa) and reviewed their distributions at a coarse inter-island scale (Schleich 1987). Later, taxonomical rearrangements made by Joger (1993), based on morphological analyses, increased up to 12 and 26 the number of species and taxa, respectively. Those framework data were compared with the now dated IUCN and German National Lists criteria (pre-2001) to produce the first Red List of Cape Verde (Leyens & Lobin 1996). The assessment considered 25% of terrestrial reptiles as Extinct or Endangered (Schleich 1996), prompting the promulgation of the law for the protection of plant and animal species (Decree nr 37/2002, 30th December). This law considered *Hemidactylus bouvieri razoensis* Gruber and Schleich, 1982 as Critically Endangered; *Tarentola gigas brancoensis* Schleich, 1984 and *Tarentola gigas gigas* (Bocage, 1875) as Endangered; *Hemidactylus bouvieri bouvieri* (Boucourt, 1870) as Rare and *Tarentola rudis* (Boulenger, 1906) and *Chioninia (=Mabuya) vaillanti* (Boulenger, 1887) as Undetermined (Anonymous 2002).

Genetic studies conducted after 2000 by Brehm *et al.* (2001), Brown *et al.* (2001), Carranza *et al.* (2000, 2001, 2002), Carranza & Arnold (2003, 2006), Jesus *et al.* (2001, 2002), and Mausfeld-Lafdgiya (2002) for phylogeographic purposes indicated the need of a complete systematic revision of the Cape Verdean reptiles. An extensive sampling of Cape Verde was carried out since 2006, which used genetic and morphological variability to review the systematics of the endemic reptiles (Arnold *et al.* 2008; Miralles *et al.* 2010; Vasconcelos *et al.* 2010, submitted). These works have increased up to 22 the number of recognised endemic reptile species in the Cape Verdes, with 31 taxa. The significant taxonomic rearrangements provided by these works represented an increase of 83% in the number of species and 19% of taxa in comparison to the most recent reptile assessment (Schleich 1996). Furthermore, they exposed the need to revise the distribution of all taxa and assess their conservation status using current IUCN criteria (IUCN SPS 2010).

The objectives of this study are to provide precise distribution data at an intra-island scale, and to assess the conservation status of the endemic Cape Verdean reptiles. The fulfilling of these two goals will provide the needed guidance for future management and conservation efforts.

STUDY AREA

The Cape Verde Islands belong to the biogeographic region of Macaronesia located in the Atlantic Ocean (Fig. VI.1). This volcanic archipelago, which has never been connected to the mainland (Mitchell-Thomé 1976), contains 10 main islands plus 13 islets, with total area of 4067 km^2. Size varies dramatically between islands: Santiago is the largest (1004 km) and Raso (6 km^2) one of the smallest. The age of the islands ranges between 2.6 to 26 Million years, with the ones closer to the mainland being the oldest, and consequently the flattest (see Mitchell-Thomé 1983; Plesner *et al.* 2002; Torres *et al.* 2002; Duprat *et al.* 2007).

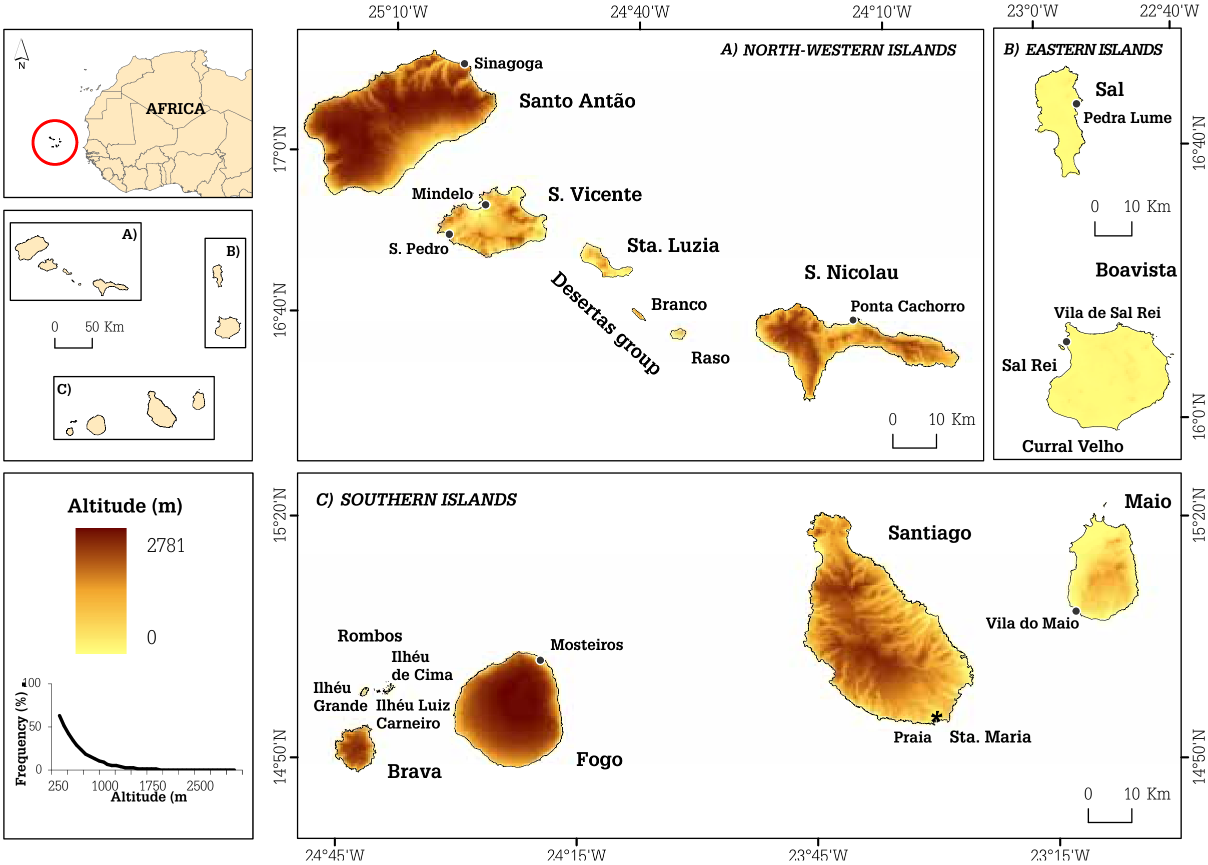


Figure VI.1 Geographic location of the Cape Verde Islands, including altitudinal variation, and toponomies mentioned in the text.

The topography of Cape Verde ranges from plains to high mountains, reaching almost 3000 m, with one active volcano in Fogo (last eruption in 1995). The elevation, steepness and orientation of mountains influence the amount of rainfall that each island receives, which can be in the form of mist or drizzle. Cape Verde is situated just north of the Intertropical Convergence Zone and has a tropical dry climate with a longer dry season, with frequent long droughts, and an irregular shorter wet season, from July to September (Lobban & Saucier 2007). The average annual temperature is rather constant (mean=22 °C) due to the moderating influence of the ocean. On the contrary, annual precipitation is spatially and temporally extremely variable, and less than 250 mm (Hijmans *et al.* 2005), resulting in almost no permanent water courses.

METHODS

The 10 islands were prospected between the years 2006 to 2008 during the dry season, from mid-May to mid-July. Sampling stations (Appendix VI.1) were randomly chosen and stratified according to habitat availability, based on agro-ecological and vegetation zoning maps (Appendix VI.2), resulting in a number of stations per habitat proportional to habitat area. This way, most of the variability between and within each habitat – altitude, topography, climate and geographic position – was contained in the different sampling stations. The sampled area, 440 stations of 1x1 square kilometres, corresponds to about 11% of the country area. Each station was sampled along transects for 35 minutes on average (range: 5 to 120 min, according to the difficulty of the terrain), by two observers walking parallel to each other, totalling nearly 264 hours of sampling. Presence or absence and abundance data of taxa (nr. individuals/km^2) were gathered.

Presence data

A total of 2139 presence observations were collected from three sources: 1) 1375 from field work, consisting of indirect (skins, eggs and skeletons) or direct observations of the animals; 2) 610 from bibliographic references and 3) 154 from GenBank. The geographic coordinates from fieldwork observations were recorded with a Global Positioning System (GPS). Coordinates from literature records (Appendix VI.3) and GenBank data were gathered manually from 59 topographical maps (1: 25,000 from Serviço Cartográfico do Exército Português for Cape Verde and Serviço Nacional de Cartografia e Cadastro de Cabo Verde). All coordinates were determined on the World Geographic Coordinate System with Datum 1984 (WGS84). Observations were inscribed in a georeferenced database and displayed in the Geographical Information System (GIS), ArcGIS 9.3 (ESRI 2008).

Conservation status

The evaluation of the conservation status was considered at specific and subspecific levels, following the methodology and the criteria of IUCN guidelines for red lists (IUCN SPS 2010). A taxon was considered 'Threatened' when it listed as one of the IUCN categories of Vulnerable (V), Endangered (EN) or Critically Endangered (CR), according to the criteria of population reduction (A), geographic range (B), small population size and decline (C), and very small or restricted population (D) (IUCN SPS 2010). Non indigenous taxa were considered as Not Evaluated (NE).

The application of criteria was implemented with RAMAS® Red List software (version 2.0) (Akçakaya & Ferson 2001), which is now recommended for assessors evaluating species by the IUCN Red List Program. Parameters for classifying taxa included: 1) population number, estimated from the number of mature individuals found during field sampling; 2) population reduction, estimated from subfossil and bibliographic data; 3) area of occupancy (AOO), calculated from the number of occupied cells × area of an individual cell (1x1 Km^2) considering only observations after 1980; 4) extent of occurrence (EOO), estimated by a minimum convex polygon method, which determines the area contained within the shortest continuous imaginary boundary which can be drawn to encompass all the present occurrences of a taxon [calculations were made using the Hawth's Tools extension for ArcGIS (Beyer 2004)]; and 5) population fragmentation, evaluated based on the number of locations (Loc) – corresponding to the number of habitats where occurrence was registered (see sampling methods section and Appendix VI.1) – and number of subpopulations (Pop), quantified by the number of islands or islets of occurrence of the taxa.

The only two exceptions were *T. darwini* and *C. spinalis santiagoensis* that presented two Evolutionarily Significant Units (ESUs) on the same island and thus Pop did not coincide with the number of islands or islets of their occurrence (see Vasconcelos *et al.* 2010; Miralles *et al.* 2010).

Taxa were considered to have restricted range (RR) if AOO was typically lower than 20 km^2 or the number of localities of occurrence was equal or lower to five (IUCN SPS 2010). An exception was considered for *C. s. spinalis*, which presented nearby limit values for AOO, but was assumed an underestimation of presences. Sampling occurred during the dry season and this, together with the very steep slopes of the island, make detection of specimens difficult. Threats for each taxa were evaluated based on information gathered from fieldwork and bibliography and followed the categories implemented in RAMAS software (Akçakaya & Ferson 2001).

Whenever an endemic taxon was found out of its distribution range within the archipelago it was considered an introduction in the following cases: if it was genetically very close to the individuals found in the island of origin of the taxon (see Vasconcelos *et al.* 2010; Miralles *et al.* 2010); if after an extensive sampling, a small number of individuals were found, and if mainly on the coast and not inland, indicating recent anthropogenic introduction via boats.

RESULTS

During fieldwork, 50 observations for exotic taxa and 1325 for native ones were collected, while analyses of bibliographic together with Genbank data gathered 21 and 743 observations of exotic and native taxa, respectively. A total of 38 taxa were referenced for Cape Verde, of which 31 are native and seven exotic (Table VI.1). From these, fieldwork only confirmed the occurrence of 34 taxa, of which 31 are native and three exotic. The distributions of observations are given in Figs. VI.2 to VI.5. Detailed information about doubtful and historical records (represented on figures as question marks) is given in Appendix VI.4.

Introductions: exotic taxa

Presently, three species of exotic reptiles were confirmed to be present on the Cape Verde Islands (Fig. VI.2). The most abundant and widespread species was *H. angulatus* which occurred at least on six islands and one islet. The most recent introduction record belonged to *Agama agama* in S. Antão. The first presence records of *H. mabouia* in S. Antão and Brava and the introduction in S. Vicente were confirmed by fieldwork.

Introductions: endemic taxa

The extensive sampling allowed confirmation of the introductions of: 1) *C. delalandii* in Vila do Maio, Maio (originally present in all other southern islands); 2) *T. maioensis* (originally from Maio) in S. Nicolau, Ponta Cachorro; and 3) *T. substituta* (originally from S. Vicente) in S. Antão, Sinagoga (Table VI.1).

Distribution of native taxa

Of the 31 endemic taxa, five belong to the genus *Hemidactylus*, 14 to *Tarentola* and 12 to *Chioninia* genus (Table VI.1). Searches for the presence of *Chioninia* (previously *Macroscincus*) *coctei* were conducted for the present work by three observers on Santa Luzia Island during five days with no positive results.

Table VI.1 Taxonomical list of Cape Verde reptile taxa, total presence data collected (*n*), and quantitative criteria used for assessment of conservation status: extent of occurrence (EOO, km^2), area of occupancy (AOO, km^2), number of localities (Loc) and number of subpopulations (Pop) (doubtful occurrences between brackets; consult Appendix VI.4). Red List category (Cat), listing of criteria and major threats standardised according to IUCN (2010). *See 'Introductions' section in Results for details. # See Methods sections for details.

Taxa	***n***	**EOO**	**AOO**	**Loc**	**Pop**	**Range**	**Cat**	**Criteria**	**Threats**
Endemic									
Geochelone atlantica López-Jurado, Mateo & García-Marquez, 1998	NO	Unk	0	0	0 (2)		EX		
Genus *Hemidactylus* Oken, 1817									
H. bouvieri (Bocourt, 1870)	34	Unk	7	8 (10)	5 (7)		CR	B1ab(i,ii,iii,iv,v)c(iii,iv)+2ab(i,ii,iii,iv,v)c(iii,iv)	1,2,7,9,12
H. bouvieri bouvieri (Bocourt, 1870)	7	Unk	1	2 (4)	2 (4)	RR	CR	B1ab(i,ii,iii,iv,v)c(iii)+2ab(i,ii,iii,iv,v)c(iii); C1+2a(ii)	1,2,7,9,12
H. bouvieri ssp., S. Nicolau	5	Unk	2	2	1	RR	CR	B1ab(i,ii,iii,iv,v)+2ab(i,ii,iii,iv,v); C1+2a(ii)	1,2,7,9,12
H. bouvieri razoensis Gruber & Schleich, 1982	22	Unk	4	4	2	RR	CR	B1ab(i,ii,iii,iv,v)c(i,ii,iii,iv)+2ab(i,ii,iii,iv,v)c(i,ii,iii,iv); C1+2a(i,ii)b; D	1,2,7,9,12
H. boavistensis Boulenger, 1906	91	723.2	47	14	4		LC		1,2,7
H. lopezjuradoi Arnold, Vasconcelos, Harris, Mateo & Carranza, 2008	3	Unk	1	1	1	RR	CR	B1ab(i,ii,iii,iv,v)+2ab(i,ii,iii,iv,v); C1+2a(ii)	1,2,7,9,12
Genus *Tarentola* Gray, 1825									
T. boavistensis Joger, 1993	39	458.1	27	7	2		VU	C1; D1	7,9
T. bocagei Vasconcelos, Perera, Geniez, Harris & Carranza, submitted	20	42.8	9	7	1	RR	VU	D2	9
T. fogoensis Vasconcelos, Perera, Geniez, Harris & Carranza, submitted	44	341.3	20	8	1		LC		7
T. darwini Joger, 1984b	152	838.5	65	9	2		LC		0
T. substituta Joger, 1984b	160	150.8	45	8	1*		LC		7
T. raziana Schleich, 1984	84	27.9	22	8	3		VU	B1ab(v)+2ab(v); C1	1,2,7
T. caboverdiana Schleich, 1984	89	545.3	37	7	1		LC		0
T. nicolauensis Schleich, 1984	111	198.2	41	10	1*		LC		0
T. gigas (Bocage, 1875)	74	<10	6	4	2		EN	B1ac(iv)+2ac(iv)	7,8,9,10
T. gigas gigas (Bocage, 1875)	39	<3	3	2	1	RR	EN	B1ac(iv)+2ac(iv)	7,8,9,10
T. gigas brancoensis Schleich, 1984	35	<6	3	2	1	RR	EN	B1ac(iv)+2ac(iv)	7,8,9,10
T. rudis Boulenger, 1906	43	254.3	22	7	2		VU	D1	8
T. protogigas Joger, 1984b	75	75.4	22	11	4		CR-VU		7,9,12
T. protogigas protogigas Joger, 1984b	13	30.7	4	3	1	RR	CR	B1ab(i,ii,v)+2ab(i,ii,v); C2a(ii)	7,9,12
T. protogigas hartogi Joger, 1993	62	44.7	18	8	3	RR	VU	D2	7
T. maioensis Schleich, 1984	57	195.3	22	6	1		LC		7

Taxa	*n*	EOO	AOO	Loc	Pop	Range	Cat	Criteria	Threats
Genus *Chioninia* (Gray, 1845)									
C. vaillanti (Boulenger, 1887)	43	445.5	20	11	3		EN	D1	7,9
C. vaillanti vaillanti (Boulenger, 1887)	19	316.7	12	5	1	RR	EN	D1+2	9
C. vaillanti xanthotis Miralles, Vasconcelos, Perera, Harris & Carranza, 2010	24	128.8	8	6	2	RR	EN	D1+2	7,9
C. delalandii (Duméril & Bibron, 1839)	341	1133.9	141	37	7*		LC		7
C. nicolauensis (Schleich, 1987)	43	183.3	21	9	1		LC		7
C. fogoensis (O'Shaughnessy, 1874)	95	344.2	46	9	1		LC		2
C. stangeri (Gray, 1845)	122	101.0	28	23	4		EN	B1ab(i,ii,iii,v)+2ab(i,ii,iii,v); C1+2a(ii)	2,7
C. coctei (Duméril & Bibron, 1839)	49	6.3	7	3	3 (5)	RR	EX		1,2,3,7,9
C. spinalis (Boulenger, 1906)	297	2034.9	129	34	9		LC		0,7,9
C. spinalis salensis (Angel, 1935)	39	141.7	17	6	1	RR	VU	D2	7,9
C. spinalis santiagoensis Miralles, Vasconcelos, Perera, Harris & Carranza, 2010	67	789.9	31	6	3		LC		0
C. spinalis spinalis (Boulenger, 1906)	37	295.3	14#	8	1		LC		7
C. spinalis maioensis (Mertens, 1955)	57	210.1	29	7	1		LC		7
C. spinalis boavistensis Miralles, Vasconcelos, Perera, Harris & Carranza, 2010	97	597.8	52	7	3		LC		7
Exotic									
Pelusios sp. Wagler, 1830	NO	Unk	0	0	0 (2)		NE		
Lygodactylus sp.Gray, 1864	NO	Unk	0	0	0 (1)		NE		
Hemidactylus angulatus Hallowell, 1852	60	1140.0	41	>6	8 (10)		NE		
Hemidactylus mabouia (Moreau de Jonnés, 1818)	12	8.2	7	3	3		NE		
Agama agama (Linnaeus, 1758)	1	Unk	1	1	1		NE		
Psammophis sibilans (Linnaeus, 1758)	NO	Unk	0	0	0 (1)		NE		

NO, Not Observed; Unk, Unkown; RR, Restricted Range

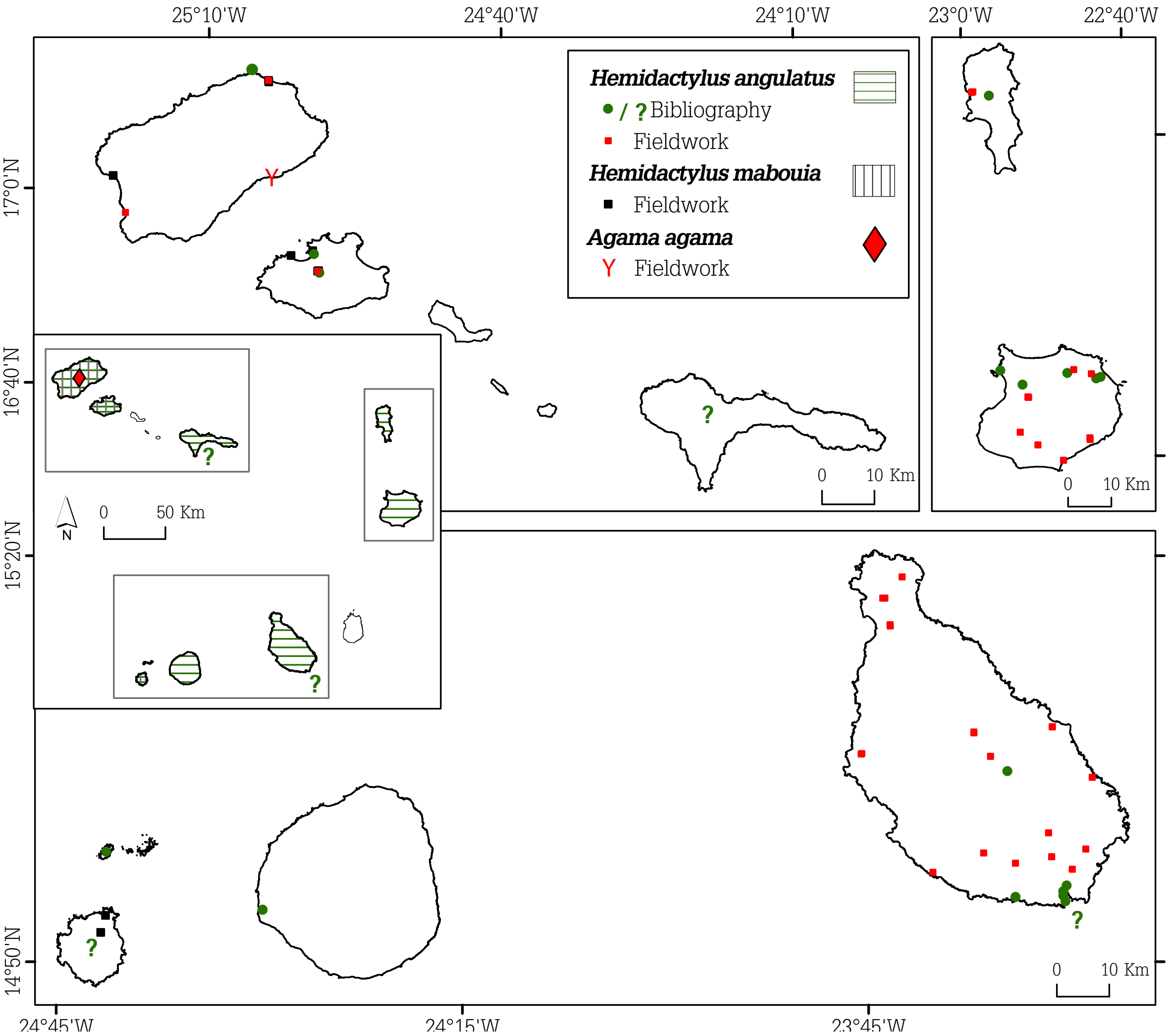


Figure VI.2 Distribution of introduced reptiles in the Cape Verde Islands. Islands of occurrence of each taxon are highlighted with a taxa-specific pattern. Doubtful records are represented as question marks.

Considering extant taxa, three broad distribution and rareness patterns were identified: 1) widespread and abundant taxa occurring on two or more islands or one island and distant islets, such as *H. boavistensis*, *T. raziana* and *C. delalandii*; 2) widespread or abundant taxa restricted to one island (and its neighbouring islets), such as *T. boavistensis*, *T. darwini* and *C. s. maioensis*; and 3) rare or limited range taxa, occurring on an islet or small portion of an island, such as *H. bouvieri spp.*, *H. lopezjuradoi*, *T. bocagei*, *T. gigas spp.*, *T. rudis, T. protogigas protogigas*, *C. vaillanti vaillanti* and *C. v. xanthotis*. (Table VI.1 and Figs. VI.3 - VI.5).

The native *C. delalandii* and *T. darwini* have the largest extents of occurrences (EOO) and areas of occupancy (AOO), while *T. gigas brancoensis* and *T. gigas gigas* have the smallest EOO, and *H. lopezjuradoi* and *H. bouvieri bouvieri* the smallest AOO (Table VI.1; Figs. VI.3 to VI.5). The *C. delalandii* skink is the taxa with the highest number of confirmed subpopulations (NP) followed by *C. stangeri* and *H. boavistensis*. Around 40% of the reptile taxa from Cape Verde have restricted AOO, geckos 1.5 times more than skinks (47% of the geckos against 33% of the skinks). About a third of all taxa present EOOs lower than 100 Km^2 (36%), especially geckos, which comparatively with skinks registered six times more restricted occupancies (53% of the geckos against 8% of the skinks).

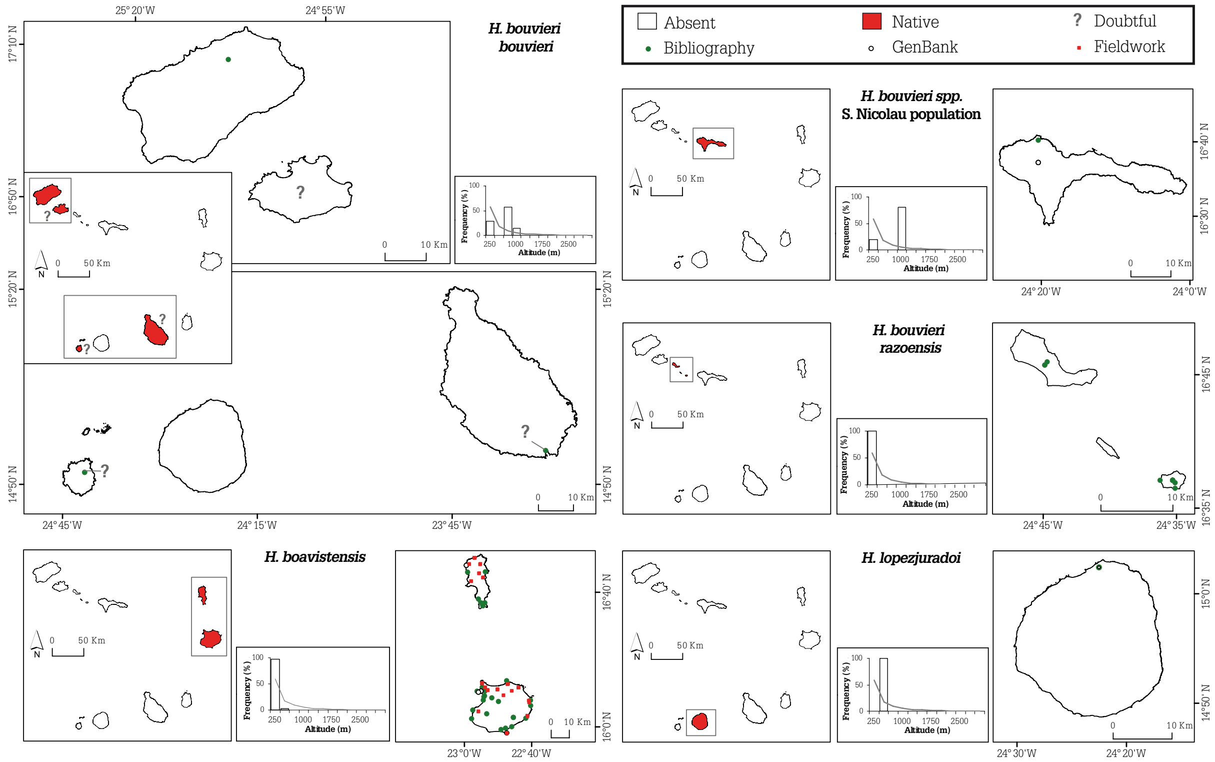


Figure VI.3 Distribution of *Hemidactylus* reptiles from the Cape Verde Islands. Islands of occurrence of each taxon are highlighted in red. Doubtful records are represented as question marks.

Around 30% of the taxa occur in less than five locations (Loc), and more than half of the taxa (58%) occur in only one island or islet, with a similar pattern among and within geckos and skinks (Table VI.1). Thirteen of the Cape Verdean reptiles (42%) were considered to have restricted ranges (RR), with higher values for geckonids in comparison to scincids.

Most of the taxa had records below 250 m of altitude (71%), although almost a third (24%) occurred between 250 and 1000 m (Figs. VI.3 to VI.5). Examples of taxa occurring at altitudes above 750 m are the S. Nicolau population of *H. bouvieri*, *T. fogoensis*, *T. darwini*, *T. caboverdiana*, *T. p. hartogi, C. v. vaillanti*, *C. v. xanthotis*, *C. delalandii*, *C. nicolauensis*, *C. fogoensis*, *C. s. spinalis*. Above 1000 m there were only records of *C. delalandii*, *C. fogoensis*, *C. s. spinalis*, *C. v. vaillanti*, *T. caboverdiana* and a few of *T. darwini*.

Conservation status of native taxa

A summary of the current conservation status of the endemic taxa are present in Table VI.1. About half of the Cape Verdean reptiles were considered Threatened (Table VI.1). One taxon was classified as Extinct (EX), around 16% of the taxa classified as Critically Endangered (CR) and Endangered (E), and 19% as Vulnerable (V). The geckos (63%) have two times more threatened taxa than skinks (33%), mostly due to 80% of *Hemidactylus* being evaluated as Critically Endangered.

The most frequently identified classifying criterion was B (56%). The most pervasive threats to Cape Verdean reptiles were natural disasters (74%), specifically droughts and volcanoes, and intrinsic factors (42%), specifically restricted range and low densities (Table VI.1, Appendix VI.5).

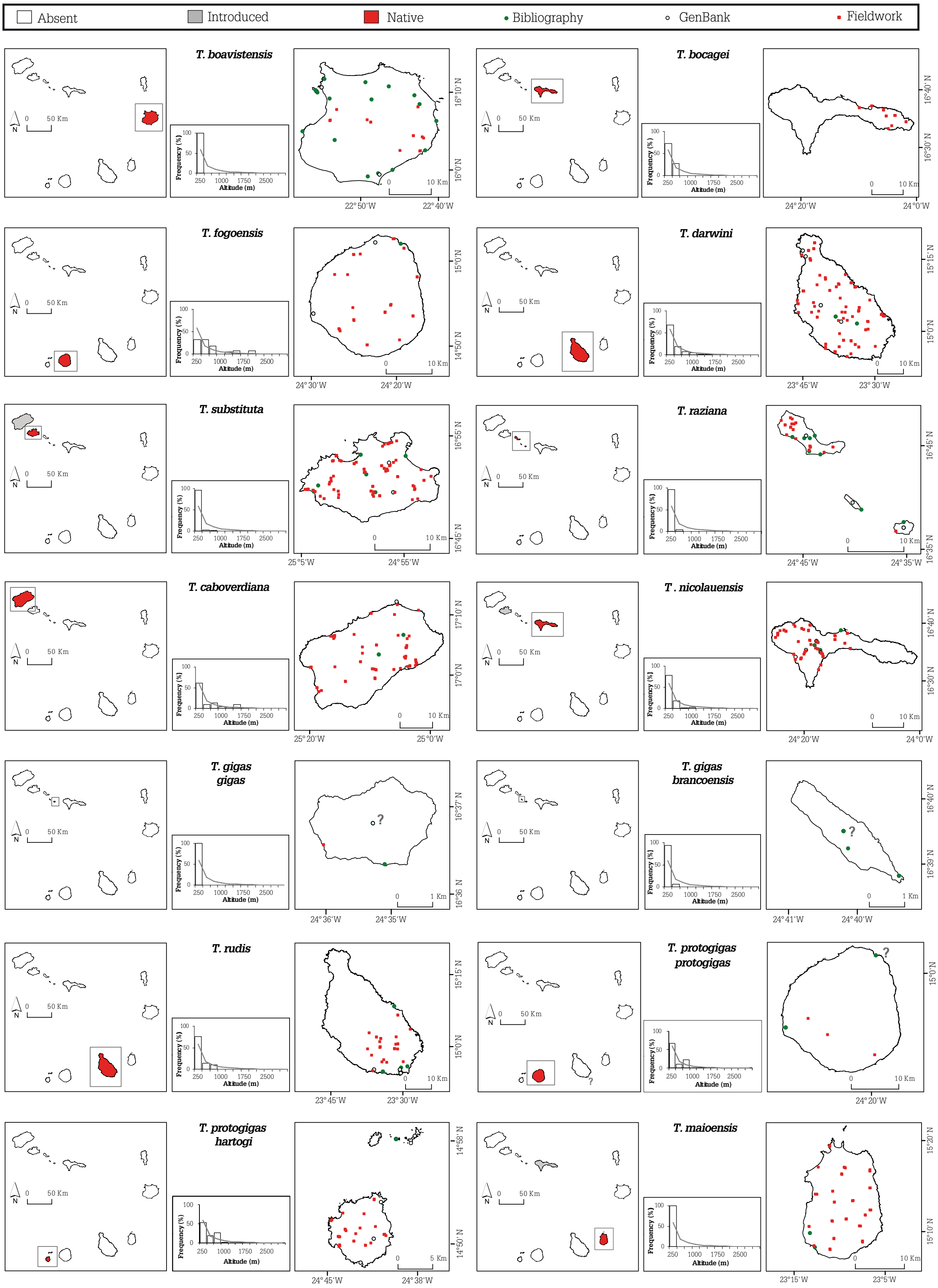


Figure VI.4 Distribution of *Tarentola* reptiles from the Cape Verde Islands. Islands of occurrence of each taxon are highlighted in light grey if they result from an introduction and in red if native. Doubtful records are represented as question marks.

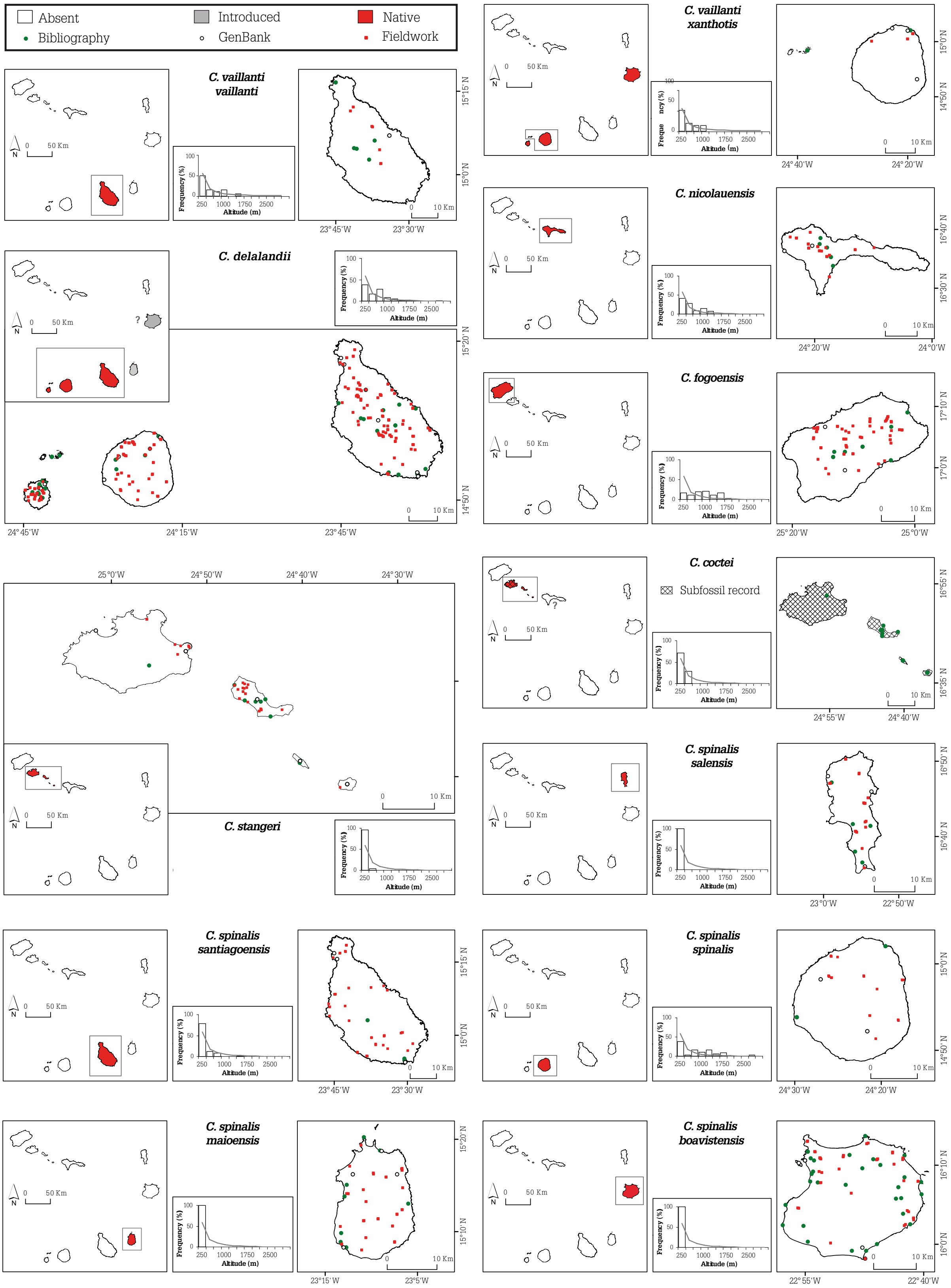


Figure VI.5 Distribution of *Chioninia* reptiles from the Cape Verde Islands. Islands of occurrence of each taxon are highlighted in light grey if they result from an introduction and in red if native. Doubtful records are represented as question marks.

DISCUSSION

The current work presents for the first time precise within-island information about the distribution of the Cape Verdean reptile species, including the newly described and revised taxa. In addition, the revised conservation status following current IUCN criteria for all taxa are presented, many of them previously categorised as DD and Undetermined, such as *T. boavistensis*, *T. substituta*, *T. rudis* and *C. vaillanti* (Schleich 1996). Furthermore, a bibliographic revision was carried out to deal with uncertain data and clarify the reptile distributions (Appendix VI.4).

IUCN criteria were applied at the subspecific level since Cape Verde is an insular system with populations that encompass conservation particularities that should be addressed at that level. On some occasions, one subspecies is assigned to one island or group of islands with particular distributions, with populations morphologically and genetically distinct from the others belonging to the same species and present in other islands. For instance, *T. protogigas* conservation status is unresolved because the population from Fogo, *T. p. protogigas*, is considered CR due to supposed continuing decline and restricted range while the other subspecies is only considered Vulnerable.

Introductions: exotic taxa

The current presence and extent of occurrence of two invasive introduced *Hemidactylus* species, *H. angulatus* and *H. mabouia* (Jesus *et al.* 2001; Arnold *et al.* 2008), is especially critical. It is known that introduced *Hemidactylus* can cause catastrophic declines and extinction of endemic geckos, as *H. frenatus* did with *Nactus* species of the Mascarene Islands probably through competition for refugia (Cole *et al.* 2005). It is also known that inland invasion can be fast and human-mediated and that recent reptile extinctions have occurred exclusively on islands (Case *et al.* 1992). Given that some endemic forms, such as *H. bouvieri* and *H. lopezjuradoi* are of conservation concern (Critically Endangered) and that *H. angulatus* is probably already displacing some populations of the endemic *H. boavistensis* (Lopéz-Jurado *et al.* 1999), knowledge regarding the extent of this threat is vital. It is alarming how widespread *H. angulatus* is in Santiago and Boavista Islands and the confirmation of the spread of *H. mabouia* to other islands. Thus, ecological studies are needed to monitor population trends. Also new taxa are being introduced in the archipelago, such as *Agama agama* in S. Antão (Vasconcelos *et al.* 2009) and thus measures should be applied to prevent the entrance of further exotic taxa on this vulnerable ecosystem.

Introductions: endemic taxa

The extensive sampling did not confirm the introductions of *T. nicolauensis* in S. Vicente, Mindelo, cited by Jesus *et al.* (2002) or of *C. delalandii* in Sal Rei, Boavista cited by Schleich (1987) and Chadwick & Slater (2005). This may be due the very low effective size or even to the extinction of the introduced populations, as suggested by López-Jurado *et al.* (1999) for the latter case.

Distribution of native taxa

Searches for *Chioninia coctei* were carried out during this study and several more in previous expeditions without recovering live animals since 1912. Thus, *C. coctei* was considered possibly extinct already in the 20th century by many authors (Chevalier 1935; Hazevoet 1994, 1995; Schleich 1982a, 1984); and officially extinct since 1986 by IUCN (Schleich 1996; Andreone & Guarino 2003; Lopéz-Jurado *et al.* 2005). Extinction was mainly the result of the action of collectors and feral cats. Already in the 19th century, Bocage (1896) noted unsustainable collection of vouchers by naturalists. Nevertheless, the doubt about the existence of few individuals left on Sta. Luzia Island and on other island of possible past distribution still remains (see Appendix VI.4) helped by the finding of an alleged mandible of a juvenile of this species in the faecal pellets of a cat (Mateo *et al.* 2005). Therefore, only further intensive sampling might refute its present conservation status. Due to the high level of interest regarding this giant skink, many citations about the absence or possible presence for this taxon were recorded, explaining the high number of data comparing to its low values of extent of occurrence, area of occupancy and number of localities.

Several threatened Cape Verde taxa exhibited restricted ranges with particular habitat associations and very low number of records. For instance, there are few presences of *H. bouvieri* on S. Vicente, Santo Antão, Santiago and possibly Brava and on S. Nicolau and of *H. lopezjuradoi* as well, known only from one site in the northern region of Fogo Island (Arnold *et al.* 2008). Rarity might be related to low population sizes and habitat specialisation. Observations of *H. lopezjuradoi* were restricted to relatively humid places such as mountain tops (Arnold *et al.* 2008) and humid valleys (Köhler *et al.* 2007a) and specimens were found under stones in deep valleys with considerable vegetation cover, at around 300 m of altitude (Arnold *et al.* 2008). Most *H. bouvieri* were found between 600 to 700 m of altitude, but the S. Nicolau population occurs from 250 m up under bushes of the endemic *Euphorbia tuqueiana* (Arnold *et al.* 2008) or under large stones (Köhler *et al.* 2007b). Also uncommon is *H. b. razoensis* which occurs on Raso islet and Sta. Luzia Island (Arnold *et al.* 2008) on dry inland streams with high vegetation density or inside the cavities of the volcanic rock and holes made by roots. It was never found on the rocks (Gruber & Schleich 1982). Only five animals were collected by Gruber & Schleich (1982), and a further four by Mateo *et al.* (1997). All these *Hemidactylus* are hence Critically Endangered.

Although not with a restricted range, the same level of habitat associations are noticed for other threatened taxa. The Vulnerable *T. boavistensis* seems to avoid the dune areas that cross from north to south of the occidental part of Boavista Island and is rare on the hyperarid flat areas on the south and northern coastal area (López-Jurado *et al.* 1999), while the Vulnerable *T. raziana*, occurs only in the small and very arid Desertas group. Also threatened, *T. rudis* was only detected on the southern part of Santiago Island and on Santa Maria Islet (Schleich 1987; Vasconcelos *et al.* submitted), preferentially on rocky barren areas and dry woody shrubland (pers. obs.). Furthermore, it was confirmed that the endangered *C. stangeri* mainly occurs, apart from the Desertas, just on the east side of S. Vicente and that it is absent between S. Pedro and Mindelo (Schleich 1987).

Most restricted range taxa and endangered taxa occurred only on one island, such as *T. p. protogigas* with only four recent records (after 1980), all on the southern part of Fogo Island (though see Appendix VI.3). Although more common, *T. bocagei* is also restricted to eastern S. Nicolau Island. Individuals were detected under rocks on rocky barren plain and arid areas and less abundant on more humid or high areas. Concerning the skinks, it was noticed that the three extant taxa with restricted range are uncommon: *C. v. vaillanti* and *C. v. xanthotis* are restricted to inland Santiago and to the northern side of Fogo Island, respectively, mainly on remains of agricultural stone walls and other rock walls on sub-humid and humid areas (pers. obs.), as in conifer and moist eucalyptus forests. Similarly, *C. s. salensis* occurs only on Sal, generally under knocked-down palm trees, rock piles and calcareous plates in dunes and sandy areas (Schleich 1987, 1996).

Some taxa are presently restricted to very small islets, such as *T. g. gigas* and *T. g. brancoensis* on Branco and Raso, respectively. The first is more abundant on the lower parts of the islet near the coast (Schleich 1982a), such as in the southern dunes (Schleich & Wuttke 1983) and on high parts and small ravines on the southern side (Schleich 1980). It is rare on the southeast peninsula due to strong wind exposure (Schleich 1982a). Wind-exposed slopes facing up, and rough and fissured stone are usually avoided by these geckos (Schleich 1980) as they are unable to use vertical surfaces (Schleich 1987) due to their high body mass. *Tarentola g. brancoensis* is also found in the coastal areas, mainly on the southern side (Schleich & Wuttke 1983) or flattened areas inside the islet (Andreone 2000). Both subspecies are usually found on rocky shores under sandstone blocks and are commensal with sea birds, using them as a food source (young, eggs, regurgitations) and inhabiting the same crevices birds use to nest (Schleich 1982a; Hazevoet 1995). This species probably had a wider range in the past, occupying Santa Luzia Island and S. Vicente, where subfossil bones were found (Mateo *et al.* 2009). Thus, the present range of the species results from the natural fragmentation of the habitat after the Pleistocenic sea-levels fluctuations that joined S. Vicente and the Desertas group, followed by the effect of human colonization and mammal predators associated with it (Mateo *et al.* 2009; Appendix VI.4).

Conservation status of native taxa

The major threats to biodiversity on this archipelago are habitat fragmentation by agriculture, cattle and introduced species; direct exploitation by hunting, collection and logging (Leyens & Lobin 1996), and severe droughts (MAAP-DGA 2004). For reptiles, natural disasters, intrinsic factors and exotic species are the main threats. The endemic *Hemidactylus* and *T. p. protogigas* are the most threatened taxa in the Cape Verde Islands. The major threats to both are related to natural disasters, as droughts and volcanic activity, intrinsic factors, such as low densities and restricted range and other unknown aspects. Very little is known about their demography and basic biology, thus further ecological studies are needed to reduce this lack of knowledge.

Criterion B, related to geographic range, was the most frequent classifying criteria to threatened taxa. This is a common pattern in reptile assessments (Pleguezuelos *et al.* 2002, 2010; Oliveira *et al.* 2005) associated to the lack of data concerning population trends and probability of extinction that are related to criteria A and E, respectively. Conversely, criterion D, related to population size or restricted range, was unusually frequent. These taxa often occur on small islands and sometimes are even restricted to islets, turning this criterion more relevant in this assessment. If comparisons were restrained to other reptile island forms of the Mediterranean basin hotspot, criterion D would turn up more significantly (Pleguezuelos *et al.* 2002; Oliveira *et al.* 2005), as is the case for *T. bischoffi* from Selvagens (Madeira archipelago) and *Gallotia bravoana* from La Gomera (Canaries).

It is disturbing that of all Macaronesian reptile taxa Cape Verde presents the highest percentage of threatened taxa (52%), followed by Madeira (50%) (Oliveira *et al.* 2005) and Canary islands (25%) (Pleguezuelos *et al.* 2002). Not considering reptiles of Madeira, since there only a maximum of five taxa, such a different proportion comparing to the Canarian reptile taxa is unexpected. It might be explained by the size of the Cape Verdes (about 50% smaller) that restricts ranges of taxa and by the increased aridity that is affecting these islands, especially in the eastern group (see Vasconcelos *et al.* 2010). Cyclic droughts were prompted by climatic changes on Cape Verde in the past century, however, projections for Sahel rainfall changes in response to global warming are highly uncertain (Biasutti *et al.* 2008). Droughts might even be more pronounced in the future, compromising the viability of some reptile populations, such as *T. boavistensis* and *C. spinalis salensis*, or not, and thus conservation efforts are needed to ensure a better future for the Cape Verdean herpetofauna.

Conservation implications

National laws to protect all threatened species are needed because current legislation is inadequate due to recent taxonomic changes and new and more precise distribution data. In addition, educational campaigns, especially directed to children and politicians, are highly recommended to increase the awareness and capacity-building of the Cape Verdeans to protect their endemic reptiles. Especial attention should be addressed to *H. bouvieri*, *H. lopezjuradoi* and *T. p. protogigas* that present few records, very restricted areas of occupancy and have Critically

Endangered status. Management plans should be implemented immediately in order to prevent their imminent extinction. Research and policy-based action, accompanied by species-based actions, such as control and eradication of invasive and probable competitor species are imperative to ensure the viability of the endemic *Hemidactylus* species. The same applies to *T. gigas* ssp. for which more precise estimates of the abundances of mature individuals are needed. Since demographic fluctuations are likely to occur within extremely restricted ranges, due to cyclic droughts and effective sizes of commensal birds, monitoring of these taxa is also essential.

The Vulnerable *C. vaillanti* also needs management plans considering that its range was already reduced probably by the increased desertification, as suggested by the finding of subfossil records on Boavista and Maio, where the species is no longer found (*in* Carranza *et al.* 2001). In addition, *C. stangeri* on S. Vicente deserves particular attention, considering its small range. Removal of introduced mammals from Santa Luzia is urgently needed to preserve not only Endangered *C. stangeri* populations but also the Vulnerable *T. raziana*.

Overall, there is a huge lack of data about basic biology and demographic parameters of all threatened reptiles in the Cape Verdes and detailed quantification of the major threats affecting them. With these new data on the distribution and conservation status, it is intended to improve the possibility of assessing conservation priorities for this group. At the moment, only four of the 46 terrestrial protected areas have been fully established and it is important to guarantee that they will encompass all taxa and ESUs for reptiles. Presently, this is not the case since, for instance, there are no protected areas projected for Brava Island, where the largest population of the vulnerable *T. p. hartogi* occurs. Thus, the opportunity to optimize the design and location of these areas for reptiles needs to be urgently grabbed.

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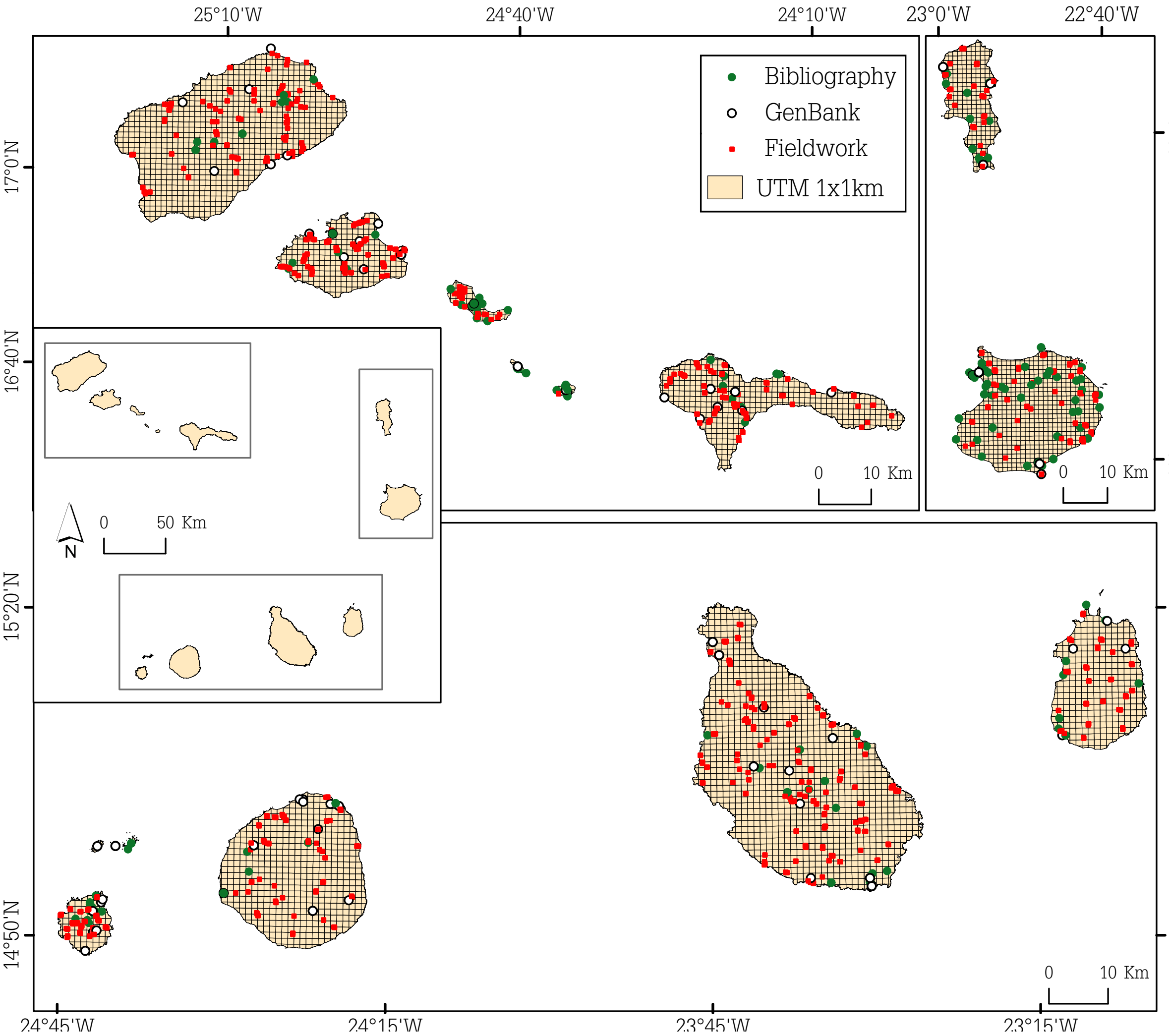
SUPPORTING INFORMATION

Appendix VI.1 Distribution of stations sampled during field work and localities from where bibliographic or GenBank data were collected (latitude and longitude in decimal degrees; Geographic Coordinate System, Datum WGS 84).



Appendix VI.2 Types and total number of habitats present in each island (•) in the Cape Verde archipelago (adapted from Diniz & Matos 1986, 1987, 1988 a, b, 1993, 1994, 1999 a, b, c).

Habitat type	SV	SL	ra	br	SA	SN	B	ro	M	F	ST	sm	S	BV
Beach	•	•			•	•			•	•	•		•	•
Dunes and sandy areas	•	•							•				•	•
Recent lavas										•				
Very arid flat areas	•	•	•		•	•			•	•			•	•
Very arid and hilly areas	•	•	•	•	•	•							•	•
Very arid and mountain areas	•	•	•	•		•								
Arid and flat areas						•	•	•		•	•	•		
Arid and hilly areas	•				•	•	•	•	•		•			
Arid and mountain areas	•				•						•			
Semi-arid and flat areas						•	•			•	•			
Semi-arid and hilly areas					•	•	•			•	•			
Semi-arid and mountain areas	•				•	•					•			
Sub-humid and flat areas										•				
Sub-humid and hilly areas					•		•			•	•			
Sub-humid and mountain areas	•				•	•	•			•	•			
Humid and mountains areas					•	•	•			•	•			
Water lines and floodplain areas	•	•			•	•	•		•		•		•	•
Coastal-salty lowland areas	•								•				•	•
Cliffs										•	•			
Urban	•				•	•	•		•	•	•		•	•
Total number	12	6	3	2	12	13	9	2	7	12	13	1	7	7

SV, S. Vicente; SL, Sta. Luzia; ra, Raso; br, Branco; SA, Santo Antão; SN, S. Nicolau; B, Brava; ro, Rombos; M, Maio; F, Fogo; ST, Santiago; sm, Sta. Maria; S, Sal; BV, Boavista.

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Appendix VI.4 Uncertain occurrences of endemic and exotic taxa on the Cape Verde Islands.

Exotic taxa

Serpa Pinto (1896) mentioned a 'tortoise' in S. Vicente. Nevertheless, Bocage, his correspondent, doubted about the presence of a terrestrial chelonid in the archipelago (Bocage 1896). Given that the common name in Creole ('cágado') is applied to the marine turtle *Eretmochelys imbricata*, frequently seen in many beaches of the archipelago, including S. Vicente, it is highly possible that a misunderstanding of common names occurred. Also the old references for *Pelusios* in Sta. Maria islet (Angel 1935, 1937) were never confirmed.

An unknown species of *Lygodactylus* geckos was observed on Santiago and mentioned on the National Red List (Schleich 1996) as Data Deficient that was never recorded on any of the following expeditions. In addition, the presence of *H. angulatus* in Maio is referred by Schleich (1982b), citing Angel (1935, 1937). However, no such reference exists in the original papers. Also Schleich (1987) cites the exotic *H. angulatus* for Santa Maria islet but with uncertainty ('?'). The presence of *H. angulatus* on Brava and S. Nicolau, at an unknown locality, was referred firstly by Mertens (1955) and Jesus *et al.* (2001), respectively and cited latter by other authors (Naurois 1994; Schleich 1982b, 1987, 1996). However, no other individuals have been observed on either island since then, including during the prospection for the present study. Indeed some authors confirmed absence of *H. angulatus* in S. Nicolau (González & López-Jurado 2004). Hence, these records could be erroneous or/and the taxon might have disappeared from these islands.

Regarding the *A. agama* voucher seen in S. Antão, after intensive sampling throughout the island in 71 sites with at least two observers, no other agamids were found. However, it might be possible that some animals remain in the wild (for details see Vasconcelos *et al.* 2009).

Finally, there is an old reference to the snake *Psammophis sibilians* on Sal by Deykeyser & Villiers (1951) which, according to the author was an accidental introduction from Guinea-Bissau that has never been recorded again.

Endemic taxa

Chevalier, in the 30s, refers to fossil records of *Testudo calcarata* in Pedra Lume crater, on Sal (*in* López-Jurado 1998). Later on, it was described as *Geochelone atlantica* López-Jurado 1998, although the validity of this new endemic taxon from Cape Verde has been questioned (Hazevoet 1995). Also Bebiano (1932) refers subfossil eggs of this terrestrial turtle from Maio. Nevertheless, this species probably went extinct after the end of the humid phase of the Quaternary, as ecological conditions no longer could sustained its presence, as confirmed by its absence from more recent historical records (López-Jurado 1998).

The actual occurrence of *Hemidactylus bouvieri* in Santiago and Brava is doubtful, since most recent records surpass 50 and 110 years, respectively (Mertens 1954; Andreone 2000). For the understanding of the accepted current distribution for the *Hemidactylus* species see Arnold *et al.* (2008).

The past occurrence of *Tarentola* in Sal (Angel 1935, 1937) is uncertain. Possible presence is based on only one voucher sent by Prof. Chevalier in 1934 that might have been incorrectly assigned to Sal. All the following authors refer to this record based on Angel (Mertens 1955; Schleich 1982b). Sal is a relatively small and almost flat island where the species presence should be relatively easy to detect, but following expeditions failed to record it, including ours. For this reason, Carranza *et al.* (2000) considers that Sal apparently has no *Tarentola* at the moment. Thus, since a recent extinction scenario is also plausible, we considered this occurence as doubtful.

The presence of *T. substituta* in Sta. Luzia and Branco islet is mentioned by López-Jurado *et al.* (2005). It is strange as this was the first record for the species in those islands and there was no reference to the fact. Even more so since references for that study were based on previous bibliographic references. Possibly it is a typographic error, as it is missing the reference for the same islands for *T. raziana* in the table where this taxon lies exactly above the former one. Thus, the above reference is considered erroneous.

There is a reference for the occurrence of *T. nicolauensis* in Mindelo, S. Vicente Island (Jesus *et al.* 2002) that could be interpreted as a recent introduction due to high genetic similarity to the samples from S. Nicolau Island. However, its absence was confirmed soon after (González & López-Jurado 2004). Unless the assessment is reconfirmed, we consider this occurrence as doubtful.

The possible presence of *T. darwini* on Sal Island (Joger 1984) was criticised by Schleich (1987) who stated that was speculative and mentioned the bad conservation status of the voucher and the identification being based only on the high number of dorsal tubercles. Even Joger (1984a) included all specimens from Sal with some reservations. Later, in 1993, Joger assumed its presence on S. Nicolau and not on Sal and thus the occurrence of *T. darwini* on the latter island is not considered valid.

Some subfossil bones of an unknown subspecies of *T. gigas* were recently found in Santa Luzia and S. Vicente (Mateo *et al.* 2009) but without genetic confirmation it is difficult to assign them to the subspecific level. Therefore, it is considered that the species had a wider range in the past, although this was not represented on either of the subspecies' current distribution maps.

A voucher of *T. protogigas* (Museo Civico 'G. Doria' di storia Naturale de Genova 28248) is recorded to have been found in Igreja (same as Mosteiros) on the northern part of Fogo in 1899 (Andreone 2000) based on Fea. However, the much more abundant *T. fogoensis*, previously referred to *T. darwini* (Vasconcelos *et al.* submitted) and also present on the island, was not described at the time. In this way, without genetic confirmation this unique northern record is considered doubtful as it could correspond to *T. fogoensis*. Also, the fact that Joger (1984a) used this same voucher to describe the new subspecies of *T. 'rudis' protogigas* but stating its origin as S. Filipe, Fogo Island, indicates that indeed an error occurred in the capture locality. '*T. rudis* cf. *protogigas*' is also reported to occur on Sta. Maria islet by Schleich (1987). However, no genetic analysis was performed because no vouchers were collected for conservation reasons, as very few animals were observed. It is possible that these animals could be in fact *T. rudis* with some morphological variation from the ones from Santiago, as a result of geographical isolation and ecological adaptation. The reference by the same author for the occurrence of *T. rudis* in Fogo (Schleich 1984) is explained by the fact that when Boulenger (1906) described *T. rudis* (at the time *T. delalandii* var. *rudis*) he recognised Santiago and Fogo as its *terra typica*. Knowing that *T.* '*rudis*' *protogigas* Joger, 1984 subspecies had not been described yet, this confusion is untangled. That is why the same voucher identified as *T. rudis* from Fogo in Schleich (1984) was used in the *T. protogigas* section in Schleich (1987). However, the error was later propagated (Schleich 1987), probably due to a typographical error as the author does not refer to its occurrence in Fogo in the article neither in the table nor in the subspecies descriptive part, but only in the 'Island by Island' part. In a later publication (Schleich 1996), the occurrence of *T. rudis* on Fogo or *T. p. protogigas* on Sta. Maria was not mentioned. So, the references until 1984 for *T. rudis* on Fogo were interpreted as referring to *T. p. protogigas*. This interpretation is also based on our intensive prospection and on the fact that after that date no other author referred the occurrence of both taxa on the same island and is supported by other experts (González & López-Jurado 2004). For analogous reasons, all references for *Tarentola* in Brava and Maio until 1984 were referred to *T. p. hartogi* and *T. maioensis* Schleich, 1984, respectively, the only *Tarentola* proven to occur respectively on each one of the islands.

Indeed *T. gigas* referred by Jesus *et al.* (2001) to occur in S. Nicolau Island is actually *T. maioensis* probably introduced in this island (see Vasconcelos *et al.* 2010). Regarding *T. protogigas hartogi* (sensu Joger, 1993) it is genetically nearly identical to *T. protogigas* from Brava (Carranza *et al.* 2000). Moreover, differences in morphology are questionable as Joger's (1993) study did not present statistical support as it was based on only five and nine specimens for each subspecies. Thus, *T. p. hartogi* was considered to occur on Brava and Rombos on this study, following Vasconcelos *et al.* (submitted).

The past presence of *C. coctei* on other islands apart from the Desertas group is defended by some authors as possible on S. Nicolau, due to Pleistocene sea level falls and based on fisherman reports (Greer 1976; Schleich 1982a). Also on S. Vicente fisherman (Schleich 1982a), subfossil records (Mateo *et al.* 2005, 2009) and old museum vouchers (Andreone 2000) might indicate its presence, even though the localities of vouchers can be considered doubtfoul (see also Miralles *et al.* 2010).

The presence of a subfossil record from Boavista and Maio apparently conspecific with *C. vaillanti* (in Carranza *et al.* 2001) might indicate a larger species range in the past, although without genetic data or a detailed study of the subfossil material it is not possible to assign them to any of the subspecies. Considering that these fossils were much larger than the individuals from Fogo and Santiago, reaching 240 mm from snout to vent, it is even possible that this would be a different and extinct form. Nevertheless, reduction in size has already been demonstrated in *Gallotia* from the Canaries and might result from the alteration of insular environments by humans (Barahona *et al.* 2000). The presence of *C. vaillanti* on Brava Island by Brehm *et al.* (2001) and Lopéz-Jurado *et al.* (2005) was interpreted as referring to Rombos Islets that lay in front of this island. The same was assumed for *T. p. hartogi* referred by the latter author also on Brava, as both taxa were considered exclusive of the Rombos Islets before the taxonomical revision of Vasconcelos *et al.* (in press). Moreover, Lopéz-Jurado *et al.* (2005) mentions in the introduction text the assignment of the presence records to islets of the island nearby.

The present study confirmed the introduction of *C. delalandii* on Maio, firstly referred by Carranza *et al.* (2001) and López-Jurado *et al.* (2005). This species is also referred in S. Nicolau by Fea (1899), Bocage (1902) and Andreone (2000) but it is probably, and following this last author, a perpetuated error originated from mislabelling. The introduction of this species in Boavista, in Vila de Sal Rei (Schleich 1987), occurred in the 1970s and its actual presence is uncertain as some authors claim that it is now extinct (Lopéz-Jurado *et. al* 1999) or that it has not been found after intensive survey (Brown *et al.* 2001). Others have referred to its presence after the 1970s (Chadwick & Slater 2005), although the photo of the individual raises doubts. In this way, we have considered the actual presence of this species in Boavista, also not confirmed during our prospection, as doubtful.

Chioninia geisthardti (Joger, 1993) and *C. fogoensis fogoensis* (O' Shaughnessy, 1874) were not considered valid taxa following some authors (Carranza *et al.* 2001; González & López-Jurado 2004; Naurois 1994) and both are presently considered as synonyms of *C. fogoensis* from Santo Antão (Miralles *et al.* 2010). In this way, the reference of *C. fogoensis* on S. Vicente is also considered doubtful (see Miralles *et al.* 2010).

Chioninia spinalis spinalis is referred to S. Nicolau by Fea (1899) but it is again probably an error originating from a mislabelling (Andreone 2000). Its presence in Sal is also mentioned by Angel (1935, 1937) even though he is the author responsible for the description of the new taxa *C. salensis* (Angel, 1935), now *C. spinalis salensis* Miralles *et al.*, 2010. This can be explained by the fact that *C. spinalis* was described by Boulenger (1905) as being present in Fogo and Sal. In this way, when Angel found differences in the few specimens analysed from Sal, he assumed the existence of the two taxa (*C. spinalis* and *C. salensis*) in the island. However, the separation of populations from Fogo and Sal in different taxa is showed by morphological and molecular data (Miralles *et al.* 2010). Only latter, Mertens (1955) divided them into *C. stangeri spinalis* and *C. stangeri salensis*, which was confirmed by Schleich (1987) and by Joger (1993), who changed the taxonomy to *C. spinalis spinalis* and *C. spinalis salensis*, respectively. For this same reason, Angel (1937) referred the presence of *C. stangeri* on Boavista, as some authors referred to *C. spinalis* as *C. stangeri* omitting the subspecific name, for example Bocage (1902), because the description of *C. spinalis* species occurred only in 1906 by Boulenger. The reference of *C. stangeri* for S. Nicolau (Bocage 1902) is again an old error (González & López-Jurado 2004) repeated in later citations. However, it was said that it was recently introduced on this island and on Santiago (Pinheiro 1990), without confirmation on any of the further prospection, including ours. The reference of this species on Brava and Sal is also made by Schleich (1982b) based on old references. Later, the same author considered those records and the presence of this taxon in Boavista as doubtful (Schleich 1996). In this way, we have considered the presence of *C. stangeri* in these three islands as probably erroneous. The hypothesis that they could be referring to *C. spinalis* in the case of Sal and Boavista islands as referred before is more plausible.

References

(References for this section already included in Appendix VI.3 are not listed)

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Appendix VI.5 Major threats acting on Cape Verdean reptiles following IUCN (2001) listing. Details on the specific threats are given by IUCN (2010): 0: None; 1: Habitat loss, degradation; 2: Invasive alien species; 3: Harvesting; 7: Natural disasters; 8: Changes in native species dynamics; 9: Intrinsic factors; 10: Human disturbance; 11/12: Other/ Unknown.

Taxa	**0**	**1**	**2**	**3**	**7**	**8**	**9**	**10**	**11/12.**
H. bouvieri bouvieri		1.1.1.2, 1.5	2.1, 2.2		7.1		9.5, 9.9		12
H. b. spp., S. Nicolau		1.1.1.2, 1.5	2.1, 2.2		7.1		9.5, 9.9		12
H. b. razoensis		1.5	2.1, 2.2		7.1		9.5, 9.9		12
H. boavistensis		1.4, 1.5	2.1		7.1				
H. lopezjuradoi		1.1.1.2, 1.5	2.1, 2.2		7.1, 7.5		9.5, 9.9		12
T. boavistensis					7.1		9.5		
T. bocagei							9.9		
T. fogoensis					7.5				
T. darwini	0								
T. substituta					7.1				
T. raziana		1.5	2.1, 2.2		7.1				
T. caboverdiana	0								
T. nicolauensis	0								
T. gigas gigas					7.1	8.3	9.9	10.6	
T. g. brancoensis					7.1	8.3	9.9	10.6	
T. rudis						8.4			
T. protogigas protogigas					7.5		9.5, 9.9		12
T. p. hartogi					7.1, 7.7				
T. maioensis					7.1				
C. vaillanti vaillanti							9.5, 9.7, 9.9		
C. v. xanthotis					7.5		9.5, 9.7, 9.9		
C. delalandii					7.1				
C. nicolauensis					7.1				
C. fogoensis			2.5						
C. stangeri			2.2		7.1				
C. coctei		1.5	2.2	3.1.1, 3.2.1, 3.4.1, 3.5.3	7.1		9.2, 9.7, 9.9		
C. spinalis salensis					7.1		9.9		
C. s. santiagoensis	0								
C. s. spinalis					7.5				
C. s. maioensis					7.1				
C. s. boavistensis					7.1				
Total	2	7	9	1	23	3	13	2	5

ARTICLE VII

Priority areas for island endemics using genetic diversity – the case of the terrestrial reptiles of the Cape Verde Islands

R. Vasconcelos[1,2,3*], J.C. Brito[1,2], S. Carvalho[1], S. Carranza[3] & D.J. Harris[1,2]

[1] CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos da Universidade do Porto,
Campus Agrário de Vairão, R. Padre Armando Quintas, 4485-661 Vairão, Portugal;

[2] Departamento de Biologia, Faculdade de Ciências da Universidade do Porto,
Pr. Gomes Teixeira, 4099-002 Porto, Portugal;

[3] Institute of Evolutionary Biology (CSIC-UPF),
Passeig Marítim de la Barceloneta, 37-49, E-08003 Barcelona, Spain.

ABSTRACT

Assessing genetic diversity is critical for conservation of endemic populations. It enhances adaptation to rapid environmental changes and persistence over evolutionary time-scales. In small and isolated populations, such as in islands, this is even more relevant. Nevertheless, few priority areas studies on islands systems have taken genetic diversity into account. The Cape Verde Islands present to resource planners unique problems and possibilities. In this biodiversity hotspot, the possibility of redesigning optimized protected areas (PAs) is real, since most of them are still proposals. This work aims to assess the adequacy of those PAs based on 'realistic' and 'ideal' scenarios of cost and to identify gaps for the conservation of the endemic evolutionary significant units (ESUs) of Cape Verdean reptiles using predictive modelling. Results indicate that most ESUs are, and will continue to be, insufficiently protected and that extra PAs are needed on all but three of the 10 islands to reach conservation targets. Surprisingly, the number of Planning Units selected in both 'ideal' and 'realistic' scenarios was identical on almost all islands, probably because scenarios are spatially congruent regarding the extra PAs; selecting optimised PAs in pristine regions does not lead to significant different results from random prioritisation, especially in small areas; or/and reptiles are good surrogates of priority areas for endemic birds and flora on which *ad hoc* planning was based on. This work provides an innovating methodological framework for using genetic diversity in reserve design and its results intend to contribute for local-scale conservation planning of endemic biodiversity.

KEY WORDS

Chioninia, ecological niche-based models, ESUs, *Hemidactylus*, Protected Areas, *Tarentola*.

INTRODUCTION

Genetic diversity is critical for conservation of endemic populations since it provides the raw material for the persistence of species over evolutionary time-scales, and is also of particular relevance at present time-scale in terms of providing the basis for adaptation to rapid environmental changes (Bradshaw & Holzapfel 2006; Höglund 2009). Genetic diversity is correlated with adaptive capacity of populations and fitness (Soulé 1986). In small populations, reduction of genetic diversity by drift and high levels of consanguine mating may cause inbreeding depression, increasing the incidence of heritable recessive diseases (Hedrick & Kalinowski 2000). Furthermore, in isolated populations, the synergy of genetic and demographic factors substantially increases their probability of extinction (Frankham 1997; Soulé & Mills 1998). Such is particularly the case of island populations (e.g. Caujapé-Castells *et al.* 2010), which tend to be highly isolated and frequently affected by stochastic catastrophic events, such as volcanic activity or droughts that can cause bottleneck effects (Whittaker & Fernández-Palacios 2007). Moreover, islands usually have higher numbers of endemic species than equivalent continental areas (Whittaker & Fernández-Palacios 2007) and high levels of uniqueness of genetic variation, especially on large or highly remote ones (Wilson *et al.* 2009). As a result, the study and protection of endemic island taxa and their genetic diversity, considering all evolutionarily significant units (ESUs), is particularly relevant on islands.

Designation of protected areas (PAs) safeguards habitats important to wildlife and preserves genetic resources and species diversity, provides a baseline against which human-caused changes can be measured, and allows evolutionary processes to continue without human disturbance (Quigg 1987). The best way to represent genetic diversity in a subset of populations is to base conservation decisions on known levels of diversity within, and distribution of diversity among, populations (Neel & Cummings 2003). Nevertheless, most studies focus on optimizing biodiversity representation at the species and/or habitat level (e.g. Cowling & Pressley, 2001; Cowling *et al.* 2003; Bonn & Gaston 2005; Kremen *et al.* 2008), while studies accounting for intra-specific genetic variability in terrestrial systems are scarce (e.g. Wei & Leberg 2002; O'Meally & Colgan, 2005; Rissler *et al.* 2006; Davis *et al.* 2007; Grivet *et al.* 2008). To our knowledge, only three studies of this nature have been performed on island-like system. Smith *et al.* (2000) and Kahindo *et al.* (2007) studied the mitochondrial lineages of avian species in the mountain regions of Africa, and considered distinctive lineages worthy of conservation. Setiadi *et al.* (2009) tested whether the two disjunct blocks constituting a National Park of an Indonesian island adequately captured the full breadth of genetic diversity of endemic species of herpetofauna. These studies showed that the study of the distribution of genetic variation within species can provide useful information for biodiversity conservation. However its concrete application to selection of protected areas at a national scale remains unexplored.

Because financial resources for conservation are limited, systematic methodologies and optimization algorithms have been developed to optimize biodiversity representation and persistence within PAs (Moilanen *et al.* 2009). The establishment of PAs is usually constrained by the existing reserve system (Pressey 1994) and forms of land use that are, in the short term, financially more viable than conservation (Ferrier *et al.* 2000). Implementation of new PAs in most developed countries is also usually hampered by high densities of human population and infrastructures. The Cape Verde Islands are an exception in some of those points, since most islands of the archipelago have less than 75 habitants/km^2 (Lobban & Soucier 2007), few impacting human infrastructures, and implementation of a PAs network is still ongoing. Nevertheless, the PAs network in the Cape Verde was chosen in a non-systematic way, based on *ad hoc* presences of nesting sites for birds and endemic flora and also on scenic and recreational reasons (Anonymous 2003a). Currently, only four of the 46 terrestrial reserves of the network (Anonymous 2003a) are established in legal terms (Fig. VII.1). These are the Natural Reserve on Santa Luzia (Anonymous 2003b) and Natural Parks of 'Monte Gordo' on S. Nicolau, 'Serra da Malagueta' on Santiago and 'Bordeira, Chã das Caldeiras e Pico Novo' on Fogo (Anonymous 2007a, b, 2008, respectively). However, only the latter three have management programs, and can thus be considered fully operational. These three areas correspond to merely 2.47% of the area of the country (IUCN & UNEP-WCMC 2010). The remaining 42 PAs are still proposals for now, and thus there is still a window of opportunity to enhance them.

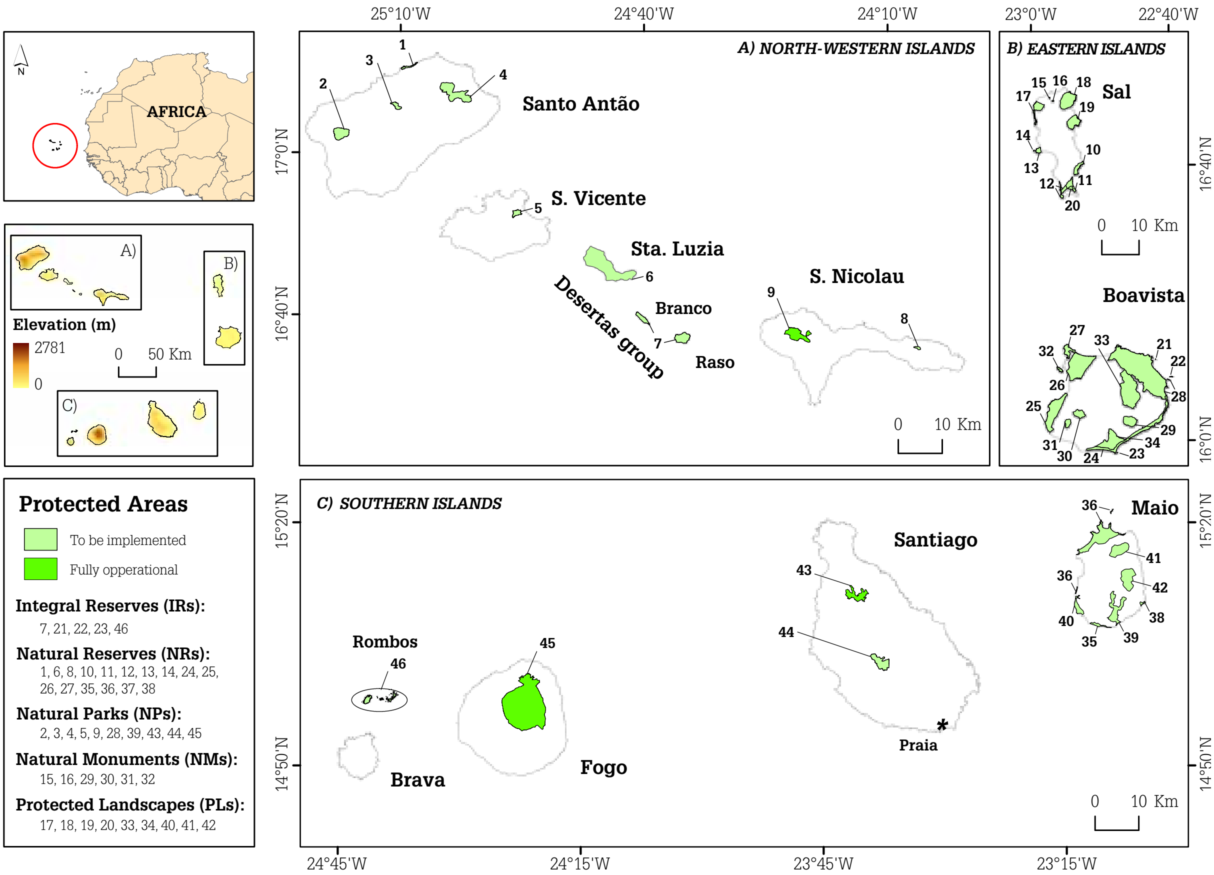

Figure VII.1 Location of the study area and distribution of the Protected Areas (PAs) in the Cape Verde Islands (see Table VII.1 for PA designations).

The insular geography of Cape Verde presents to resource planners unique problems and possibilities for reserve design. Its complex system with numerous islands with different climate and topography, each one with unique habitats and biodiversity is challenging, and the possibility of including new or modified optimized areas for representing and ensuring long-term persistence of its endemic biodiversity is real. In addition, biodiversity inventories are still scarce, and chorological data are still poorly documented, although this archipelago is of highly conservation importance given that it was included in the Mediterranean biodiversity hotspot (Conservation International 2005). Hence, the degree that implemented and proposed PAs serve to protect important elements of biodiversity in the country, especially genetic diversity, is unknown. One of the first steps in assessing how well reserves achieve their goal of preserving biodiversity is to investigate the extent to which specific resources are being protected within the reserve system (Scott & Csuti 1997). Therefore, assessing the adequacy of the fully established and proposed PAs for conservation of the ESUs of endemic groups and identifying gaps in the representation of ESUs are high-priorities.

Among vertebrates, the biodiversity of reptiles in the Cape Verde Islands stands out in total number of taxa and endemisms, since it is the richest of all Macaronesian islands (Vasconcelos *et al.* submitted a). Contrary to other groups, all native taxa are endemics (Schleich 1987) and present recently updated taxonomy, well-known genetic diversity and defined ESUs for conservation (Arnold *et al.* 2008; Vasconcelos *et al.* submitted b; Miralles *et al.* 2010). Furthermore, it is a group that was generally neglected in the design of the PAs network due to the lack of chorological data. It also presents a manageable number of extant taxa, 30, within only three genera: the *Hemidactylus* and *Tarentola* geckos and the *Chioninia* skinks (Vasconcelos *et al.* submitted). Hence, Cape Verdean reptiles are ideal models to study reserve design and perform gap analyses taking into account genetic diversity.

The general aims of this study are to assess the adequacy of the PAs network and to identify its gaps for the conservation of the endemic ESUs of Cape Verdean reptiles. The specific objectives are: 1) to map priority Planning Units (PUs) using a 'realistic' scenario of reserve design (considering PUs inside PAs with lower cost) and an 'ideal' scenario (considering all non-humanized PUs with higher potential for conservation); 2) to quantify the protection that the PAs network guarantees or will guarantee and the amount that is still missing for achieving the conservation targets for each ESU; 3) to quantify the amount of selected PUs that will be inside PAs in each island considering both scenarios. For achieving these goals, predictive models of taxa occurrence delimited for each ESU will be used. Hence, this work attempts to provide innovating methodological framework for using genetic diversity in reserve design and its results are intended to contribute for local scale conservation planning of endemic biodiversity on islands.

MATERIALS AND METHODS

Study area

The study region is the Cape Verde archipelago, located in the Atlantic Ocean around 500 kilometres off the west coast of Africa (Fig. VII.1). With an area of 4067 km^2, the study area was divided into 76,414 grid cells, of 225x225 m each, hereafter referred as Planning Units (PUs), the units for reserve design.

Data on the existing PAs was compiled from MAAP-DGA (2010) website. Digital maps of the proposed Cape Verdean PAs were created based on information available from government internal reports (Table VII.1; Fig. VII.1). Only the terrestrial portion of PAs which also cover marine zones was considered.

Taxa occurrence data and distribution models

Given that only a small fraction of the territory was sampled (around 11%), and that sampled locations were spatially biased, it is most appropriate to use ecological models to predict the potential distribution of each taxa occurrence, when attempting to identify priority areas for conservation (Carvalho *et al.* 2010).

Taxa occurrence data

A total of 953 observations of all 30 extant Cape Verdean reptile taxa from the most recent distribution atlas were used to develop models (Vasconcelos *et al.* submitted a). For 752 observations, the geographic location was recorded with a Global Positioning System (GPS) on the WGS84 datum, whereas the remaining 201 observations were georeferenced using topographical maps to a precision of 225 m. Given that there was spatial bias in survey effort that resulted in presence clumps, observations were removed from clusters of occurrences to decrease the level of spatial autocorrelation in taxa presences (for details see Brito *et al.* 2009). The Nearest Neighbour Index was used to assess the degree of data clustering: 0.42, 0.66, 0.85 and 0.89 in *Chioninia delalandii*, *Hemidactylus boavistensis*, *Tarentola fogoensis* and *Tarentola substituta*, respectively, and above 0.90 for the remaining taxa, indicating some degree of clustering for the former four species and dispersed distribution for the remaining ones. Spatial analyses were accomplished with 'Spatial Analyst' extension of ArcGIS 9.3 (ESRI 2008). From the observations available, 791 were used for developing distribution models for each taxon.

Environmental factors

Fourteen ecogeographical variables (hereafter EGVs), were used in the ecological models (Appendix VII.1 in Supplementary Material) and included altitude (Jarvis *et al.* 2006), slope derived from altitude with the 'Slope' function

Table VII.1 Location, area (km2) and perimeter (km) of the Protected Areas (PAs) of the Cape Verde Islands. PAs presently fully established are marked (*); (land) indicates the terrestrial portion of PAs that also cover marine zones.

Code	Name	Island	Area	Perimeter
1	NR Cruzinha	SA	1.11	1.04
2	NP Tope de Coroa	SA	7.08	1.14
3	NP Moroços	SA	1.87	7.28
4	NP Cova/Ribeira Paúl/Torre	SA	14.71	2.59
5	NP Monte Verde	SV	2.12	8.30
6	NR Santa Luzia	SL	34.8	3.49
7	IR Ilhéu Branco e Raso	br, ra	8.58	10.69
8	NR Monte do Alto das Cabeças	SN	0.62	3.73
9	NP Monte Gordo (*)	SN	9.52	2.21
10	NR Serra Negra (land)	S	3.28	1.26
11	NR Costa da Fragata (land)	S	3.47	1.20
12	NR Ponta do Sinó (land and Peripheral Zone of Protection)	S	2.37	6.75
13	NR Rabo de Junco	S	1.53	5.78
14	NR Baía da Murdeira (land: Ilhéu Rabo de Junco)	S	0.03	0.81
15	NM Morrinho do Açúcar	S	0.05	0.84
16	NM Morrinho do Filho	S	0.11	1.26
17	PL Buracona-Ragona	S	5.35	1.99
18	PL Monte Grande	S	13.09	1.97
19	PL Salinas de Pedra Lume e Cagarral	S	8.04	1.56
20	PL Salinas de Santa Maria	S	0.74	3.68
21	IR Ilhéus dos Pássaros	BV	0.01	0.41
22	IR Ilhéu de Baluarte	BV	0.10	2.02
23	IR Ilhéus de Curral Velho	BV	0.01	0.55
24	NR Tartaruga (land)	BV	17.57	6.65
25	NR Morro de Areia (land)	BV	21.42	2.97
26	NR Boa Esperança	BV	31.25	2.59
27	NR Ponta do Sol (land)	BV	4.61	1.58
28	NP do Norte (land and islets)	BV	89.74	8.68
29	NM Monte Estância	BV	7.31	1.07
30	NM Monte Santo António	BV	4.56	8.97
31	NM Rocha Estância	BV	2.52	6.69
32	NM Ilhéu de Sal-Rei	BV	0.93	6.34
33	PL Monte Caçador e Pico Forçado	BV	33.6	2.84
34	PL Curral Velho	BV	16.36	2.44
35	NR CasaVelhas (land)	M	1.39	1.07
36	NR Praia do Morro (land)	M	0.22	3.64
37	NR Terras Salgadas (land)	M	19.79	7.11
38	NR Lagoa Cimidor (land)	M	0.51	4.38
39	NP Barareiro e Figueira (land)	M	10.55	3.01
40	PL Salinas de Porto Inglês (land)	M	3.42	1.37
41	PL Monte Santo António	M	8.76	1.23
42	PL Monte Penoso e Monte Branco	M	11.1	1.48
43	NP Serra da Malagueta (*)	ST	7.74	2.71
44	NP Serra do Pico de Antónia	ST	7.98	1.94
45	NP Bordeira, Chã das Caldeiras e Pico Novo (*)	F	84.79	4.92
46	IR Ilhéus do Rombo	ro	3.04	16.08

Categories: IR, Integral Reserve; NR, Natural Reserve; NP, Natural Park; NM, Natural Monument; PL, Protected Landscape; Islands: SA, Santo Antão; SV; S. Vicente; SL, Santa Luzia; br, Branco; ra, Raso; SN, S. Nicolau; S, Sal; BV, Boavista; M, Maio; ST, Santiago; F, Fogo; ro, Rombos

of ArcGIS, normalised difference vegetation index (NDVI), and 11 habitat types digitised from agro-ecological and vegetation zoning maps (for details on habitats see Vasconcelos *et al.* 2010). NDVI 16-day L3 Global 250 m data series from 01.01.2006 to 31.12.2008 were downloaded from USGS (2009) website, corresponding to the years when sampling was performed, and then the maximum of that data series was calculated to input into the models. The Euclidean distance of each grid cell to the closest habitat-type was calculated for each individual habitat grid using the 'Euclidian Distance' tool of ArcGIS. Finally, the resolution of EGVs was decreased from 0.00083 to a grid cell size average of 0.00211 degrees (about 225 m) to match the resolution of observations.

Predicted occurrences

Models were developed for each taxon (Appendices VII.2 and VII.3) using the Maximum Entropy approach (Phillips *et al.* 2006, Phillips & Dudík 2008). This modelling technique requires only presence data as input, but consistently performs well in comparison to other methods (Elith *et al.* 2006), especially with low samples sizes (Hernandez *et al.* 2006; Wisz *et al.* 2008). Even so, for seven taxa with extremely low sample size ($n \leq 5$) models were not developed. In these cases, the pixels of occurrence of the taxa and/or all pixels of the islet where the taxon occurs were used in subsequent analyses (Appendix VII.4).

Reptile observations and EGVs were imported into Maxent 3.3 software (Phillips *et al.* 2006). A total of 10 model replicates were run with random seed which allows a different random training/ testing data partition in each run. Observations for each replicate were chosen by bootstrapping. Percentages assigned for testing models varied according to sample size: 10% for four taxa with less than 20 observations, 20% for 18 taxa with more than 20 observations, and 15% for one taxa with only seven observations (Appendix VII.4). Models were run with auto-features (Phillips *et al.* 2006), and the Area under the Curve (AUC) of the receiver-operating characteristics (ROC) plot was taken as a measure of individual model fit (Fielding & Bell 1997).

The individual model replicates (n =10) were used to generate an average probability forecast of species occurrence (Marmion *et al.* 2009). Standard deviation between individual model probabilities of presence was used as an indication of prediction uncertainty (Buisson *et al.* 2010). Average models were reclassified to display areas of probable absence and presence for each taxon. For that purpose, 10 percentile training thresholds calculated by Maxent were used, which corresponds to the model probability where 90% of the observations with the highest model probabilities are considered as presences. To evaluate the model quality, the total observations (n= 953) were intersected with the threshold models to calculate the percentage of correct classification of presences for each taxa (Appendix VII.4).

Conservation planning prioritisation

A systematic approach was performed to identify the priority PUs for conservation of the endemic reptiles. To include genetic diversity into the reserve design, conservation targets were applied on ESUs.

Evolutionarily Significant Units delimitation

Considering the definition of Fraser & Bernatchez (2001) ESUs, the units for conservation action, are defined as lineages demonstrating highly restricted gene flow from other such lineages within the higher organisational level of species. Delimitation of ESUs for endemic species of each genus were performed on recent published papers that updated the taxonomy of the three reptile groups based on molecular markers, population and morphological analyses (see Arnold *et al.* 2008; Vasconcelos *et al.*, submitted b; Miralles *et al.* 2010). Hence, the 23 reclassified models with predicted taxa occurrence (Appendices VII.2 and VII.3) were clipped into individual files to correspond to the 38 previously identified extant ESUs. For example, the reclassified model for *C. delalandii* was clipped by Santiago, Fogo, Brava and Rombos shape files, respectively, to obtain the predicted distributions of the four genetically identified lineages (see Table VII.2). In the case of two taxa (*T. darwini* and *C. s. santiagoensis*) with two ESUs occurring on the same island (Santiago), the distribution data of lineages was plotted over the reclassified models to define the extent of occurrence of each ESU. For the seven taxa for which distribution models were not developed, only observed records were accounted for reserve selection. The ESU corresponding to the extinct *C. coctei* was not considered in the analyses.

Table VII.2 Number (*n*) of Planning Units (PUs) where each evolutionarily significant unit (ESU) is predicted to occur, targeted for conservation, inside Protected Areas (PAs) fully operational (present) or to be implemented (future), and missing to meet conservation targets (see Material and Methods for details). Percentages (%) are given between brackets.

Taxon/ ESU	**Island**	**Predicted**	**Targeted**		**Inside PAs**				**Missing**	
					Present		Future			
		n	*n*	%	*n*	%	*n*	%	*n*	%
Hemidactylus lopezjuradoi	F	1	1	(100)	0	(0.0)	0	(0.0)	1	(100)
H. boavistensis	BV, S	5901	708	(12)	0	(0.0)	2991	(50.7)	0	(0.0)
ESU Sal	S	2225	267	(12)	0	(0.0)	517	(23.2)	0	(0.0)
ESU Boavista	BV	3676	441	(12)	0	(0.0)	2474	(67.3)	0	(0.0)
H. bouvieri, SN population	SN	2	2	(100)	1	(50.0)	1	(50.0)	1	(50.0)
H. bouvieri bouvieri	SA	1	1	(100)	0	(0.0)	0	(0.0)	1	100.0)
H. bouvieri razoensis	SL	108	108	(100)	0	(0.0)	108	(100.0)	0	(0.0)
Tarentola boavistensis	BV	2994	359	(12)	0	(0.0)	1261	(42.1)	0	(0.0)
T. bocagei	SN	384	46	(12)	0	(0.0)	0	(0.0)	46	(12.0)
T. fogoensis	F	1099	132	(12)	17	(1.5)	17	(1.5)	115	(10.5)
T. darwini	ST	9801	1176	(12)	153	(1.6)	318	(3.2)	858	(8.8)
ESU North	ST	3819	458	(12)	153	(4.0)	153	(4.0)	305	(8.0)
ESU South	ST	5982	718	(12)	0	(0.0)	165	(2.8)	553	(9.2)
T. substituta	SV	1934	232	(12)	0	(0.0)	24	(1.2)	208	(10.8)
T. raziana	SL, ra, br	592	71	(12)	0	(0.0)	592	(100.0)	0	(0.0)
T. caboverdiana	SA	4180	502	(12)	0	(0.0)	97	(2.3)	405	(9.7)
T. nicolauensis	SN	2359	283	(12)	78	(3.3)	78	(3.3)	205	(8.7)
T. gigas brancoensis	br	46	46	(100)	0	(0.0)	46	(100.0)	0	(0.0)
T. gigas gigas	ra	107	107	(100)	0	(0.0)	107	(100.0)	0	(0.0)
T. rudis	ST	2380	286	(12)	0	(0.0)	29	(1.2)	257	(10.8)
T. maioensis	M	2013	242	(12)	0	(0.0)	601	(29.9)	0	(0.0)
T. protogigas protogigas	F	4	4	(100)	0	(0.0)	0	(0.0)	4	(100.0)
T. protogigas hartogi	B, ro	667	80	(12)	0	(0.0)	59	(8.8)	21	(3.2)
ESU Brava	B	608	73	(12)	0	(0.0)	0	(0.0)	73	(12.0)
ESU Rombos	ro	59	7	(12)	0	(0.0)	59	(100.0)	0	(0.0)
Chioninia vaillanti vaillanti	ST	3510	3510	(100)	157	(4.5)	233	(6.6)	3277	(93.4)
C. vaillanti xanthotis	F, ro	574	574	(100)	0	(0.0)	59	(10.3)	515	(89.7)
C. delalandii	ST, F, B,ro	7828	939	(12)	253	(3.2)	483	(6.2)	456	(5.8)
ESU Santiago	ST	4541	545	(12)	167	(3.7)	338	(7.4)	207	(4.6)
ESU Fogo	F	2238	269	(12)	86	(3.8)	86	(3.8)	183	(8.2)
ESU Brava	B	990	119	(12)	0	(0.0)	0	(0.0)	119	(12.0)
ESU Rombos	ro	59	7	(12)	0	(0.0)	59	(100.0)	0	(0.0)
C. nicolauensis	SN	1432	172	(12)	149	(10.4)	149	(10.4)	23	(1.6)
C. fogoensis	SA	3668	440	(12)	0	(0.0)	319	(8.7)	121	(3.3)
C. stangeri	SV, SL, ra, br	1036	1036	(100)	0	(0.0)	811	(78.3)	225	(21.7)
ESU Desertas	SL, ra, br	811	811	(100)	0	(0.0)	811	(100.0)	0	(0.0)
ESU S. Vicente	SV	235	235	(100)	0	(0.0)	0	(0.0)	235	(100.0)
C. spinalis salensis	S	2356	283	(12)	0	(0.0)	465	(19.7)	0	(0.0)
C. spinalis santiagoensis	ST	4740	569	(12)	0	(0.0)	0	(0.0)	569	(12.0)
ESU North	ST	684	82	(12)	0	(0.0)	0	(0.0)	82	(12.0)
ESU South	ST	4056	487	(12)	0	(0.0)	0	(0.0)	487	(12.0)
C. spinalis spinalis	F	2118	254	(12)	303	(14.3)	303	(14.3)	0	(0.0)
C. spinalis maioensis	M	1635	196	(12)	0	(0.0)	559	(34.2)	0	(0.0)
C. spinalis boavistensis	BV	5496	660	(12)	0	(0. 0)	2947	(53.6)	0	(0.0)
TOTAL		76414	9170	(12)	1111	(1.5)	12657	(16.6)	9552	(12.5)

Islands: SA, Santo Antão; SV; S. Vicente; SL, Santa Luzia; br, Branco; ra, Raso; SN, S. Nicolau; S, Sal; BV, Boavista; M, Maio; ST, Santiago; F, Fogo; ro, Rombos.

Priority areas for conservation

A software for spatial conservation prioritisation, Zonation v 2.0 (Moilanen *et al.* 2009) was used to evaluate if the proposed and already established areas were optimal for protecting all the ESUs of endemic reptiles from Cape Verde. Zonation uses a gradient-like iterative heuristic, which gives a solution very close to the global optimal (van Teeffelen & Moilanen 2008) to produce a sequential removal of units throughout the planning region. Planning units with less conservation value are removed first, thus, PUs with highest rank are the ones with highest conservation value.

Target-based planning was chosen as the PUs removing rule since the goal was to find the best solution in which the maximum number of ESUs met conservation targets. Conservation targets were set as 12% for this analysis because it appears to be widely used in similar types of analyses (Wright & Mattson 1996; Cantú *et al.* 2004). Hence, any resource category with at least 12% of its area protected was considered 'adequately protected'. The only exception was applied to taxa considered endangered, (Critically Endangered or Endangered) according to IUCN Red List criteria (Vasconcelos *et al.* submitted a) to which a higher target was set (100%), following the recommendations of Carvalho *et al.* (2010) and the principals of similar works (e.g. Jackson *et al.* 2004).

In order to generate spatial aggregation into the solution, the rule 'only remove from edges' was selected, but 15282 points (about 20% of total PUs) were randomly selected as additional edge points set. The warp factor was set to one. The Boundary Length Penalty (BLP), which devalues reserve structures with lots of edge, was chosen as the method for inducing reserve network aggregation since it is quick, effective and most commonly used (Moilanen & Kujala 2008). Several runs were performed with different aggregations levels and the level of 0.04 was chosen since it presented reasonable results of network aggregation.

Two cost scenarios, one 'realistic' and one 'ideal', were simulated, constrained and unconstrained by the 46 PAs, respectively. In the 'realistic' scenario, cells with main roads and small and large urban areas and infrastructures (with a buffer radius of 112 m or 1 km, respectively) were given a cost of 100, with secondary roads a cost of 75, with PAs 1, and remaining cells 50. All different categories of PAs were thus treated with the same weight. In the 'ideal' scenario, PAs were not taken into account, thus cells with main roads and urban areas were given a cost of 100, with secondary roads 50, and remaining cells 1. The minimum set of PUs with higher rank in the final solution, which assured that all ESUs were represented with the desired target, was selected for each scenario.

Gap analyses

The ESU files were intersected with the PAs polygons to assess the percentages of each ESU distribution which are currently protected or that will be protected if the full PAs network is implemented in the future, and the amount of PUs still missing to reach conservation targets (Table VII.2).

The selected PUs in each scenario were intersected with the PAs polygons using ArcGIS to calculate the amount of units encompassed in the 46 PAs network on each island and to identify gaps in the PAs network for conservation (Table VII.3).

RESULTS

Evaluation of ecological niche-based models

The ROC plots exhibited high average AUCs with low standard deviations (SD) for both training and test datasets in all model types (Appendix VII.4). Average AUCs for the training and test datasets were 0.985±0.003 and 0.970±0.018, respectively. Thresholded models identified suitable cells for each species. The average percentage of observations identified in suitable cells was 80.8% (Appendix VII.4).

Table VII.3 Number (*n*) of total Planning Units (PUs) and PUs inside the 46 Protected Areas (PAs) on each island for the available and selected PUs for each model scenario. Percentages (%) are given between brackets.

	Available			**Realistic Scenario**			**Ideal Scenario**		
Island	Total	Inside PAs		Total	Inside PAs		Total	Inside PAs	
	n	*n*	%	*n*	*n*	%	*n*	*n*	%
Santo Antão	14899	601	(4.0)	505	72	(14.3)	505	7	(1.4)
São Vicente	4275	58	(1.4)	419	19	(4.5)	420	0	(0.0)
Santa Luzia	656	656	(100.0)	655	655	(100.0)	655	655	(100.0)
Branco	49	49	(100.0)	49	49	(100.0)	49	49	(100.0)
Raso	108	108	(100.0)	108	108	(100.0)	108	108	(100.0)
São Nicolau	6515	258	(4.0)	334	52	(15.6)	334	11	(3.3)
Sal	4187	862	(20.6)	374	374	(100.0)	283	61	(21.6)
Boavista	11930	4743	(39.8)	655	655	(100.0)	657	440	(67.0)
Maio	5141	1283	(25.0)	244	244	(100.0)	242	90	(37.2)
Santiago	18829	409	(2.2)	4085	225	(5.5)	4084	225	(5.5)
Fogo	8841	1713	(19.4)	521	0	(0.0)	521	0	(0.0)
Brava	1176	0	(0.0)	119	0	(0.0)	119	0	(0.0)
Rombos	59	59	(100.0)	9	9	(100.0)	8	8	(100.0)
Total	76665	10799	(39.7)	8077	2462	(56.9)	7985	1654	(41.2)

Adequacy of the Protected Areas network

Presently, with the three PAs fully operational, only *Chioninia spinalis spinalis* fulfils the 12% target of protection (Table VII.2). All the remaining ESUs are insufficiently protected. When considering the complete PAs network to be implemented, these figures are quite different. In these circumstances, 15 of the 38 ESUs' potential distributions considered in the analyses will have the target percentage of its distribution inside a PA (Table VII.2). However, 10 of those 38 ESUs would not have a single PU inside a PA and only *Hemidactylus bouvieri razoensis*, *Tarentola gigas brancoensis* and *T. g. gigas* would be fully protected (Table VII.2). Also several threatened taxa (*Hemidactylus bouvieri bouvieri*, *H. bouvieri* from S. Nicolau, *H. lopezjuradoi*, *T. protogigas protogigas*, *C. vaillanti vaillanti*, *C. v. xanthotis*) would not be adequately protected, and *C. stangeri* would miss protection on S. Vicente Island.

Planning Units selection

Overall, more PUs inside PAs were selected in the 'realistic' (56.9) than in the 'ideal' (41.2) scenario (Table VII.3). The number of PUs selected in both 'ideal' and 'realistic' scenarios was identical, except on Sal Island (Table VII.3). It was also on Sal where the PUs selected by each scenario spatially coincided by the least amount, followed by Maio; in the remaining islands, the concordance of PUs selected by both scenarios was relatively high (Fig. VII.2 and Appendices VII.5 to VII.9).

Gap analyses

On uninhabited islets and islands of the archipelago, such as the Rombos islets and the Desertas island group, 100% of the selected PUs would be inside PAs according to both scenarios (Table VII.3). Under the case of the 'realistic' scenario, also Sal, Boavista and Maio presented all selected PUs within PAs. These islands would also reach conservation targets under the 'ideal' scenario, although in lower percentages (Table VII.3). On the other hand, Fogo and Brava presented all PUs selected by both scenarios outside PAs. Considering the 'ideal' scenario, S. Vicente would also present no selected PUs inside PAs (Table VII.3). Apart from those three latter islands, several others presented selected PUs below the 12% threshold of protection. These islands were S. Vicente and Santiago, considering the 'realistic' scenario, and also S. Antão and S. Nicolau, considering the 'ideal' scenario.

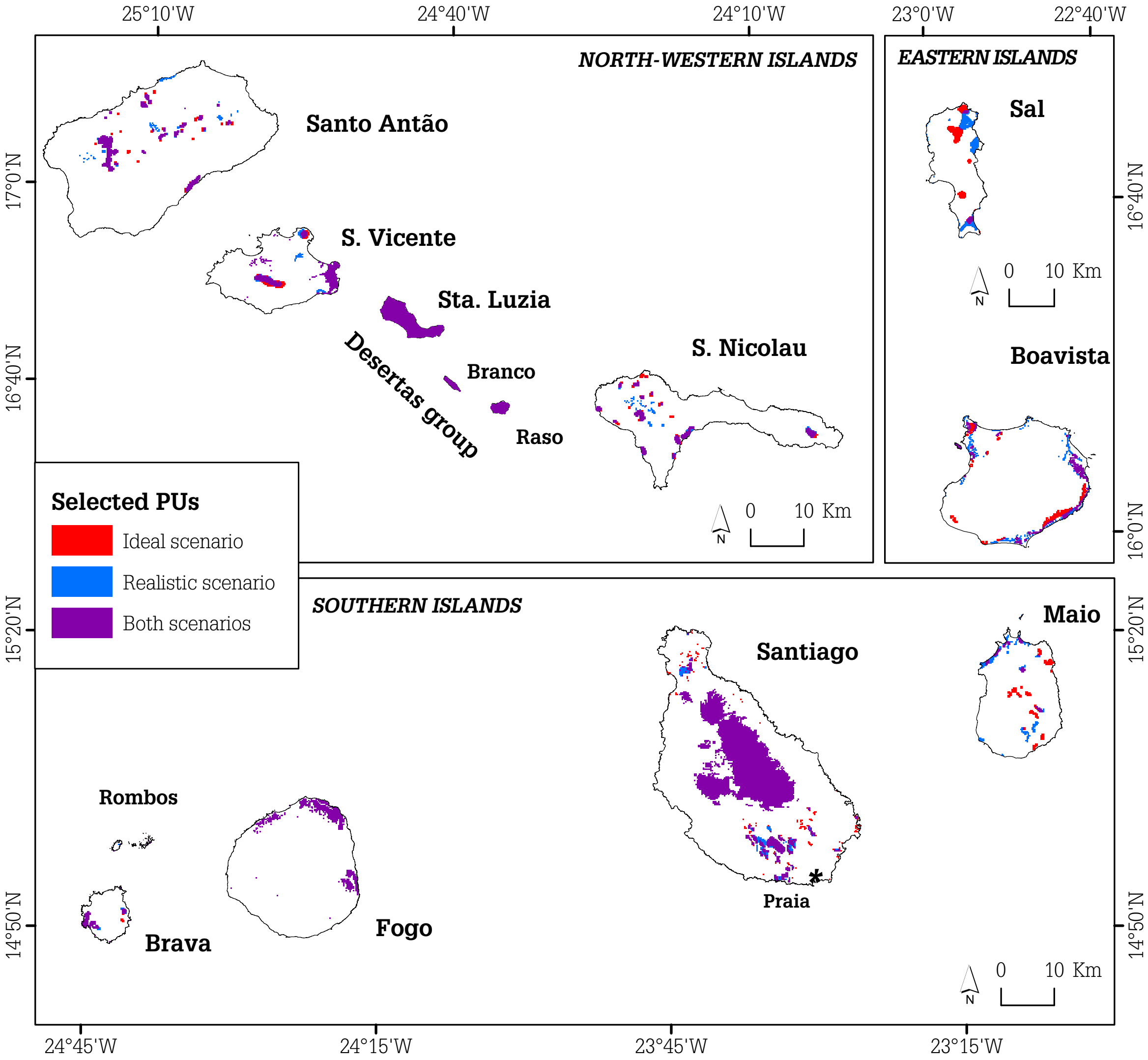

Figure VII.2 Selected planning units (PUs) necessary to reach conservation targets for all reptile ESUs from the Cape Verde Islands considering the 'realistic' and 'ideal' scenarios (see materials and methods and Appendices VII.5 to VII.9 for details).

DISCUSSION

Evaluation of the Methodology

The ecological niche-based models provided fairly robust predictions of occurrences and the reserve design algorithm identified priority PUs for conservation of endemic reptiles. Hence, this study may turn into an important tool in the planning and designation of protected sites in Cape Verde. Additionally, the novel approach used may prove useful to other studies attempting to maximize the representation of genetic diversity in conservation prioritization. Several studies assumed predicted probabilities of occurrence of taxa to be surrogates to probability of persistence, and targeted areas where probabilities were high (e.g. Margules & Stein 1989; Williams & Araújo 2000). In this study, the selection algorithm incorporated the most probable occurrence areas of all ESUs, thus potentially enhancing taxa persistence even more. Nevertheless, potential pitfalls might have emerged because patterns of neutral variation, as measured by molecular markers, may not reflect levels of adaptive variation for all traits across all populations. However, given the difficulty in measuring adaptive variation for wild species, molecular markers are valuable surrogates and, in some cases, may be conservative estimates of the expectations of loss and recovery of quantitative genetic variation (Lynch *et al.* 1999). In addition, adaptive features may be best protected by maintaining the context for selection, such as heterogeneous landscapes (Höglund 2009). Since habitats in this archipelago are most different among islands than within them (data not shown), targeting 12% of the area of each island for conservation potentially enhances the cover of adaptive variation. Another question that might be addressed is if ecological models should have been based on ESUs instead of taxa. Nevertheless, in doing so, sample sizes would have been greatly reduced, which would probably compromise the analytical method. Furthermore, in the case of islands, almost all the distinct ESUs within a taxon correspond to a different island population. Hence, the probability of occurrence of an ESU on each island is more related to isolation by the ocean, genetic drift and other factors than with ecogeographical factors, with no evidence for local adaptation, a determinant condition for modeling those (Pearman *et al.* 2010).

Concerning the representation targets set for each ESU, choosing the 12% target turns these results comparable to other natural resources conservation studies but does not suggest that this figure has any established scientific validity to assure that populations selected for conservation are viable. The question of which percentage would assure is a paramount of conservation planning but remains largely unsolved (Tear *et al.* 2005).

Regarding the PUs selection, the 'ideal' model spatially coincided with the 'realistic' model scenario (Fig. VII.2) in most cases. In addition, both scenarios always presented identical efficiency (similar number of selected PUs), except on Sal Island, where the ideal model would be more effective, since much less area would be needed to protect reptile diversity (Table VII.3). These results are surprising since 'ideal' scenarios theoretically minimize costs for PUs selection in comparison with scenarios constrained by PAs, because PAs are generally biased for other factors rather than protecting biodiversity. Three complementary rationales might explain this result. First, both scenarios are congruent in selecting many PUs outside PAs, in order to encompass 12% of most ESUs distributions (100% in threatened taxa), and in those areas, selected PUs by both scenarios are likely to overlap. Second, in regions less affected by anthropogenic disturbance, selecting an ideal network that maximizes representation of diversity most times does not lead to significantly different results from a selection by chance (Bonn & Gaston 2005). This pattern might be especially noticeable in small areas. In Cape Verde, where few impacting human infrastructures are present in most islands and PAs were designed using *ad-hoc* criteria, reptile distributions are little restricted by anthropogenic actions. Thus, some PUs inside PAs selected by the realistic scenario (that prioritizes PUs inside protected areas) are likely to be also selected by the ideal model. This is most noticeable in islands like Boavista and Maio. Third, alternatively, the extensive overlap of solutions from both models may suggest that PUs selected *ad hoc* for other endemic groups on which PAs locations were based on, such as birds, are also good for reptiles and vice-versa. Thus, reptiles may be good surrogates of priority PUs for endemic birds and flora, although they might not be as good for other groups such as invertebrates (Rodrigues & Gaston 2001). In fact, some recent *ad hoc* data on endemic birds confirms several selected PUs outside the PAs depicted by this work as important for conservation. For instance, the threatened Cape Verde cane warbler (*Acrocephalus brevipennis*) also occurs on the north-eastern part of Fogo, and a large colony of the Critically Endangered purple heron was confirmed (*Ardea purpura*) around 'Montanha' on Santiago (see Appendices VII.9 and VII.8, respectively), following Hazevoet (2010). It would be important to cross updated information about georeferenced nesting sites of the endemic birds and accurate distribution maps of the endemic flora with the performed analyses, whenever they become available, to confirm this result.

Adequacy of the Protected Areas network and Planning Units selection

Presently, Cape Verde presents the lowest proportion of land (about 2%) devoted to conservation in comparison to several other oceanic islands (40% on average) (Caujapé-Castells *et al.* 2010). The implementation of the full PAs network is thus needed to guarantee the partial protection of the biodiversity of the endemic reptiles and their habitats (Table VII.2 and VII.3). In addition, implementation of new PAs based on the 'ideal' scenario, is needed to fully protect the genetic diversity of these reptiles.

The reserve design analyses indicated two main patterns in the Cape Verde Islands. On a group of islands, namely Santa Luzia, Branco, Raso, Sal, Boavista, Maio and Rombos, designation of new PAs is not a priority, since the PAs that are going to be implemented will guarantee total targeted protection of all endemic reptile taxa and ESUs occurring within these islands and islets and their habitats (Table VII.2 and VII.3; Appendices VII.6, VII.7, VII.8 and VII.9). On the remaining islands, the planned PAs are clearly insufficient, since about 60% of the ESUs would not achieve the conservation targets (Table VII.2), namely on Santo Antão, S. Nicolau, S. Vicente, Santiago, Fogo and Brava (Table VII.3 and Appendices VII.5, VII.6, VII.8 and VII.9). Hence, new PAs proposed by the realistic and ideal model should be implemented on each of this latter island group to reach conservation targets for all ESUs.

Among the island group that needs extra PAs three cases of priority were detected. In some islands, the figures of 12% widely cited as the percentage of a nation that should be dedicated to nature reserves (WCED 1987) would be achieved (Table VII.3), despite not protecting all ESUs, namely on Santo Antão and S. Nicolau. Thus, those two islands, would at least contribute, after the PAs implementation, to the potential protection of the habitat diversity of the archipelago. Nevertheless, the creation of two new PAs on Santo Antão and the establishment of a corridor between the 'Moroços' and the 'Cova/Ribeira Paúl/Torre' Natural Parks (Fig. VII.1 and Appendix VII.5) would be necessary to protect the two single island endemics, *T. caboverdiana* and *C. fogoensis* and the Critically Endangered *H. bouvieri* gecko, respectively. On S. Nicolau, extensions of the already existing 'Monte Gordo' National Park (Fig. VII.1 and Appendix VII.6) would be needed as a partial and least costly solution for protecting unique diversity on that island, including *T. nicolauensis* and *C. nicolauensis*. It is also needed to create new PAs along the coast to reach the conservation targets for those taxa and above all to also fully protect the threatened and genetically differentiated *H. bouvieri* population and the Vulnerable *T. bocagei*, another island endemic.

On other islands, neither the target of 12% of their areas to be protected nor the 12% target of their ESUs would be achieved (Table VII.2 and VII.3; Appendices VII.5 and VII.8), such as on S. Vicente and Santiago. Hence, the creation of three PAs on S. Vicente is especially important to protect the ESU of both the Endangered *C. stangeri* and its habitat and the island endemic gecko, *T. substituta* (Appendix VII.5). On Santiago, all the inland mountainous area should be protected to guarantee the viability of the two allopatric ESUs of *T. darwini* (see Vasconcelos *et al.* 2010), the Endangered *C. vaillanti vaillanti*, the southern lineage of *C. spinalis santiagoensis*, and the distinct lineage of *C. delalandii* and their habitats. This measure will ensure that the largest possible pool of genetic material of the metapopulations to which they belong is protected and that opportunities for gene flow are provided. Also new PAs should be designed to ensure the conservation of the northern lineage of the *C. spinalis* and the Vulnerable *T. rudis*; both single island endemic taxa (Appendix VII.8). Santiago is one of the islands with the highest number of reptile taxa and the island with the highest number of ESUs, so creation of PAs and implementation of the planned ones is even more crucial. Nevertheless, this goal might be difficult to fulfil since Santiago contains more than half of the national inhabitants (Lobban & Soucier 2007) and a large part of its habitat modified by humans.

Finally, in the extreme case of some islands, neither the 'realistic' nor the 'ideal' scenario selected a single PU inside a PA (Table VII.3 and Appendix VII.9) such as on Fogo and Brava. The PA implemented on Fogo, although it might be important to protect endemic flora (Miller 1993; Duarte *et al.* 2008), is totally inadequate to preserve the diversity of the reptiles. The priority PUs selected by both scenarios depicted the north-eastern part of the island as optimal for covering the targeted distributions of two island endemics, *T. fogoensis* and the Endangered *C. vaillanti xanthotis*. Also Brava presents no PUs inside PAs but for a different reason: there are no planned PAs for this island. However, both scenarios are congruent in depicting at least two important areas for conserving the genetic variability of *C. delalandii* and the Vulnerable *T. p. hartogi*, which has its largest population on this island (see Vasconcelos *et al.* submitted). Brava also might harbour the Critically Endangered *H. bouvieri* (see Arnold *et al.* 2008) highlighting the importance of establishing a PA on the island. Previous studies already depicted Brava as important in conservation terms due to high diversity for both total and endemic species of flora; jointly occupying with São Nicolau the leading position (Duarte *et al.* 2008).

This study contributes to address one of the major constraints of conservation in the Cape Verde Islands biodiversity hotspot, namely the lack of basic information in formats that policymakers and administrators can interpret and use (Miller 1993). It is expected that this innovating framework can be applied to other island systems with well-know genetic diversity such as the Canary Islands, where extensive work has been carried out on the endemic reptiles (e.g. Brown & Pestano 1998; Carranza *et al.* 2000, 2002; Cox *et al.* 2010; Gübitz *et al.* 2000) or other island-like systems, such as mountain ranges.

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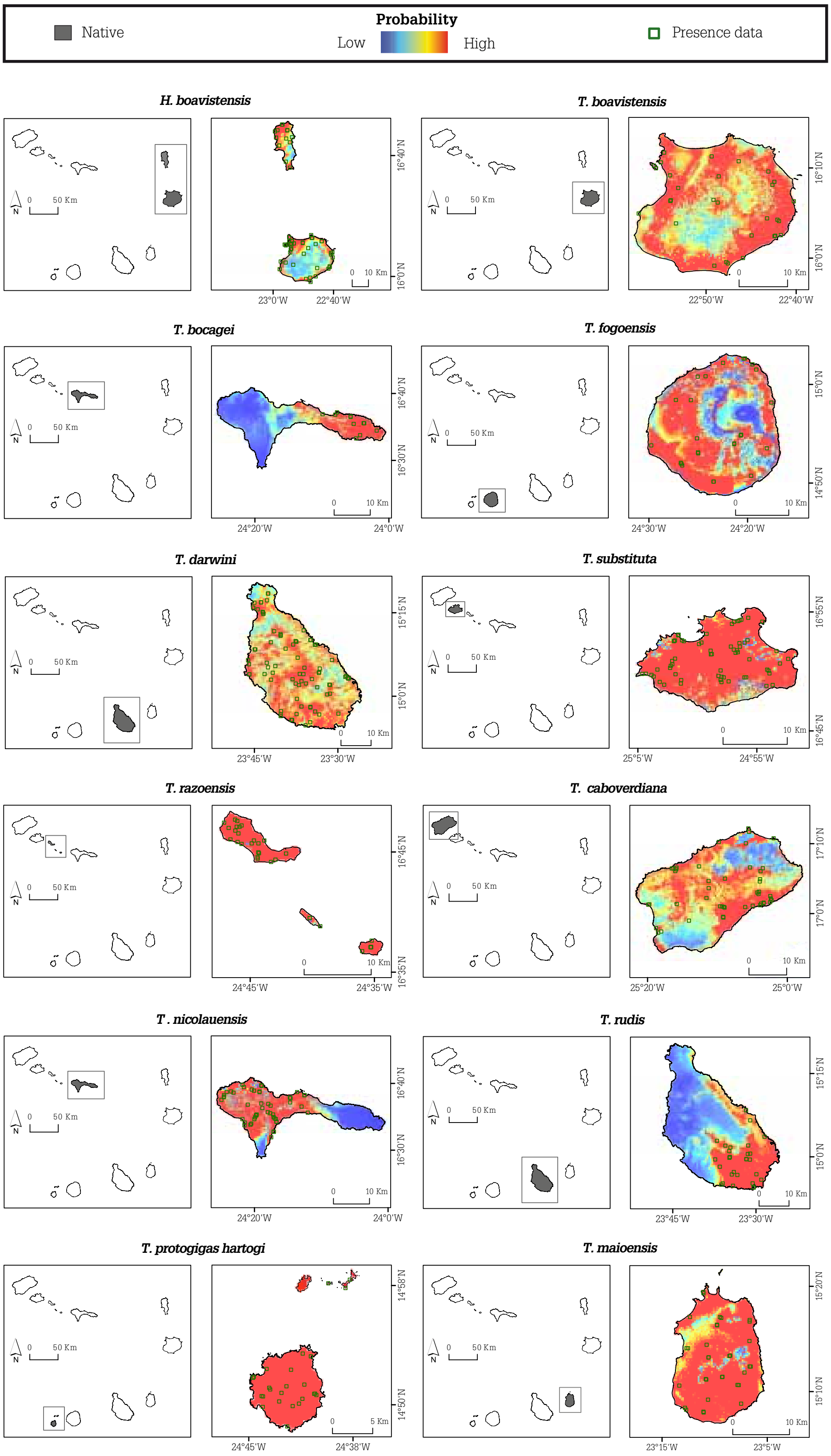
SUPPLEMENTARY MATERIAL

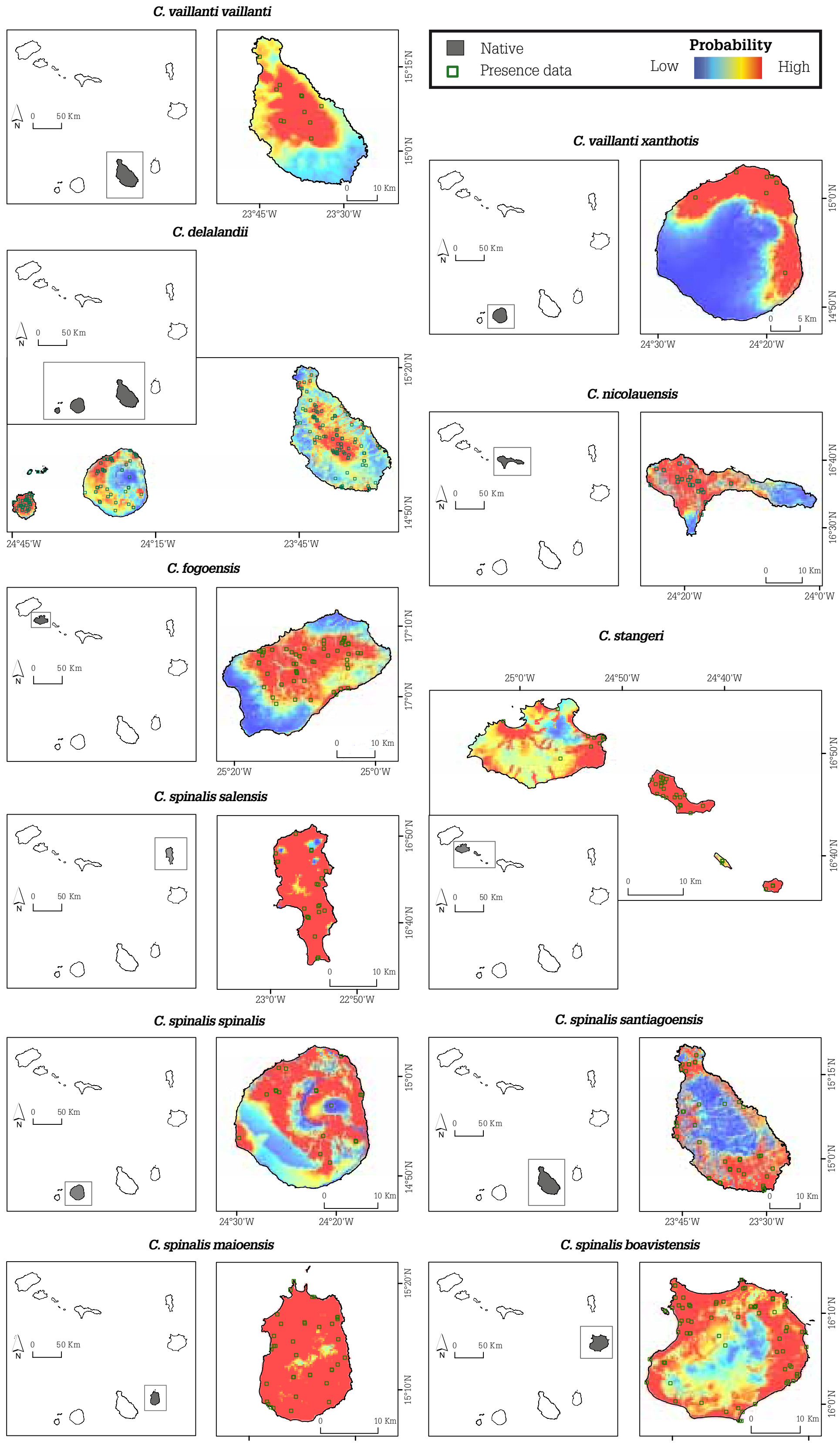
Appendix VII.1 Environmental factors used for model the distribution of reptiles in Cape Verde and their codes, units and original resolution.

Code	**Environmental factor**	**Original resolution** (degrees)
alt	Altitude	0.00083
slope	Slope	0.00083
NDVI	Normalised difference vegetation index	0.00211
d_salty	Distance to costal-salty lowland areas	0.00083
d_beach	Distance to beaches	0.00083
d_cliff	Distance to cliffs	0.00083
d_dune	Distance to dunes and sandy areas	0.00083
d_lava	Distance to recent lavas	0.00083
d_v_arid	Distance to very arid areas	0.00083
d_arid	Distance to arid areas	0.00083
d_s_arid	Distance to semi-arid areas	0.00083
d_s_humid	Distance to sub-humid areas	0.00083
d_humid	Distance to humid and mountains areas	0.00083
d_water	Distance to water lines and floodplain areas	0.00083

Appendix VII.2 Probability of occurrence of Cape Verdean endemic *Hemidactylus* and *Tarentola* geckos at a 225x225 m scale estimated using Maximum Entropy environmental niche-based models (see Material and Methods for details).



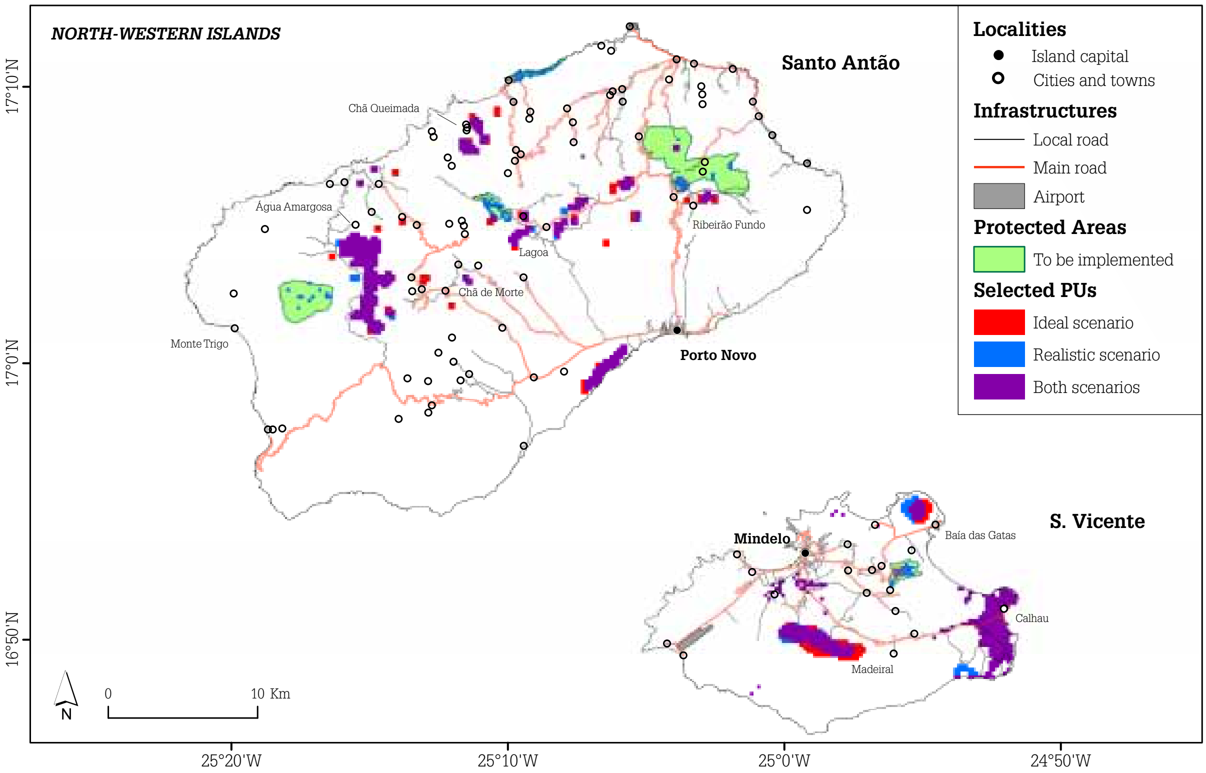
Appendix VII.3 Probability of occurrence of Cape Verdean endemic *Chioninia* skinks at a 225x225 m scale estimated using Maximum Entropy environmental niche-based models (see Material and Methods for details).



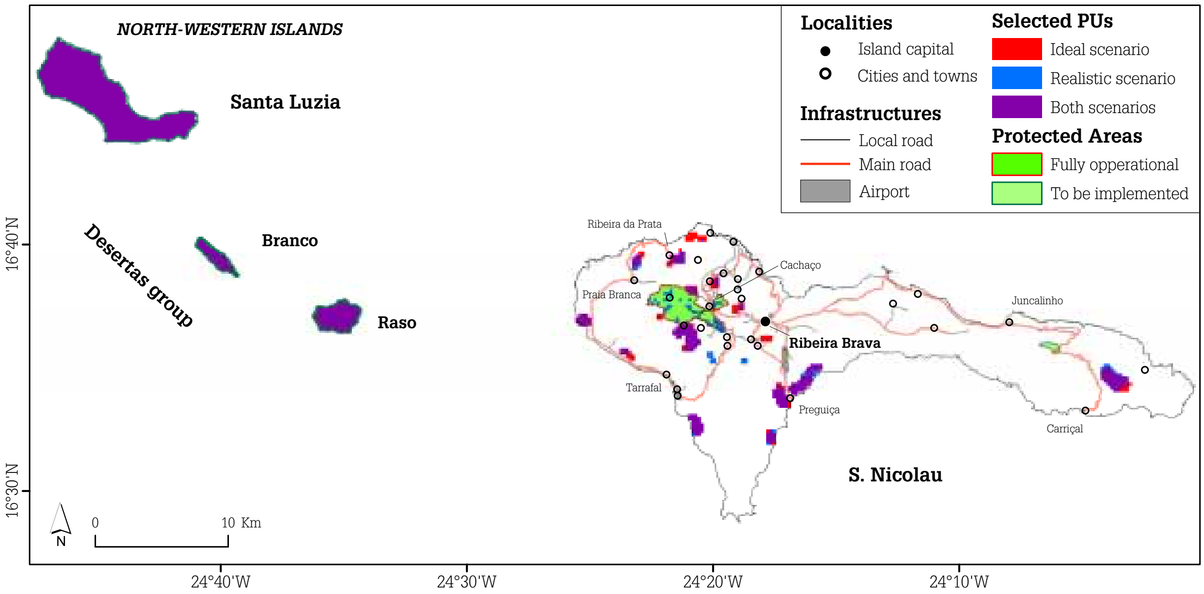
Appendix VII.4 Number of observations (*n*) of endemic Cape Verdean reptile taxa in each data set, average (and standard deviation, SD) of training and test AUC for the 30 model replicates, correct classification rate (CCR) of training data according to the threshold models (see Methods for details), and average percent contribution of each variable for the models. Taxa that were not modelled due to low sample size are marked (*). Description of the environmental factors codes are given in Appendix VII.1.

Taxon	*n* training/ test	% test	AUC training	AUC test	CCR %	d_salty	d_beach	d_cliff	d_dune	d_lavas	d_v_arid	d_arid	d_s_arid	d_s_humid	d_humid	d_water	alt	slope	NDVI
Hemidactylus lopezjuradoi	1*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
H. boavistensis	44/ 9	20	0.977±0.005	0.964±0.017	85.2	2.7	7.8	0.0	11.7	0.5	1.0	57.6	1.5	4.1	1.6	3.5	4.9	1.6	1.8
H. bouvieri, SN pop.	2*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
H. bouvieri bouvieri	4*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
H. bouvieri razoensis	5*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Tarentola boavistensis	30/ 6	20	0.983±0.006	0.956±0.025	76.7	1.1	12.9	0.0	2.4	0.9	3.6	64.9	5.2	1.0	0.2	1.6	2.5	3.1	0.5
T. bocagei	11/ 1	10	0.997±0.001	0.994±0.002	63.6	26.3	14.0	4.6	0.0	0.4	19.4	8.2	5.9	0.3	0.7	13.0	2.4	4.3	0.6
T. fogoensis	25/ 5	20	0.991±0.003	0.977±0.015	76.0	0.0	0.8	2.4	0.2	47.2	5.4	2.6	4.2	0.7	0.8	27.7	2.0	5.6	0.5
T. darwini	62/ 12	20	0.958±0.007	0.924±0.016	87.5	1.3	1.7	3.2	0.1	0.4	73.0	1.3	2.3	1.3	3.0	3.4	1.7	6.2	1.0
T. substituta	45/ 9	20	0.991±0.001	0.982±0.006	82.3	40.7	1.3	18.7	2.3	0.0	3.4	1.2	17.9	6.4	3.2	0.6	1.1	2.9	0.2
T raziana	26/ 5	20	0.998±0.000	0.997±0.001	84.6	7.7	1.0	7.1	7.7	0.0	0.8	29.7	30.4	10.8	0.2	0.8	0.6	0.5	2.6
T. caboverdiana	35/ 7	20	0.980±0.005	0.965±0.023	80.4	2.4	3.5	56.8	4.0	4.0	1.5	2.8	1.9	3.7	2.0	3.3	6.3	7.0	1.0
T. nicolauensis	33/ 7	20	0.990±0.001	0.985±0.008	89.8	36.3	4.1	29.7	0.0	6.2	1.9	0.7	1.9	3.0	4.5	2.3	3.9	4.7	0.7
T. gigas brancoensis	3*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
T. gigas gigas	3*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
T. rudis	28/ 6	20	0.986±0.004	0.954±0.026	71.4	1.7	0.8	4.1	0.0	0.0	66.4	4.3	3.0	10.5	1.9	1.9	0.8	3.7	0.6
T. maioensis	21/ 4	20	0.992±0.004	0.981±0.010	75.8	2.4	5.3	3.9	2.6	9.0	3.3	21.7	42.4	0.0	0.0	2.5	1.9	3.5	1.4
T. protogigas protogigas	4*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
T. protogigas hartogi	22/ 4	20	0.998±0.000	0.996±0.002	86.4	9.4	0.0	0.4	77.7	0.9	0.4	0.8	0.7	1.6	1.1	2.5	0.9	3.1	0.4
Chioninia vaillanti vaillanti	11/1	10	0.970±0.014	0.972±0.050	72.7	0.4	1.8	16.8	1.1	0.6	40.1	1.8	2.0	19.4	1.0	10.0	1.8	0.6	2.6
C. vaillanti xanthotis	7/ 1	25	0.996±0.003	0.989±0.010	71.4	0.2	0.4	5.5	0.0	8.3	12.9	0.3	0.0	2.2	4.2	49.6	2.5	3.3	10.5
C. delalandii	140/ 28	20	0.964±0.005	0.927±0.015	81.1	6.5	1.5	11.2	2.3	42.2	2.6	0.9	2.7	2.7	9.6	1.5	5.0	6.6	4.8
C. nicolauensis	21/ 4	20	0.994±0.002	0.985±0.008	85.7	32.8	2.8	28.8	0.0	5.6	3.1	5.0	2.4	4.4	4.9	2.4	0.9	6.0	0.7
C. fogoensis	52/ 10	20	0.981±0.003	0.969±0.011	84.6	0.4	8.7	64.2	0.4	1.0	2.0	2.1	1.1	0.7	4.9	2.6	5.5	4.2	2.1
C. stangeri	33/ 7	20	0.995±0.001	0.989±0.007	84.8	3.8	1.4	15.9	36.0	1.5	4.0	7.2	7.8	13.9	3.3	2.7	0.3	0.8	1.6
C. spinalis salensis	15/ 2	10	0.989±0.002	0.953±0.098	71.4	0.3	0.2	0.1	0.2	0.8	0.9	78.7	1.0	1.5	11.3	0.9	3.0	1.0	0.2
C. spinalis santiagoensis	28/ 6	20	0.978±0.003	0.956±0.019	84.6	0.0	0.8	2.3	0.0	0.1	63.0	0.9	1.8	11.3	0.5	2.3	3.0	12.8	1.1
C. spinalis spinalis	18/ 2	10	0.993±0.002	0.964±0.034	94.4	0.0	0.5	0.4	0.3	52.9	4.9	1.9	4.8	4.0	5.0	17.9	3.2	4.2	0.1
C. spinalis maioensis	29/ 6	20	0.990±0.003	0.981±0.008	78.4	2.1	4.7	2.7	1.2	14.3	2.3	20.5	46.7	0.0	0.0	1.9	1.6	1.4	0.6
C. spinalis boavistensis	55/ 11	20	0.976±0.004	0.954±0.009	89.7	0.8	8.7	0.1	5.5	3.1	1.9	65.4	3.4	0.1	0.6	2.0	3.3	3.0	2.2
TOTAL	791/ 153		0.985±0.003	0.970±0.018	80.8	8.5±13.5	3.3±4.1	10.2±14.3	7.1±18.4	7.8±15.0	15.6±24.2	16.0±24.6	9.3±14.0	4.8±5.5	2.4±2.7	7.5±12.1	2.2±1.4	3.9±2.8	1.5±2.3

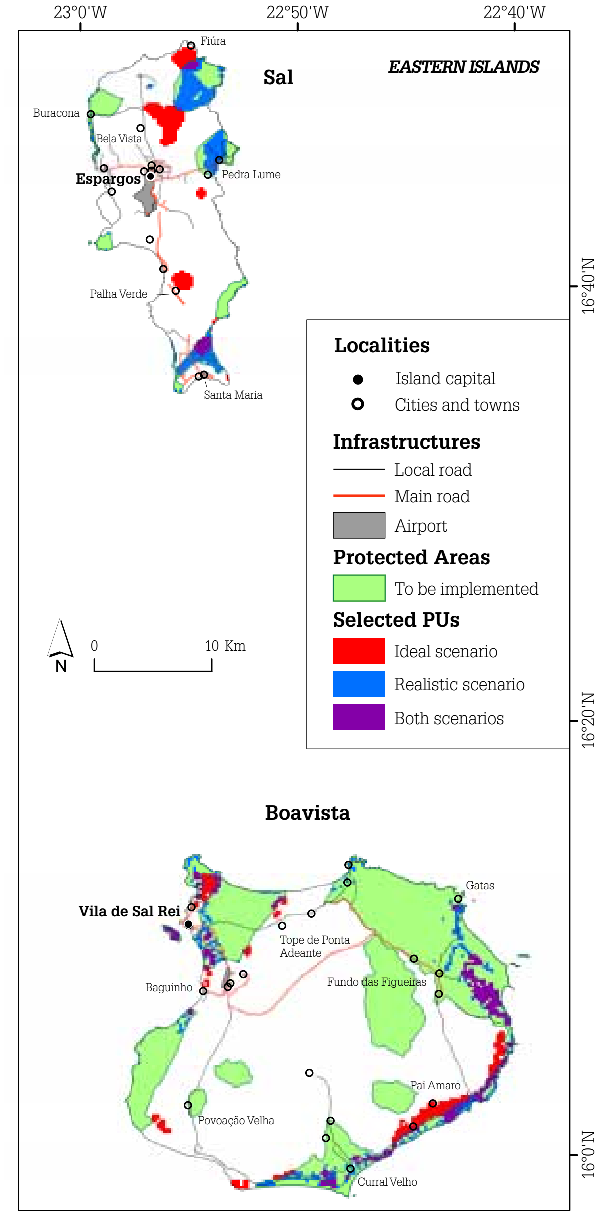
Appendix VII.5 Selected planning units (PUs) necessary to reach conservation targets for all reptile ESUs from Santo Antão and S. Vicente Islands considering the ‘realistic’ and ‘ideal’ scenarios (see Material and Methods for details).



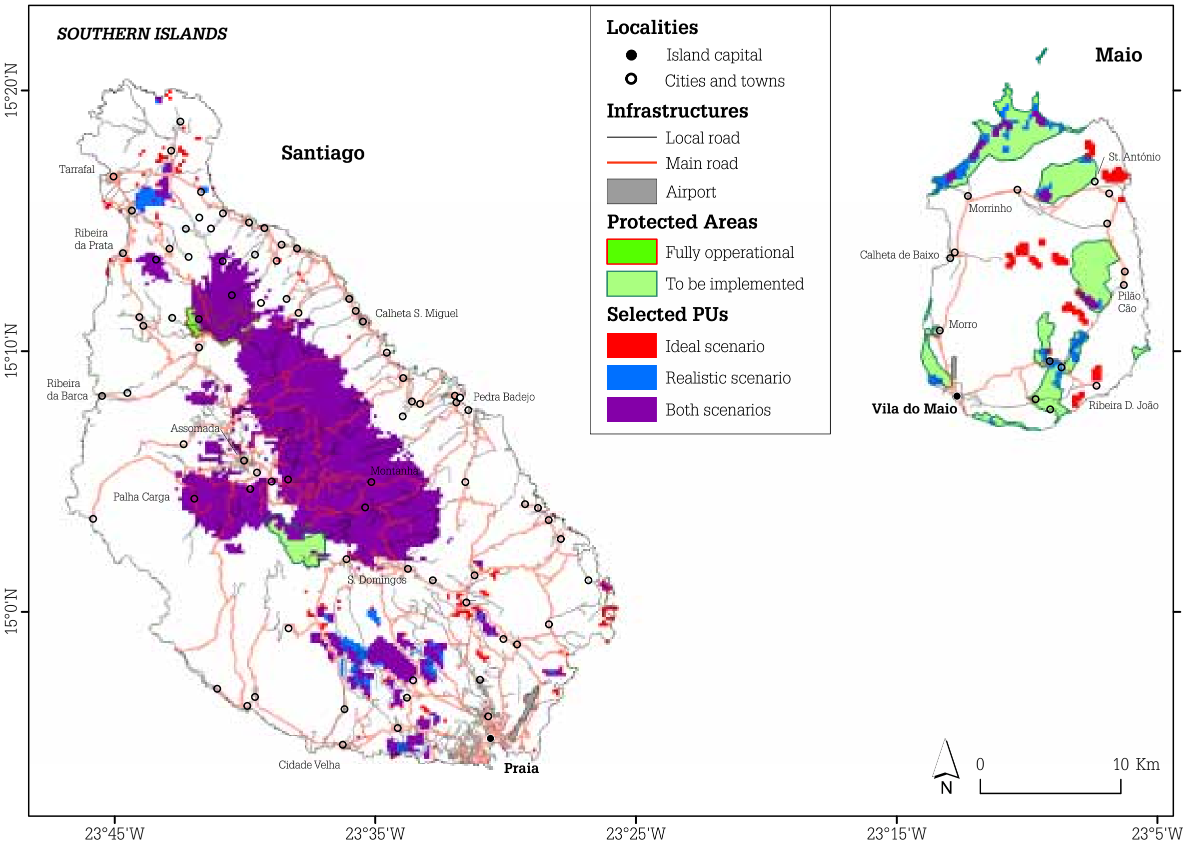
Appendix VII.6 Selected planning units (PUs) necessary to reach conservation targets for all reptile ESUs from Desertas and S. Nicolau Islands considering the 'realistic' and 'ideal' scenarios (see Material and Methods for details).



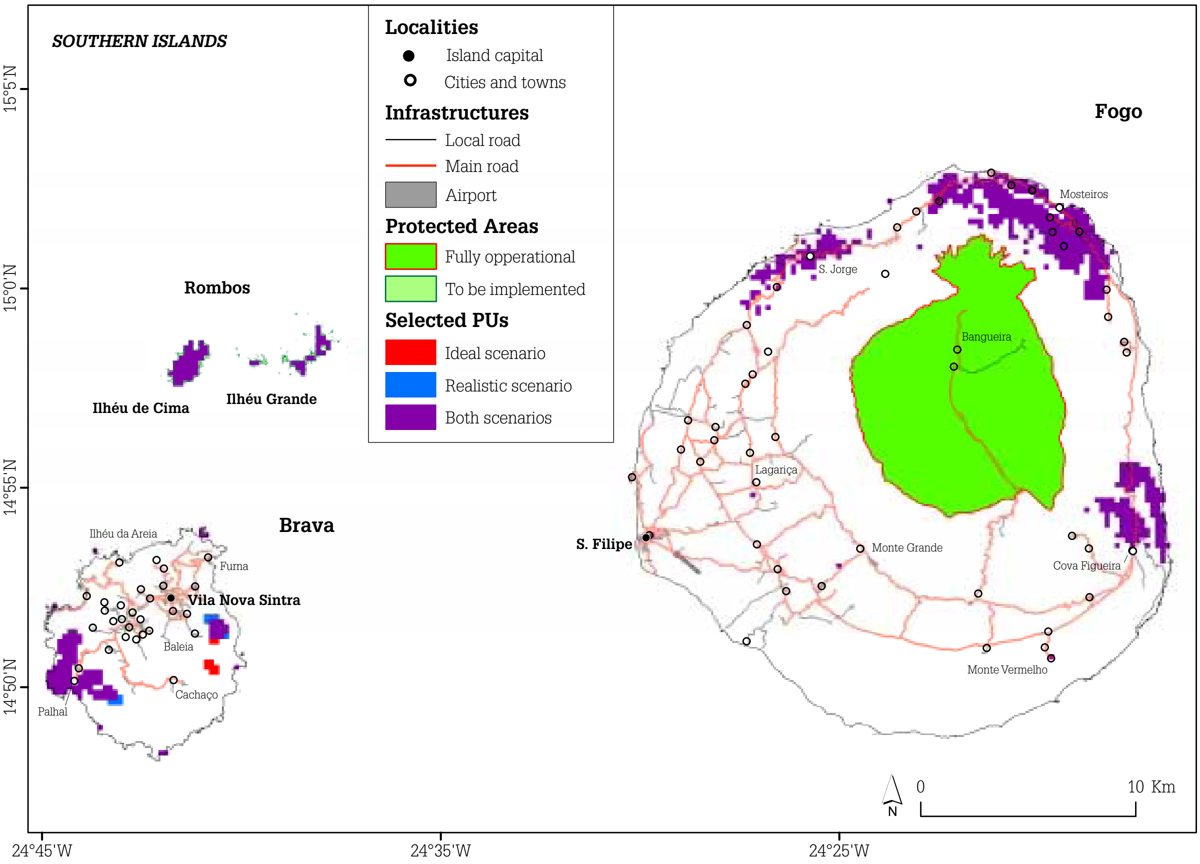
Appendix VII.7 Selected planning units (PUs) necessary to reach conservation targets for all reptile ESUs from Sal and Boavista Islands considering the 'realistic' and 'ideal' scenarios (see Material and Methods for details).



Appendix VII.8 Selected planning units (PUs) necessary to reach conservation targets for all reptile ESUs from Maio and Santiago Islands considering the 'realistic' and 'ideal' scenarios (see Material and Methods for details).



Appendix VII.9 Selected planning units (PUs) necessary to reach conservation targets for all reptile ESUs from Fogo and Brava Islands and Rombos Islets considering the ‘realistic’ and ‘ideal’ scenarios (see Material and Methods for details).

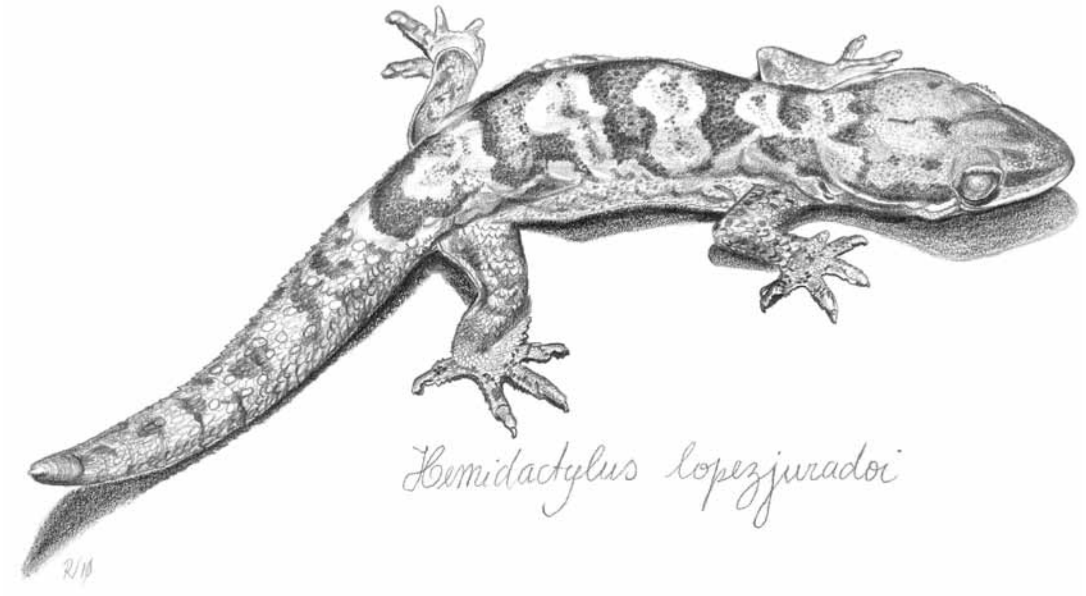


“Oneness is the secret of everything.”

Swami Vivekananda

CHAPTER 4

General Discussion and Concluding Remarks



SECTION 4.1. GENERAL DISCUSSION

The broad objective of this thesis was to address the integration of distinct disciplines for systematics and conservation planning of biodiversity. Two of the main sensitivities of Conservation Biogeography are the inadequacies in taxonomic and chorological data, the so-called Linnean and Wallacean shortfalls, respectively (Whittaker *et al.* 2005). These shortfalls increase in the more remote areas such as oceanic islands. This thesis contributed towards filling those shortfalls in one remote and isolated area, the Cape Verde Islands, for one of its least studied groups, the reptiles. It intended to answer to **what** diversity occurs there, **where** it can be found and to address putative biogeographic factors that explain **why** reptile richness is unevenly distributed. Then, conservation studies were implemented based on all the gathered data to plan **how** to optimise the protection of biodiversity at different levels. In the first part of this discussion, the key findings are summarised and integrated and their implications for conservation are discussed. In addition, future research is suggested. The second part of this chapter focuses on the concluding remarks that could be drawn from this work.

Section 4.1.1. Key findings

What is there?

Before this study, 12 species of native terrestrial reptiles and a total of 26 taxa (Fig. 4.1.1.A) were recognised in the Cape Verde Islands (Schleich 1996). After this study, these figures have increased to **22 species with 31 recognised taxa** (see articles II, IV and V). Hence, ten subspecies have been upgraded to the specific status and three new cryptic species (*Hemidactylus lopezjuradoi*, *Tarentola bocagei* and *T. fogoensis*) and three subspecies (*Chioninia vaillanti xanthotis*, *C. spinalis boavistensis* and *C. s. santiagoensis*) have been described, using an integrative approach, combining morphology, phylogenies and population genetics (Table 4.1.1.A).

Generally, each taxon corresponded to a single evolutionarily significant unit (ESU), except in the cases where a taxon occurred on more than one island. In that case, each ESU was generally assigned to each island population. The only exception was recorded in Santiago Island where two taxa, *T. darwini* and *C. spinalis santiagoensis*, presented two allopatric ESUs with a southern and a northern distribution.

Presently, *Tarentola* is the most taxonomically diverse genus of all the endemic reptile genera occurring on the Cape Verde archipelago and *Hemidactylus* the least diverse one. In the Canary Islands, *Tarentola* is not as diverse and *Gallotia* is the most diverse genus of the archipelago (Carranza *et al.* 2002, 2008). On the other hand, *Chioninia* presents more ESUs than the remaining genera (Fig. 4.1.1.B).

Answering the question 'What diversity is there' is not a straightforward task. For some taxa cryptic differentiation may exist, and apparently wide ranges (e.g. occurrence in multiple islands) may harbour in fact multiple lineages. This was the case of the close-resembling and morphologically conservative '*T. darwini*' geckos, from Santiago, Fogo and S. Nicolau islands, which in fact contained three distinct species corresponding to each island. In that case, the study of mitochondrial DNA (mtDNA) variation has proven once again to be a valuable tool in defining evolutionary units, in which traditional approaches to systematics were unable to do so. On the other hand, morphological plasticity may also be high, and taxa may present high morphological variation within each group, sometimes even overlapping with other groups, encumbering chorology and taxonomy. This was the case of the five *Chioninia spinalis* that presented reliable morphological differentiation among most, but not all, inter-group comparisons due to high variability of characters. In that case, also mtDNA was needed to support the five subspecies. It is now clear the usefulness of integrative datasets in the fields of taxonomy and phylogeography for the improvement of taxa estimations and relationships (article IV and V). The comprehension that a single line of evidence is but one realisation of a complex speciation process and that its direct equation with the taxon history may be

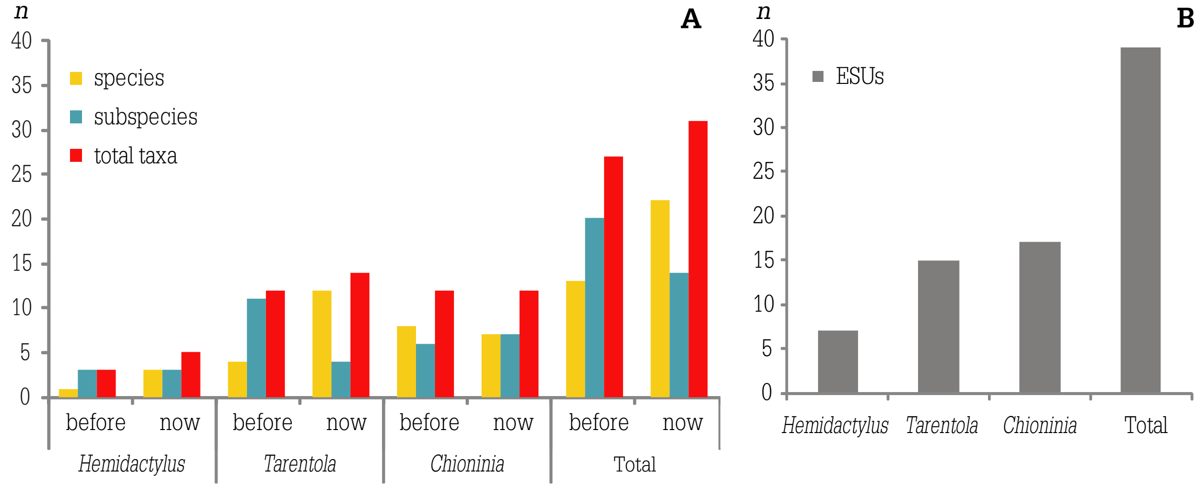


Figure 4.1.1. A) Number (*n*) of species, subspecies and total taxa recognised for each genus and for all genera of Cape Verdean terrestrial reptiles before and after the current study. **B)** Number (*n*) of evolutionary significant units (ESUs) currently recognised per genus and for all genera of Cape Verdean terrestrial reptiles.

misleading (Shaw 2002; Wiens 2007) allowed this paradigm change, but also innovations at the experimental and computational levels. In the case of morphological characters, it was showed that meristic and biometric variables should be taken into account together with coloration patterns, only easily observable in live specimens, since some cryptic taxa might be overlooked if these are not considered altogether, as was the case of *Chioninia vaillanti* subspecies (article V). In the case of molecular markers, the considerable degree of introgression observed between *Tarentola darwini* and *T. rudis* (article III and IV) highlights how processes like hybridisation can impact island populations and distort inferences based on single markers and the need of multi-locus approaches to correctly assign taxa and to properly reveal phylogeographic patterns.

It is important to highlight that discordance among lines of evidence does not imply that a species hypothesis is invalid. It may just reflect either sampling biases (e.g. the studied characters did not reflect existing divergences), or the decoupling of character evolution during the divergence of lineages (Smith *et al.* 2005; Lougheed *et al.* 2006) due to faster divergence in some characters than in others, promoted by different evolutionary processes. For example, rapid adaptive radiations can result in morphologically divergent species with low levels of genetic differentiation (e.g. Cunha *et al.* 2005). Conversely, genetic drift could promote rapid genetic differentiation despite morphological stasis (Sturmbauer & Meyer 1992). Moreover, the absence of any one or more of the species delimiting properties (e.g. reproductive isolation, niche-overlap, fixed differences, monophyly), does not constitute evidence contradicting a hypothesis of lineage separation and only the absence of all of those properties should be considered evidence against the hypothesis that two sets of populations represent different species (De Queiroz 2007).

Another result of this study was the detection of the **introduction of a new taxo**n, *Agama agama*, in the archipelago (article I), as well as the confirmation of two of the six reported introduced species, *H. angulatus* and *H. mabouia* (article VI). These observations highlighted the importance of restricting the entrance of, and the need to tackle potential invasive species in island settings, where introduced taxa can more easily establish and spread mainly due to poorer community structuring (Case & Bolger 1991). In fact, after the publication of that article, agamids were detected on other two island (J. Teixeira and B. Martins, pers. com.), indicating a possible human-mediated spread or a new introduction event, supporting that this is indeed one of the top-ten most successful introduced families in the world (Bomford *et al.* 2005).

Table 4.1.1.A Taxonomy of the endemic terrestrial reptiles of the Cape Verde Islands before and after this study.

	Before		Now	
	Species	**Subspecies**	**Species**	**Subspecies**
Hemidactylus	*H. bouvieri* (Bocourt, 1870)	*H. bouvieri bouvieri* (Bocourt, 1870)	*H. lopezjuradoi* Arnold, Vasconcelos, Harris, Mateo & Carranza, 2008	
			H. bouvieri (Bocourt, 1870)	*H. bouvieri bouvieri* (Bocourt, 1870)
				H. bouvieri ssp., S. Nicolau
		H. bouvieri razoensis Gruber & Schleich, 1982		*H. bouvieri razoensis* Gruber & Schleich, 1982
		H. bouvieri boavistensis Boulenger, 1906	*H. boavistensis* Boulenger, 1906	
Tarentola	*T. darwini* Joger, 1984b		*T. bocagei* Vasconcelos, Perera, Geniez, Harris & Carranza, submitted	
			T. fogoensis Vasconcelos, Perera, Geniez, Harris & Carranza, submitted	
			T. darwini Joger, 1984b	
	T. caboverdiana Schleich, 1984	*T. caboverdiana substituta* Joger, 1984b	*T. substituta* Joger, 1984b	
		T. caboverdiana raziana Schleich, 1984	*T. raziana* Schleich, 1984	
		T. caboverdiana caboverdiana Schleich, 1984	*T. caboverdiana* Schleich, 1984	
		T. caboverdiana nicolauensis Schleich, 1984	*T. nicolauensis* Schleich, 1984	
	T. gigas (Bocage, 1875)	*T. gigas gigas* (Bocage, 1875)	*T. gigas* (Bocage, 1875)	*T. gigas gigas* (Bocage, 1875)
		T. gigas brancoensis Schleich, 1984		*T. gigas brancoensis* Schleich, 1984
	T. rudis Boulenger, 1906	*T. rudis rudis* Boulenger, 1906	*T. rudis* Boulenger, 1906	
		T. rudis protogigas Joger, 1984b	*T. protogigas* Joger, 1984b	*T. protogigas protogigas* Joger, 1984b
		T. rudis hartogi Joger, 1993		*T. protogigas hartogi* Joger, 1993
		T. rudis maioensis Schleich, 1984	*T. maioensis* Schleich, 1984	
		T. rudis boavistensis Joger, 1993	*T. boavistensis* Joger, 1993	
Chioninia	*C. vaillanti* (Boulenger, 1887)		*C. vaillanti* (Boulenger, 1887)	*C. vaillanti vaillanti* (Boulenger, 1887)
				C. vaillanti xanthotis Miralles, Vasconcelos, Perera, Harris & Carranza, 2010
	C. delalandii (Duméril & Bibron, 1839)		*C. delalandii* (Duméril & Bibron, 1839)	
	C. fogoensis (O'Shaughnessy, 1874)	*C. fogoensis nicolauensis* (Schleich, 1987)	*C. nicolauensis* (Schleich, 1987)	
		C. fogoensis antaoensis (Schleich, 1987)	*C. fogoensis* (O'Shaughnessy, 1874)	
		C. fogoensis fogoensis (Schleich, 1987)		
	C. geisthardti (Joger, 1993)			
	C. stangeri (Gray, 1845)		*C. stangeri* (Gray, 1845)	
	M. coctei (Duméril & Bibron, 1839)		*C. coctei* (Duméril & Bibron, 1839)	
	C. spinalis (Boulenger, 1906)	*C. spinalis salensis* (Angel, 1935)	*C. spinalis* (Boulenger, 1906)	*C. spinalis salensis* (Angel, 1935)
				C. spinalis boavistensis Miralles, Vasconcelos, Perera, Harris & Carranza, 2010
		C. spinalis spinalis (Boulenger, 1906)		*C. spinalis spinalis* (Boulenger, 1906)
				C. spinalis santiagoensis Miralles, Vasconcelos, Perera, Harris & Carranza, 2010
		C. spinalis maioensis (Mertens, 1955)		*C. spinalis maioensis* (Mertens, 1955)

Molecular tools also allowed the detection or confirmation of the introduction of endemic taxa in other Cape Verde islands outside their natural ranges. This was the case of a *T. substituta* individual, endemic of S. Vicente Island, which was detected in Santo Antão using mtDNA (article III) and a nuclear marker (article IV) and of *C. delalandii* individuals which were confirmed to occur in Maio (article V).

Where are they?

Despite inventories on the terrestrial reptile fauna of the Cape Verdes dating back to the 18th century and the performance of systematic studies since the 1980's (e.g. Joger 1984; Schleich 1987; Carranza *et al.* 2000, 2001, 2002; Brehm *et al.* 2001; Brown *et al.* 2001), precise distribution records were largely lacking and most intra-island distributions were clearly incomplete. Thus, extensive sampling and compilation of data gathered over roughly five months of fieldwork provided an **updated distribution record** of reptiles across islands (Table 4.1.1.B). Over 440 stations distributed across the ten islands of the three topological groups were sampled, covering around 11% of the territory and resulting in approximately 1400 observations (article VI). Furthermore, many historical location records were doubtful or erroneous, due to *ad hoc* sampling by naturalists in the past, perpetuation of bibliographic errors, incomplete sampling, and lack of technological tools that presently allow accurate georeferencing and management of geographic data, such as military maps, GPS and digital databases. For instance, *T. gigas* was mentioned to occur on S. Nicolau by Jesus *et al.* (2002) but in fact it was a misinterpretation due to the previous lack of samples from Maio Island – it is confirmed to be a specimen of *T. maioensis* probably introduced in S. Nicolau (article III and VI). Thus, a revision of records was needed to clarify distributions.

The distribution data gathered allowed the depiction of some broad biogeographic patterns, such as the perception that the southern islands of Santiago and Fogo are the richest of the archipelago both in total number of taxa and ESUs (Fig. 4.1.1.C). Considering the number of single-island endemics (SIEs), S. Nicolau Island also stands out together with the latter islands. Thus, conservation efforts for reptiles should be prioritised for these three islands.

Predictive maps of occurrence based on ecologic niche-based models (article VI) allowed the detection that richness is also unevenly distributed within each island too. In the case of mountainous islands, such as Santo Antão, S. Nicolau and Santiago, the inner mountainous areas are generally richer than the costal parts (Fig. 4.1.1.D). On the contrary, most of the flatter islands, such as Santa Luzia, Sal and Maio, and also Brava seem to depict an unclear pattern for the distribution of taxa richness.

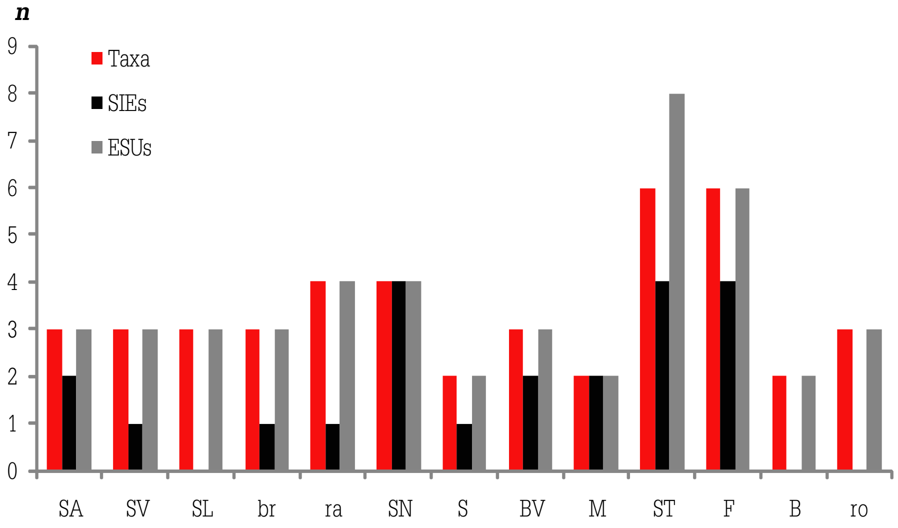


Figure 4.1.1.C Distribution of the total number (*n*) of extant terrestrial reptile taxa, single-island endemics (SIEs) and evolutionarily significant unit (ESUs) for the different islands of the archipelago (introduction of endemics not included). SA, Santo Antão; SV, S. Vicente; SL, Santa Luzia; br, Branco; ra, Raso; SN, S. Nicolau; S, Sal; BV, Boavista; M, Maio; ST, Santiago; F, Fogo; B, Brava; ro, Rombos.

Table 4.1.1.B Summary distributions of the endemic terrestrial reptiles on the Cape Verde Islands and islets. Presence records (▪), introductions (i), extinctions (e) and doubtful occurrences (?) are signalled.

	North-western Islands						**Eastern Islands**				**Southern Islands**					
Taxon/ Island-Islet	SA	SV	SL	br	ra	SN	S	BV	sr	cv	M	ST	sm	F	B	ro
H. bouvieri (Bocourt, 1870)	▪	▪	▪		▪	▪						▪			?	
H. bouvieri bouvieri (Bocourt, 1870)	▪	▪										▪?			?	
H. bouvieri ssp., S. Nicolau						▪										
H. bouvieri razoensis Gruber & Schleich, 1982			▪		▪											
H. boavistensis Boulenger, 1906							▪	▪	▪	▪						
H. lopezjuradoi Arnold, Vasconcelos, Harris, Mateo & Carranza, 2008														▪		
T. boavistensis Joger, 1993								▪	▪							
T. bocagei Vasconcelos, Perera, Geniez, Harris & Carranza, submitted						▪										
T. fogoensis Vasconcelos, Perera, Geniez, Harris & Carranza, submitted														▪		
T. darwini Joger, 1984b												▪				
T. substituta Joger, 1984b	i	▪														
T. raziana Schleich, 1984			▪	▪	▪											
T. caboverdiana Schleich, 1984	▪															
T. nicolauensis Schleich, 1984		i				▪										
T. gigas (Bocage, 1875)				▪	▪											
T. gigas gigas (Bocage, 1875)					▪											
T. gigas brancoensis Schleich, 1984				▪												
T. rudis Boulenger, 1906												▪	▪			
T. protogigas Joger, 1984b														▪	▪	▪
T. protogigas protogigas Joger, 1984b														▪		
T. protogigas hartogi Joger, 1993															▪	▪
T. maioensis Schleich, 1984						i					▪					
C. vaillanti (Boulenger, 1887)								e			e	▪		▪		▪
C. vaillanti vaillanti (Boulenger, 1887)												▪				
C. vaillanti xanthotis Miralles, Vasconcelos, Perera, Harris & Carranza, 2010														▪		▪
C. delalandii (Duméril & Bibron, 1839)								i?			i	▪	▪	▪	▪	▪
C. nicolauensis (Schleich, 1987)						▪										
C. fogoensis (O'Shaughnessy, 1874)	▪															
C. stangeri (Gray, 1845)		▪	▪	▪	▪											
C. coctei (Duméril & Bibron, 1839)		e	e	e	e	e?										
C. spinalis (Boulenger, 1906)							▪	▪	▪	▪	▪	▪	▪	▪		
C. spinalis salensis (Angel, 1935)							▪									
C. spinalis santiagoensis Miralles, Vasconcelos, Perera, Harris & Carranza, 2010												▪	▪			
C. spinalis spinalis (Boulenger, 1906)														▪		
C. spinalis maioensis (Mertens, 1955)											▪					
C. spinalis boavistensis Miralles, Vasconcelos, Perera, Harris & Carranza, 2010								▪	▪	▪						

SA, Santo Antão; SV, S. Vicente; SL, Santa Luzia; br, Branco; ra, Raso; SN, S. Nicolau; S, Sal; BV, Boavista; M, Maio; ST, Santiago; F, Fogo; B, Brava; ro, Rombos

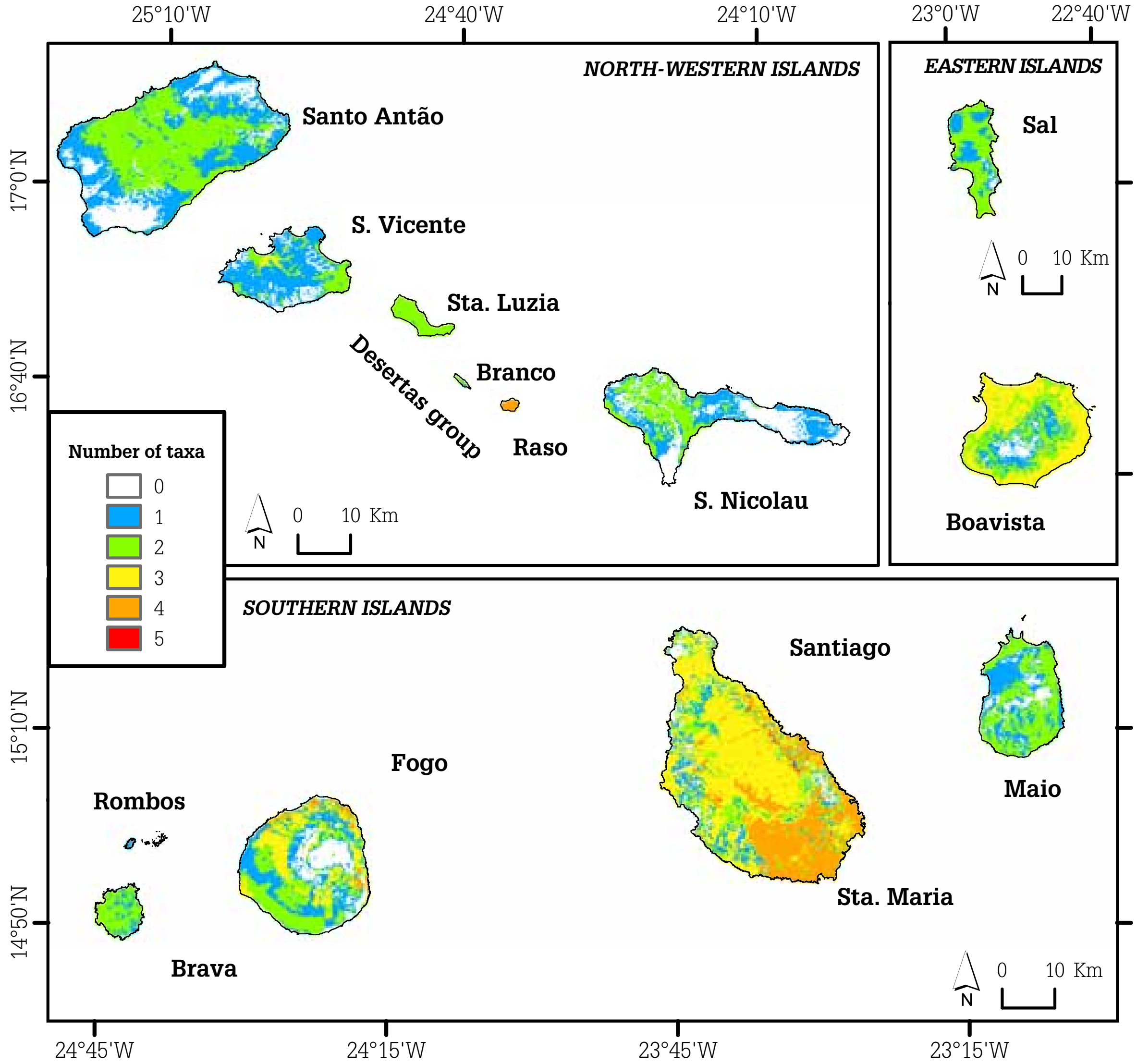


Figure 4.1.1.D Predicted distribution of extant taxa richness of endemic terrestrial reptiles on the Cape Verde Islands.

Considering the introduced species, it was imperative to determine how common and widespread they were on the islands (Jesus *et al.* 2001). Knowing their precise distributions allowed evaluating the extent of that threat (article VI). It is now clear the broad range of the introduced gecko *H. angulatus* throughout the archipelago, especially within Santiago and Boavista. It is also evident that the other introduced gecko, *H. mabouia*, although uncommon, is currently present in three islands, which is of concern since it had been previously recorded in only one (Jesus *et al.* 2001). This might be explained by a recent human-mediated spread of this species to other islands but also by a previous failure to detect it due to lack of extensive sampling.

Finally, in Chapter IV, it was demonstrated how species distribution models (SDMs) are useful tools to infer ranges on relatively under-sampled and remote areas with high accuracies and how they can be applied to conservation, maximising efficiency of reserve designs, as previously shown by other authors (Papes & Gaubert 2007; Brito *et al.* 2009; Carvalho *et al.* 2010). Knowing the predicted taxa distributions and all their lineages (ESUs) allowed identifying the most important areas to protect the reptile diversity in the Cape Verde Islands (article VII).

Why?

The reasons why the taxonomic and genetic diversity of the Cape Verde reptiles was unevenly distributed were explored in the different articles in Chapter 2 and can be summarised into two main causes: 1) historical and 2) environmental factors.

1) The most revealing **historical factors** that influenced colonisations across islands, explaining the present patterns and amounts of diversity of these reptiles are related with the geology and geography of the Cape Verde archipelago as well as the oceanic currents.

Considering geological events, the Pleistocene sea-level falls was one major shaping factor. During that time, S. Vicente and the Desertas island group were connected, which may have allowed migration among them and, therefore, gene flow. This affected taxa which colonised those north-western islands, for instance *T. substituta* and *T. raziana* and also the different island populations of *C. stangeri*, that now present haplotype sharing and/or low levels of genetic divergence at the mitochondrial level (article III, IV and V).

Another case of distributions explained by geological events is related to volcanic activity. The presence of the two allopatric species on São Nicolau (*T. bocagei* and *T. nicolauensis*) might be explained by the fact that this island consisted of two independent units until 4.7–2.6 Mya, when they were finally united by volcanic activity (Duprat *et al.* 2007). Allopatric speciation of the common ancestor of both species might have occurred on each unit, influencing their present distribution pattern, that is, the former occurring exclusively in the eastern part and the latter in the western and central part of the island (article III, IV and VI).

Furthermore, the ages of the islands seem to be strongly correlated with the number of SIEs (Whittaker *et al.* 2008). This trend was found as well for the total number of taxa, SIEs and ESUs of endemic terrestrial Cape Verdean reptiles and also for haplotype diversity in *Tarentola* (article III) and less markedly for *Chioninia* of the Cape Verdes (Fig. 4.1.1.E). The above findings are congruent with the general dynamic model (GDM) of oceanic island biogeography postulated by Whittaker *et al.* (2008). This model predicts that speciation rates peak when an island reaches its maximum area and elevational range, meaning that the maximum habitat diversity, and therefore the maximum opportunity for within-island allopatry, occurs during 'middle age' of the island. As only a snapshot of this archipelago can be analysed simultaneously, the Cape Verdes' 'middle age' corresponds to those islands that are in the mature phase of ontogeny, such as Santiago (see Fig. 1.3.1.A). The model also predicts that loss of taxa on old, declining islands should gradually occur due to habitat loss, as could be the case of *Tarentola* from Sal (article III) and *C. vaillanti* from Boavista and Maio (article V and VI).

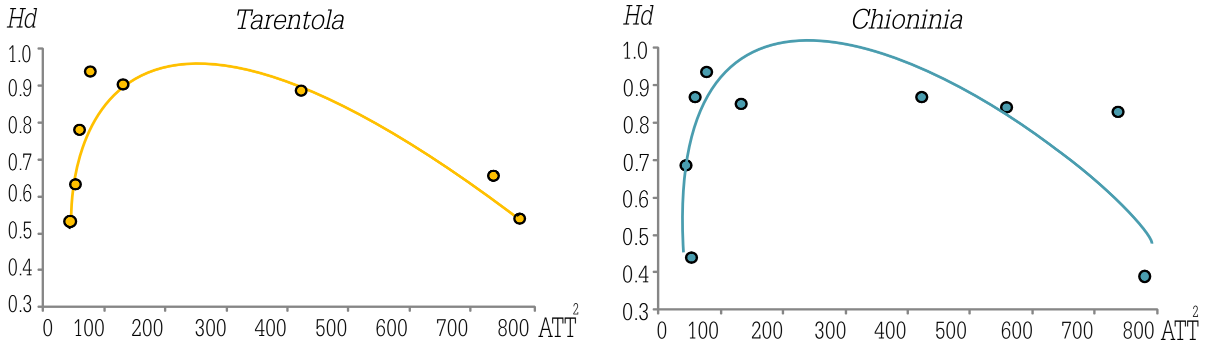


Fig. 4.1.1.E Hump-shape trend relationship between area, maximum age of the islands and haplotype diversity (*Hd*) in *Tarentola* and *Chioninia* from Cape Verde following the general dynamic model, GDM (GDM= log Area + Time + Time^2; ATT^2). To retrieve the maximum age of the islands consult Section 1.3.2 or Fig. 1.3.1.A.

Considering oceanic currents, the main trajectory of particles at surface of the ocean around the archipelago is South-West (Medina 2008), which coincides with the direction of trade winds (Duarte & Romeiras 2009). This fact may explain why all Cape Verdean reptile ancestors from all the three genera first colonised the northern islands (Fig. 4.1.1.F). The Saharan archipelago, a group of 4 to 5 emerged seamounts located some 300 km South of the Canarian island of El Hierro (Patriat & Labails 2006) might have acted as stepping-stones, facilitating the movement of populations during glacial periods towards Cape Verde, as has already been shown to have occurred in endemic flora and gastropods from Macaronesia (Carine 2005; van de Broeck *et al.* 2008, respectively).

Oceanic currents may also explain why the southern islands are richer in taxa, since they favour multiple colonisations towards this island group. Thus, reptile diversity within the Cape Verde Islands appears to be largely attributable to multiple colonisation events of individual islands by different species groups followed by within-island differentiation. Parallel patterns have previously been described for reptiles and invertebrates in the Canary Islands (Juan *et al.* 2000).

Specific small-scale oceanic currents may also explain distribution patterns at taxa level. For instance, a circum-Leeward current existing around the southern Islands (see Fig. 1.3.2) may be related to the range of *C. delalandii*, which is restricted to this island group. It might also be related to the low levels of mtDNA and nuclear (nDNA) differentiation observed between the island populations (article V) resulting from facilitated dispersion patterns among those islands, alternatively to the recent expansion hypothesis proposed.

The agreement between the phylogenetic structure within the different clades in all three reptile genera and the three ecogeographical regions of the archipelago is also strong evidence suggesting that distances between islands is another important historical factor (Fig 4.1.1.G.). Indeed, there are no confirmed taxa shared between north-western and southern islands (except the genetically unconfirmed *H. bouvieri* from Santiago) or between north-western and eastern islands in any of the three endemic groups and only one species occurs in both eastern and southern islands, *C. spinalis*, even though with different subspecies on each of the islands. Instead there are deep lineage splits between island groups, that is, entire clades that are unique to only one of these groups, such as '*boavistensis*' clade A and '*lopezjuradoi*' clade C in *Hemidactylus*; '*caboverdiana*' clade B and '*nicolauensis*' clade C in *Tarentola*, and '*delalandii*' clade A and '*stangeri*' clade B in *Chioninia* (Fig 4.1.1.G.1-3, respectively). However, in *Tarentola* this pattern is less clear, with clade A and D not confirming this structuring.

This pattern is expected since these reptiles are terrestrial and non-volant organisms with very limited marine dispersal. However, also other Cape Verde vertebrates with higher marine dispersal abilities exhibit a similar pattern of differentiation to the endemic terrestrial reptiles. For example, demersal fishes occurring around the north-western, southern (Brava and Rombos) and eastern islands (including Maio) present higher ecological similarity driven by the combination of physical isolation of geographic distance and average depth (Medina *et al.* 2007). Interestingly, even volant organisms, for which dispersal is independent of oceanic currents, such as the kestrel *Falco tinnunculus,* present three geographical units in microsatellite data in the north-western, eastern and southern islands. This species has only two presently recognised subspecies in the archipelago but three ESUs, with low rates of gene flow among them determined mainly by geographical distance but also south-westerly trade winds (Hille *et al.* 2003).

Inter-island distances was also suggested to be one of the most important factors explaining faunistic similarity and dissimilarity of reptiles in another Macaronesian archipelago, the Canary Islands (Guerrero *et al.* 2005), and in other island groups, such as the Seychelles (Rocha 2010). This may as well be explained by the fact that the different island groups also present high habitat dissimilarities and hence environmental factors may be enhancing this topological split. This is the case for the Canary Islands (Guerrero *et al.* 2005) and it seems to be the case of the Cape Verde Islands too. For instance, the eastern islands are much flatter and more arid than the remaining

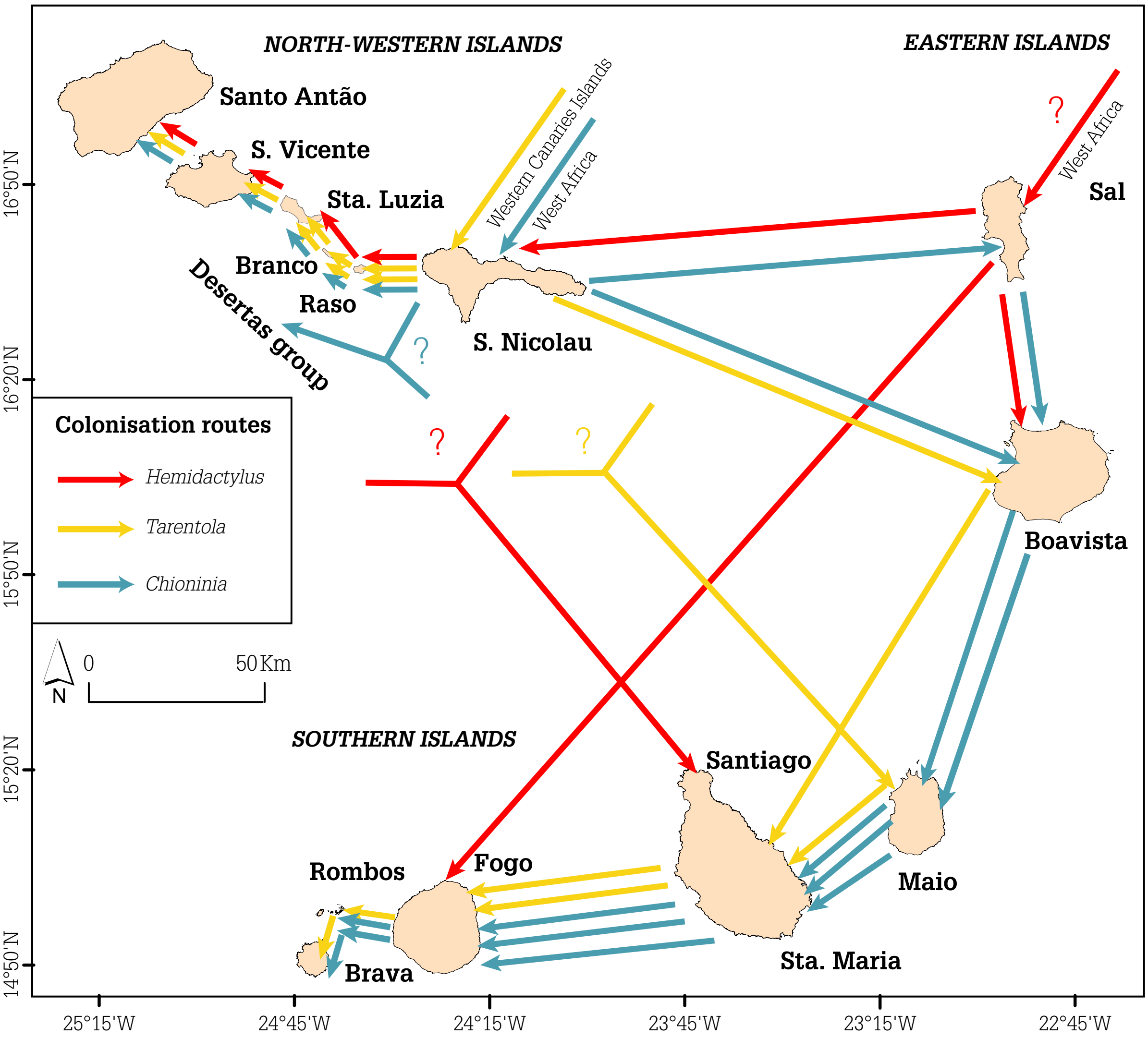


Fig. 4.1.1.F Putative colonisation routes of the three extant genera of the endemic terrestrial reptiles of the Cape Verde Islands inferred by the phylogenetic relationships among clades, direction of the main currents and trade winds and the age of the islands (article II, III and V).

island groups (see Fig. 1.3.1.A, B, C). Thus, organisms adapted to the environmental conditions of this island group, would have more difficulties to colonise the humid and mountainous southern islands.

2) Regarding the **environmental factors**, it seems that they are related to the distribution of richness of the terrestrial Cape Verde reptiles at different levels. These factors include topography, habitat, climate and vegetation.

At the inter-island level, higher maximum and average altitudes are positively related to the number of SIEs and taxa (r= 0.6 and r= 0.7, respectively; $P < 0.05$). Habitat diversity, maximum slope and average NDVI present the same relationship with SIEs richness, and average NDVI with the number of ESUs (all r≥ 0.6, $P < 0.05$). Taking into account the area of the islands, which is significantly correlated with the number of SIEs, ESUs and habitat diversity (r= 0.6, r= 0.7 and r= 0.7, respectively; $P < 0.05$), Raso Islet seems to be an exception since it is very small, homogeneous and nevertheless bears a high number of ESUs. In addition, at least in *Tarentola,* haplotype diversity is also significantly and positively correlated with altitude and this relationship holds true also for habitat diversity (see article III).

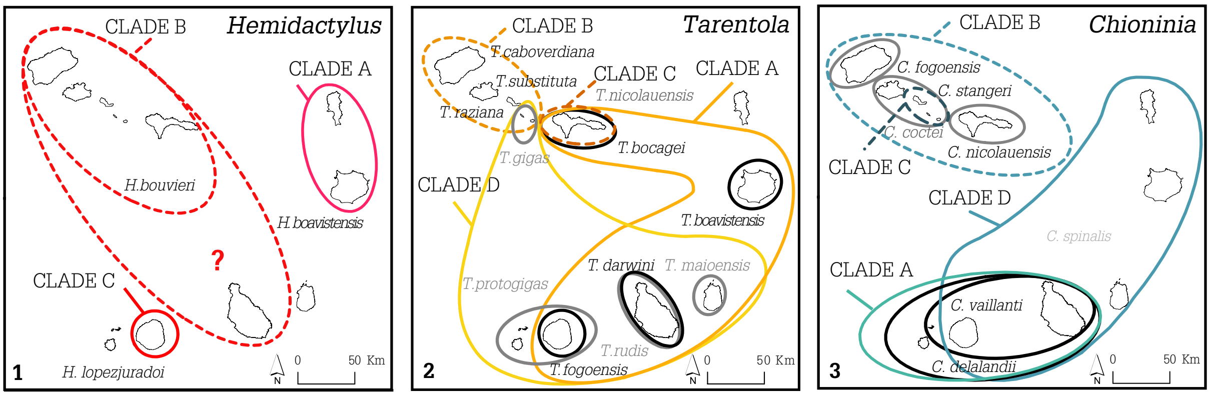


Fig. 4.1.1.G Distribution of the mitochondrial clades identified within each genera in articles II, III and V among the three island groups.

At the intra-island level, and as seen above in Fig. 4.1.1.D, apparently higher, inner and more humid areas of mountainous islands are richer in taxa. Fogo is an exception to this pattern possibly due to the recent volcanic activity that wiped out life around its highest point in 1995. Its richest areas are currently in the north-eastern parts of the island, not affected by the eruption of lavas and where the main trade winds bring more humidity (see Brochmann 1993 and Fig. 4.1.1.D). A different pattern is depicted in one of the flatter islands, Boavista, where the coast is richer in comparison to the inner part of the island. This is probably because the centre south is very arid and avoided by its two gecko taxa (López-Jurado *et al.* 1999).

An advantage of the use of SDMs is that they allow identification of the environmental factors which contribute the most to explain distributions at the taxonomic level (Guisan & Zimmermman 2000; Elith & Leathwick 2009). It is important to highlight that the available number of EGV images with a small pixel size freely available of the Cape Verde archipelago is relatively low compared to other areas. This is mostly due to the low global interest in this area and the low number of weather stations in the country. For instance, all WordClim images were affected by the lack of information on one-side of the island borders. Therefore, it was not possible to use direct climatic variables to input the distribution models. This problem was partially circumvented by the manual digitalisation of polygons from habitat maps, even thought it constrained the inference of the correlations between presence data and direct climatic variables to broad habitat types. Nevertheless, some of this information can be used to infer the major ecological constrains and features of the groups and taxa, since habitat types are considered reasonable surrogates for EGVs (Manel *et al.* 1999).

At a taxonomic level, the habitat variables, especially distance to arid and very arid habitats, contributed more than NDVI and topographic variables to explain distributions of all reptiles. Modelling data also allowed the inference that the presence of *Chioninia* in Sal, where *Tarentola* seems to be absent (Carranza *et al.* 2000), might indicate a better adaptation to salty and sandy habitats by skinks than by *Tarentola* geckos in the Cape Verde Islands. In fact, *C. spinalis* in Sal and Boavista are commonly found on dunes and sandy areas, habitats that Cape Verdean *Tarentola* taxa tend to avoid (López-Jurado *et al.* 1999). Another example is *C. spinalis maioensis*, which appears to occur with a higher probability at intermediated distances to semi-arid arid habitats and close to arid habitats. Proximity to 'dunes and sandy areas' also seems to be important to *H. boavistensis*, contrary to the other endemic *Hemidactylus*. This variable has one of the highest percentages of contribution to the ecological niche-base model of the former species (article VII), presenting a positive association with shorter distances to this habitat type, what is concordant with our field observations and those from other authors (Schleich 1987; Chadwick & Slater 2005). On the other hand, some *Tarentola* taxa also present morphological adaptations to aridity, such as keeled dorsal tubercles that possibly minimise water loss (Maderson *et al.* 1978). This is the case of

T. rudis, which occurs on the driest area of Santiago, and also *T. boavistensis* and *T. maioensis*, which occur on the very arid Boavista and Maio Islands (see Fig 1.3.1.B-C and article VI), contrary to *T. darwini* that presents smooth tubercles (Joger 1984) and for which distribution is negatively related to proximity to very arid habitats (article VII). The NDVI variable seems to be less important, although it partially explains the presence of *C. vaillanti* in Fogo Island, since the probability of occurrence of the subspecies is higher in areas with dense vegetation cover.

Generally, it is the combination of both historical and environmental factors that explains the spatial patterns of diversity of reptiles in the archipelago, even though they were explored separately. At the infra-specific level, lineage and haplotype diversity, this is clearly noticeable, as showed in article III.

Low intraspecific diversity between reptile lineages of the same island have been found in the three genera of terrestrial Cape Verdean reptiles, contrary to what was found in the Canary Islands (e.g. *Chalcides sexlineatus* and *Chalcides viridanus*: Pestano & Brown 1999; Brown *et al.* 2000; Carranza *et al.* 2008; *Tarentola delalandii* and *Tarentola boettgeri*: Nogales *et al.* 1998; Gübitz *et al.* 2000, 2005; *Gallotia galloti* and *Gallotia intermedia/ Gallotia goliath*: Thorpe *et al.* 1996; Maca-Meyer *et al.* 2003; Cox *et al.* 2010). Only two taxa (*T. darwini* and *C. spinalis santiagoensis*) among the 30 presented more than one ESUs within the same island (Santiago). This has been hypothetically explained by both geological and ecological factors, namely the recent volcanic activity and high ecological stress that could lead to population extinctions, and the low habitat diversity within some islands that could restrain opportunities for allopatric diversification comparing to the Canaries. In addition, haplotype diversity in *Tarentola* is positively correlated with size but also with elevation and habitat diversity of the islands, and apparently related to the age of the islands following the GDM, as discussed above.

For explaining the distribution of the exotic reptiles, **anthropogenic factors** must be taken into account. Since *Hemidactylus* species are frequently associated to humanised habitats, living around or inside houses, human-mediated introductions are facilitated. In this way, it seems easily explained why *H. angulatus* is more widespread in the island with the highest human density, Santiago. Considerable evidence exists of possible anthropogenic introductions of this genus in several other island groups, based on both direct observations and genetic markers (Vences *et al.* 2004; Jesus *et al.* 2005; Rocha *et al.* 2010; Carranza & Arnold 2006).

How to conserve?

One of the first steps to provide the needed guidance for future management and conservation efforts is to **assess conservation status** of endemic taxa (Butchart *et al.* 2006). The improved accuracy of the extent of occurrence and area of occupancy data, together with the new taxonomic revisions of the genera, allowed the reclassification of the conservation status of all extant endemic terrestrial reptile taxa (article VI). Analyses performed with Ramas depicted a concerning scenario of 53.3% of threatened extant endemic terrestrial reptile taxa plus one extinct skink (see article VI), with a higher percentage of threatened taxa for *Hemidactylus* (Fig. 4.1.1.H). This is twice the proportion of threatened extant taxa than in the Canaries, what might be related to the smaller area of the Cape Verdes and to the increased aridity of the archipelago.

The most frequent classifying criterion was B (geographic range), followed by D (very small or restricted population) and C (small population size and decline). This is a common pattern in reptile assessments (Pleguezuelos *et al.* 2002, 2010; Oliveira *et al.* 2005) associated to the lack of data concerning population trends and probability of extinction that are related to criteria A and E, respectively.

The most pervasive threats are related to natural disasters, as droughts and volcanic activity, intrinsic factors, such as low densities and restricted range, and introduced species (article VI). Some unknown threats may be affecting some taxa, since very little is known about their demography and basic biology. Thus, further ecological studies, as the one presented in Appendices IV and V, are needed to reduce this lack of knowledge.

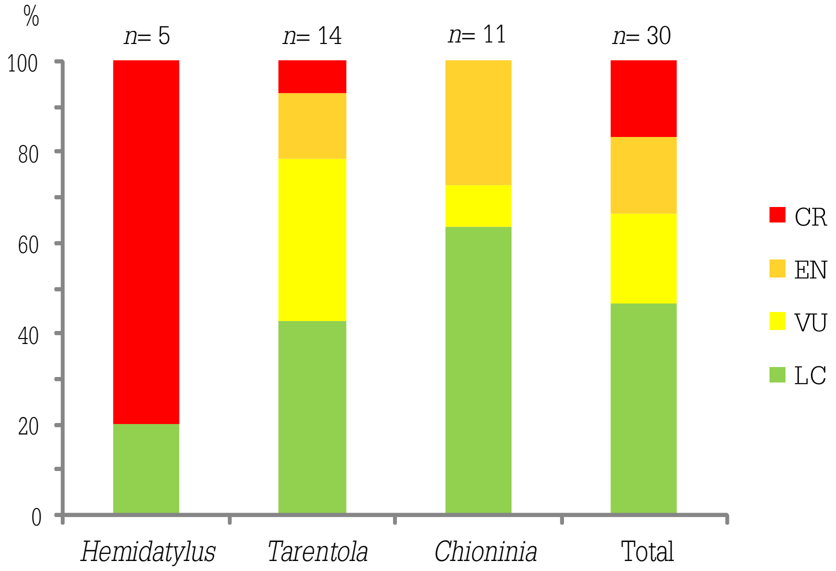


Fig. 4.1.1.H Conservation status of the extant endemic terrestrial reptile taxa of the Cape Verde Islands following the IUCN guidelines and criteria implemented in Ramas. CR, critically endangered; EN, endangered; VU, vulnerable; LC, least concern; *n*, total taxa.

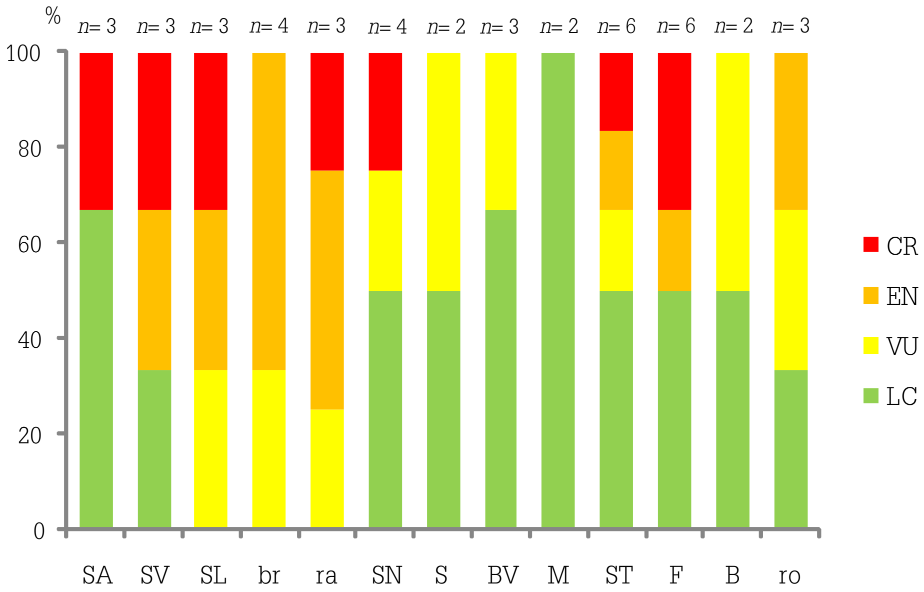


Fig. 4.1.1.I Distribution of the conservation status of the extant endemic terrestrial reptile taxa for the different Cape Verde Islands. CR, critically endangered; EN, endangered; VU, vulnerable; LC, least concern; *n*, total taxa.

Conservation status categories are also unevenly distributed in terms of islands, and this data can guide priority efforts. For instance, 100% of the taxa from Desertas island group are threatened, and Santo Antão, S. Vicente and Fogo, present the highest percentages of Critically Endangered taxa (Fig. 4.1.1.I).

A second step for conservation planning is **optimised design of protected areas** (PAs). Protected area planning frameworks and their resulting map outputs are amongst the most powerful and influential applications within conservation biogeography (Whittaker *et al.* 2005). Selecting priority areas is vital since implementation of reserve system usually takes years or decades, during which time the agents of biodiversity loss continue to operate (Cowling & Pressey 2001). Thus, the study presented in article VII is an important tool in the planning and designation of protected sites in Cape Verde. These islands present a unique opportunity for conservation achievements since the protected areas network is still not fully implemented and hence the possibility of including new better areas for conserving reptiles is real. Coincidentally or not, it is on the three islands with higher number of taxa, ESUs and SIEs of reptiles (S. Nicolau, Santiago and Fogo) that protected areas are already fully implemented (article VII). Probably reptile diversity is a good surrogate of diversity for other groups on which *ad hoc* protected areas were based on the Cape Verde Islands, such as flora and birds, and that may explain why these islands were chosen in the first place.

In article VII, a novel approach was developed to incorporate molecular data on conservation prioritisation. Targeting evolutionary processes in conservation planning has been fully acknowledged in scientific literature but rarely implemented in terrestrial systems. As a result, a clear picture of how the proposed PAs performed to protect the diversity of reptiles at lineage level was presented. In Santa Luzia, Branco, Raso, Sal, Boavista, Maio and Rombos, the designation of new protected areas is not a priority since the PAs that are going to be implemented will already reach the targets of protection of all endemic reptile taxa and ESUs existing within these islands and islets. Conversely, in Santo Antão, S. Nicolau, S. Vicente, Santiago, Fogo and Brava, the planned PAs will be insufficient to achieve the conservation targets for its ESUs. These islands were grouped in three priority levels: 1) In Santo Antão and S. Nicolau, as in the first island group, the figures of 12% widely cited as the percentage of a nation that should be dedicated to nature reserves (WCED 1987) would be achieved. Thus, those two islands, would at least contribute, after the PAs implementation, to the protection of the habitat diversity of the archipelago, since habitats are most different among islands than within them; 2) In Santiago and S. Vicente, the planned PAs will guarantee partial protection of some ESUs, but extra PAs should follow. Since Santiago is one of the islands with the highest number of reptile taxa and the island with the highest number of ESUs, this measure is even more crucial to be implemented there. However, on Santiago implementation of PA may be constrained due to the high population density, since it contains more than half of the national inhabitants (Lobban & Soucier 2007) and higher level of habitat modification by humans; 3) Finally, neither the realistic nor the ideal scenario selected any planning unit (PU) inside a PA on Fogo or Brava. In the first case, although the existing PA might be partially important to protect endemic biodiversity, such as flora (Miller 1993; Duarte *et al.* 2008) and geomorphologic features, it seems totally inadequate to preserve the diversity of the reptiles. In the second case, there are no planned PAs for Brava, even though previous studies already depicted this island as important in conservation terms due to fact that it bears one of the highest diversity of both total and endemic species of flora of the archipelago (Duarte *et al.* 2008). It is noteworthy that Brava presents the largest population of the Vulnerable *T. p. hartogi* and that might also harbour the Critically Endangered *H. bouvieri* gecko (article II).

Hence new PAs proposed should be designed and implemented on Santo Antão, S. Nicolau, S. Vicente, Santiago, Fogo and Brava to reach conservation targets for the remaining 60% of all ESUs in the manner summarised in the following Table 4.1.1.C. Implementation of these measures would allow protecting unique taxonomic and genetic diversity of reptiles, a large portion of them threatened. The failure to apply them would imply a total absence of protection for nine endemic ESUs.

Taking into consideration that the PAs network programme only began in 1988 and what has been achieved, there are reasons to be optimistic about future developments concerning the implementation of the full PAs network and conservation management plans. The Cape Verdean Government and their organisations have shown great interest in the programme and have provided outstanding assistance and support considering their budgetary constraints (Hazevoet 1994). Thus, it is realistic to expect the proposed measures to be taken into account before the implementation of the full PAs network. Nevertheless, it will be imperative that research biologists are available locally to oversee future developments and provide guidance. In the end, outcomes on effective protection of

Table 4.1.1.C Recommended conservation actions to change the protected areas network in order to attain conservation targets for all taxa and ESUs of endemic terrestrial reptiles.

Island	**Targeted taxon/ ESU**	**Conservation action**
Santo Antão	*T. caboverdiana / Tc*	Expansion to the East of the Tope da Coroa Natural Park, untill near Água Amargosa; Creation of two new PAs around Chã da Queimada and near Chã de Porto Novo; Corridor between the Moroços and the Cova/Ribeira Paúl/Torre Natural Parks.
	C. fogoensis / Cf	
	*H. bouvieri bouvieri / Hbb*SA	
S. Vicente	*C. stangeri / Ct*SV	Creation of a new PA around Calhau.
	T. substituta / Ts	Creation of two new PAs at West of Madeiral and North-West of Baía das Gatas.
S. Nicolau	*H. bouvieri spp. / Hb*SN	Extensions to South and East of the implemented Monte Gordo National Park; Creation of three new PAs along the coast around Preguiça, around Ribeira da Prata and Praia Branca; Addition of Fajã de Cima e Lombo Pelado Natural Park (excluded from Decree nr. 3/2003).
	T. nicolauensis / Tn	
	C. nicolauensis / Cn	
	T. bocagei / Tb	Creation of a new PA at North-East of Carriçal.
Santiago	*H. bouvieri bouvieri / Hbb*ST	Creation of a new PA at inland mountainous area or a corridor connecting the two Natural Parks; Expansion to the North of the Serra da Malagueta Natural Park untill Ribeirão Sal; Expansion to the North-West of the Serra do Pico de Antónia Natural Park untill Palha Carga and beyond João Teves.
	T. darwini / Td_{North}, Td_{South}	
	C. vaillanti vaillanti / Cvv	
	C. spinalis santiagoensis / CstST_{North}	Creation of a new PA at South-East of Tarrafal.
	T. rudis / Tr	Creation of a new PA at North of Cidade Velha.
	C. spinalis santiagoensis / CstST_{South}	
Fogo	*H. lopezjuradoi / Hl*	Expansion to the North-East of the Bordeira, Chã das Caldeiras e Pico Novo Natural Park until the coast; Creation of two new PA at North of Cova Figueira and around S. Jorge.
	T. fogoensis / Tf	
	C. vaillanti xanthotis / Cvx	
	*C. delalandii / Cd*F	
	C. spinalis spinalis / Css	
	*T. protogigas protogigas / Tph*B	Creation of new small PAs around Lagariça, Monte Grande and Monte Vermelho.
Brava	*T. protogigas hartogi / Tph*B	Creation of two new PAs at North-east of Baleia and around Palhal.
	*C. delalandii / Cd*B	

Tc, T. caboverdiana; Cf, C. fogoensis; Hbb, H. bouvieri bouvieri; Ct, C. stangeri; Ts, T. substituta; Tn, T. nicolauensis; Cn, C. nicolauensis; Tb, T. bocagei; Td, T. darwini; Cvv, C. vaillanti vaillanti; Cst, C. spinalis santiagoensis; Tr, T. rudis; Hl, H. lopezjuradoi; Tf, T. fogoensis; Cvx, C. vaillanti xanthotis; Cd, C. delalandii; Css, C. spinalis spinalis; Tpp, T. protogigas protogigas; Tph, T. protogigas hartogi.
SV, S. Vicente; SA, Santo Antão; SN, S. Nicolau; B, Brava; F, Fogo; ST, Santiago.

Cape Verdean biodiversity are dependent on the necessary funds becoming available to support this crucial step in the conservation (Hazevoet 1994).

Following Gibbons *et al.* (2000) recommendations, several measures should be followed to prevent the decline of the Cape Verdean reptile populations. First, the impact of habitat degradation, introduced invasive species, and unsustainable use can be controlled immediately through legislation and cultural shifts in environmental attitudes by means of educational campaigns. Second, the release of invasive non-native species and trade of threatened taxa must be proscribed. Finally, long-term monitoring of reptile populations is essential, for example, to determine demographic parameters important in determining variation in the conservation status (IUCN SPS 2010). Since in the near future, human pressure on ecosystems will likely increase more markedly on islands than on continents (Millennium Ecosystem Assessment 2005), a systematic conservation planning should urgently be followed in the Cape Verde Islands.

Section 4.1.2. Future prospects

Despite the contribution of this work to a general better understanding of reptile taxa biogeography in the Cape Verde Islands, many relevant questions remain to be answered and others were generated through this work.

Further molecular analyses with fast-evolving nuclear markers should follow to understand if the two endemic *Tarentola* from S. Nicolau, *T. nicolauensis* and *T. bocagei*, hybridise or not, and if so, to what extent. Extensive sampling between Belém and Juncalinho was accomplished to determine more precisely the contact zone inferred by the predictive maps of occurrence. The collected material needs to be sequenced and analysed with microsatellites or fast evolving introns, similarly to what was performed in other insular reptiles (Thorpe *et al.* 2010). In addition, the methods applied in the morphological analyses were mainly restricted to traditional analyses of allometric and meristic characters. In further studies, using methods of geometric morphometric should be recommended, which might elucidate possible differences between these two cryptic taxa (Kaliontzopoulou *et al.* 2010). It would also be interesting to confirm if other taxa or groups with different vagilities, namely terrestrial invertebrates and more birds, follow similar phylogeographic patterns to the ones detected for most of the reptiles.

Gathering enough ecological data to produce mechanistic SDMs for some taxa would be valuable to compare those results with the SDMs obtained with ecological niche-modelling. Mechanistic models would ensure obtaining real cause-effect relationships between the species distribution patterns and environmental factors (Guisan & Zimmermann 2000). This data would be also valuable to further understand the vulnerable aspects of the taxon ecology that should be taken into account in a conservation management plan, such as the reproduction mode. To feed this type of models, many ecological, behavioural and physiological studies are needed, as few data are presently available for the Cape Verdean reptiles.

Other interesting questions that deserve further attention relate to the study of priority areas. Following Hazevoet (2010), recent data confirms some of the selected PUs for reptiles as important for endemic birds too, such as the threatened Cape Verde cane warbler (*Acrocephalus brevipennis*) that also occurs on the north-eastern part of Fogo, but further work is needed to gather all published data. It would be important to check, once that data is available, if the nesting areas of all endemic birds are included in the protected areas or in the PUs proposed by this study and if endemic flora taxa are protected at least on 12% of their distributions.

4.2. CONCLUDING REMARKS

This work integrated phylogeography, taxonomic revisions, ecological modelling and reserve design, contributing for cataloguing and mapping the diversity (at both genetic and specific level) of Cape Verdean terrestrial reptiles and promoting its conservation. This knowledge has allowed updating the conservation status and optimising the reserve design of the protected areas for this group. Furthermore, it has provided a better understanding of the biogeographic and phylogeographic patterns of reptiles and some insight on how historical and environmental factors shaped the diversification of these island endemics. In summary, the major conclusions of this work are:

1. New records of introductions of terrestrial reptiles were detected after extensive sampling on the Cape Verde Islands: a new anthropogenically introduced species, identified as *Agama agama*, and also new locations for some already known introduced species, highlighted the need to take actions as quickly as possible to prevent further cases of introductions and to diminish the extent of this threat.

2. The phylogenetic relationships among all taxa of each endemic genus were unravelled for the first time and detected similar strong division between Windward and Leeward clades for the three genera. Some paraphyletic/ polyphyletic taxa were noticed.

3. Cryptic diversity was unveiled using integrative approaches combining mitochondrial and nuclear markers with population and morphological analyses within the three genera of endemic reptiles at specific, subspecific and lineage levels, confirming the high taxonomic richness of the archipelago but a low substructuring in lineages within islands when compared with the Canary Islands.

4. The taxonomy of the three endemic reptile genera was reviewed based on mitochondrial and nuclear DNA, and morphological data of live and museum specimens, with all the synonyms and chresonyms identified for each taxon and identification keys elaborated for each genus. The taxonomic status of some taxa was resolved and new species and subspecies were described using congruence approaches for promoting taxonomic stability.

5. Colonisation patterns described by previous authors were generally confirmed and proved to be common among genera, with the northern islands being the first to be colonised and then the southern ones, and with dispersion from east to west. Also the colonisation ages of the archipelago by the ancestors of the three genera were broadly similar to previous works, ranging between 5.7 and 15.1 Mya.

6. High taxonomic diversity in the archipelago might be better explained by multiple colonisations and drift and founder effect among the different islands followed by adaptive radiation. The low lineage diversity within island taxa is probably explained by the recent volcanic activity and high ecological stress that could lead to population extinctions, and the poor habitat diversity within some islands that could restrain opportunities for allopatric diversification.

7. Taxa distributions were clarified based on new chorological and bibliographic data and intra-island precise observed and potential distributions were mapped depicting that more than a third of taxa present restricted ranges. This result is related to the fact that about 52% of them present threatened conservation status following updated IUCN criteria, twice the proportion of the Canaries, what might be explained by the smaller area of the Cape Verdes and by the increased aridity of the archipelago.

8. The main threats to reptiles were identified and related to natural disasters, intrinsic factors and introduced species. However basic biology and demographic parameters of all threatened reptiles in the Cape Verdes and detailed quantification of the major threats affecting each one of them are lacking and thus lack of knowledge seems to be one of the main threats that should be first circumvented. Several conservation measures were proposed of which implementation of protected areas encompassing all taxa and ESUs was suggested to be top priority.

9. Implementation of all the currently proposed protected areas is definitely needed and in some cases still insufficient to cover at least 12% of all ESUs of endemic reptiles in most of the islands except Sal, Boavista and Maio. Hence, new areas were proposed based on an algorithm for spatial conservation prioritisation, taking cost layers into account, to cover gaps of protection for some islands, taxa and their genetic diversity. Since both real and ideal scenarios surprisingly presented similar efficiencies, the real model scenario should be followed to minimise bureaucratic processes and hence accelerate the much needed conversation planning for the archipelago.

SECTION 4.3. REFERENCES

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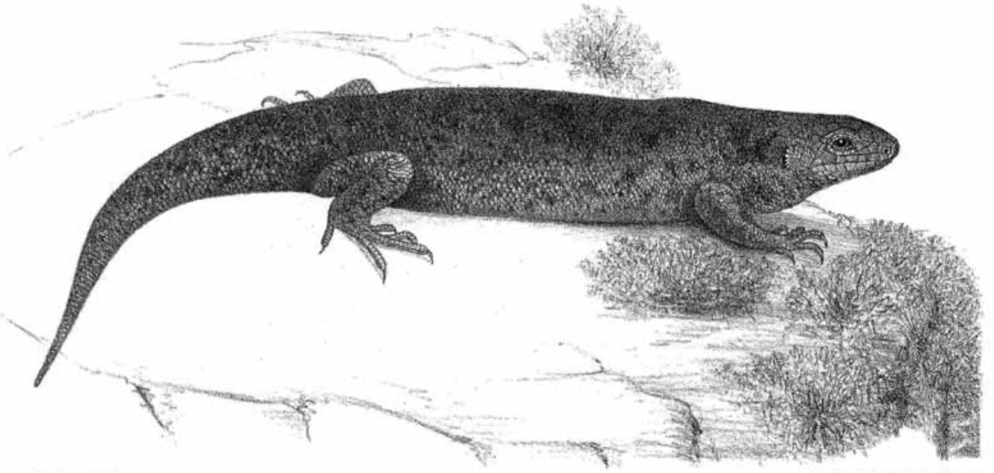
Appendices



MACROSCINCUS COCTEI

APPENDIX I

Phylogeography of the African common toad, *Amietophrynus regularis*, based on mitochondrial DNA sequences: inferences regarding the Cape Verde population and biogeographical patterns

R. Vasconcelos [1,2,3*], E. Froufe[4], J.C. Brito[1], S. Carranza[3] & D.J. Harris[1,2]

*E-mail: raquel.vasconcelos@mail.icav.up.pt

[1] CIBIO-UP, Centro de Investigação em Biodiversidade e Recursos Genéticos,
Campus Agrário de Vairão, R. Padre Armando Quintas, 4485-661 Vairão, Portugal.

[2] Departamento de Biologia, Faculdade de Ciências da Universidade do Porto,
R. Campo Alegre, s/n, 4169-007 Porto, Portugal.

[3] Institute of Evolutionary Biology (CSIC-UPF),
Passeig Marítim de la Barceloneta, 37-49, E-08003 Barcelona, Spain.

[4] CIIMAR, Centro Interdisciplinar de Investigação Marinha e Ambiental,
R. dos Bragas, 289, 4050 - 123 Porto, Portugal.

ABSTRACT

The amphibian Amietophrynus regularis is distributed throughout equatorial Africa, with presumed introduced populations in the Cape Verde archipelago. Portions of the 12S and 16S rRNA mitochondrial regions of 30 specimens from Kenya, Uganda, Niger, Mali, Burkina-Faso, Ghana, Guinea-Bissau and Cape Verde were used to assess genetic diversity and to identify the most probable geographic origin for the introduction of this toad on the latter archipelago. Two lineages with 1.4% genetic divergence between them were identified in western and eastern Africa. All sequences from the different Cape Verde Islands were identical to each other and to the Guinea-Bissau samples, indicating, together with other historical evidences, that an anthropogenic introduction event probably occurred, possibly from Guinea-Bissau, but further work is needed to confirm this. As previously noted, several individuals from previous genetic studies seem to have been misidentified.

KEY WORDS

Amietophrynus regularis, "*Bufo*", Mitochondrial DNA, 12S and 16S rRNA, Cape Verde Islands.

INTRODUCTION

Amietophrynus is a large genus of 38 species of true toads native to Africa, with typically 20 chromosomes, with a complex and unresolved taxonomy. Originally, all *Amietophrynus* species groups were part of the genus *Bufo*, but were separated primarily based on molecular analyses by Frost *et al.* 2006 (although see criticisms in Smith & Chiszar 2006; Pauly *et al.* 2009). The African common toad, *Amietophrynus regularis* (Reuss, 1833), also known as the Square-marked toad, Egyptian and Reuss's toad, is listed as Least Concern by the IUCN in view of its wide distribution in a broad range of habitats and presumed large populations. It occurs in savannas, shrublands, grasslands, forests, rural gardens, urban areas, rivers and freshwater lakes, from near sea level up to 2 500 m high (Tandy *et al.* 2006). Its range appears to be restricted by increasing aridity; in drier areas, away from permanent water, it is replaced by species such as *A. garmani* and *A. xeros* (Tandy *et al.* 2006), which are morphologically similar and sympatric with *A. regularis* to some extent (Tandy *et al.* 2004, Rödel et al. 2006).

Amietophrynus regularis ranges from Senegal to Nilotic Egypt, Sudan and Ethiopia, southwards to western Democratic Republic of the Congo, north-western Angola, Uganda and central-southern Kenya (Fig. A.I.1). It is also present in the Cape Verde Islands where it is thought to have been introduced deliberately in water tanks to control mosquitoes (Schleich 1987). The oldest reference concerning the presence of toads on this archipelago, where no native amphibians occur (Schleich 1987), is from 1844 by Lopes de Lima (*in* Bocage 1896). It is only known to occur in Santiago, S. Nicolau and Santo Antão Islands (López-Jurado *et al.* 2005) (Fig. A.I.1). The introduction of *A. regularis* to the Cape Verde Islands remains unconfirmed and the geographic origin of introduced populations and the number of introduction events undetermined.

With such a wide range, it is important to determine genetic diversity within the species, in order to evaluate if geographical structure is present. By sequencing part of the 12S and 16S rRNA mitochondrial region, this work will also increase the amount of data available to infer comparative phylogeographical patterns of African amphibians, as this region was already the focus of studies of "*Bufo*" *mauritanicus* (Harris & Perera 2009), present in the Maghreb, and *A. xeros* (Froufe *et al.* 2009), occurring in the sub-desert belt. In addition, some sequences of *Amietophrynus* species from previous publications appear to be misidentifications, as noted by Froufe *et al.* (2009). Thus, a detailed reassessment of *A. regularis* with multiple individuals analysed across its range and including near relatives is needed to establish the recognition of the species group, considered paraphyletic by Frost *et al.* (2006) based on analyses of DNA sequences, and to ascertain if this is due to misidentification, the presence of cryptic species or because of hybridization followed by introgression. Subsequently, the objectives of this study are: 1) to determine genetic diversity across the range of *A. regularis*, 2) to ascertain the origin and number of introduction events in the Cape Verde Islands, and 3) to resolve discrepancies regarding previously published sequences.

MATERIALS AND METHODS

Sampling and gathering of molecular data set

A total of 29 sequences of *Amietophrynus* and one of "*Bufo*" *mauritanicus* were used in the analysis (Fig. A.I.1): a) 10 from new specimens collected in the Cape Verde Islands, including one specimen from Brava where this study recorded its presence for the first time; b) eight from new specimens collected in Northern African countries; and c) 12 from several African countries available on GenBank (Table A.I.1). Digital photographs of the collected specimens were taken and a piece of toe was removed and stored in 100% ethanol. Sampled animals were released immediately afterwards. Identification codes, localities and all GenBank accession numbers are listed in Table A.I.1.

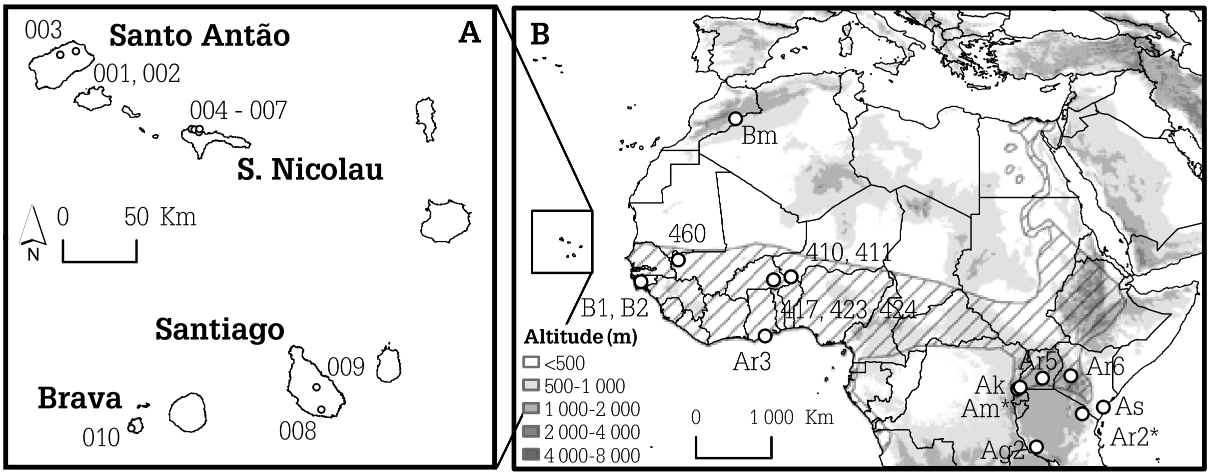


Figure A.I.1 Locations of the *Amietophrynus* and "*Bufo*" sequences used in this study **A**) from the Cape Verde Islands and **B**) North Africa. The distribution of *A. regularis* is indicated in dashed lines (adapted from Tandy *et al.* 2006). For codes with an asterisk (*), refer to the Discussion section.

Total genomic DNA was extracted using standard methods, following Harris (2001). Polymerase Chain Reaction (PCR) primers used in amplification and sequencing of the two mitochondrial (mtDNA) genes were 12Sa and 12Sb for the 12S rRNA, 16SL and 16SH for the 16S rRNA from Kocher *et al.* (1989) and Palumbi *et al.* (1991), respectively. Thermocycling consisted of an initial 3 min at 95 °C followed by 35 cycles of 30 s at 95 °C, 50 °C and 72 °C and then a single cycle of 7 min at 72 °C. Amplified mitochondrial fragments were sequenced from both strands on a 3100 Applied Biosystems DNA Sequencing Apparatus. Alignment was performed with ClustalW using Bioedit v. 5.0.9. (Hall 1999) and adjusted by hand.

Phylogenetic analyses

Sequences were imported into PAUP* 4.0b10 (Swofford 2003). Four GenBank sequences of *A. kisoloensis*, *A. gutturallis*, *A. steindachneri* and '*Bufo*' *mauritanicus* were used as outgroups (Table A.I.1).

For the phylogenetic analyses, Maximum Likelihood (ML) and Maximum Parsimony (MP) methods were used with random sequence addition (100 replicate heuristic searches). Support for nodes was estimated through bootstrap techniques (Felsenstein 1985) with 1000 replicates. Modeltest 3.06 (Posada & Crandall 1998) was used to select the model of sequence evolution that fit the data set better using the Akaike information criterion (AIC). This model was implemented in the ML and Bayesian analyses. The Bayesian analysis was carried out using MrBayes v.3.1 (Huelsenbeck & Ronquist 2001), model parameters estimated as part of the analysis and four incrementally heated Markov chains with the default heating values. The analysis was run for 107 generations, saving one tree each 1000 generations. Twenty five percent of the saved trees were discarded as burn in. It was confirmed that all parameters had ESSs above 100 after burn in using the software Tracer v1.5 (Rambaut & Drummond 2007). The remaining trees (7500) were combined in a 50% majority consensus tree, in which the frequency of any particular clade represents its posterior probability (Huelsenbeck & Ronquist 2001).

Table A.I.1 Details of material and sequences used in the present study. For codes with an asterisk (*), refer to the Discussion section.

Species	Code	Country	Region/ Island	Latitude	Longitude	12S/16S Genbank
"Bufo" mauritanicus	Bm	Morocco	Errachidia Province	-	-	AY680265
A. kisoloensis	Ak	Uganda	Rukungiri District	-	-	AY325995
A. steindachneri	As	Kenya	Arubuko Sokoke forest	-	-	AY325981
A. gutturalis	Ag1	Tanzania	-	-	-	FJ882851
A. gutturalis	Ag2	Tanzania	Mumba Village	-8.15000	31.85100	DQ283436
*A. regularis**	Ar1*	-	North Africa	-	-	AY680264
*A. regularis**	Ar2*	Tanzania	Kilimanjaro Region	-3.99979	37.37750	DQ283163
*A. maculatus**	Am*	Uganda	Rukungiri District	-0.79114	29.92490	U52762/28
A. regularis	Ar3	Ghana	Eastern Region	-	-	DQ158485
A. regularis	Ar4	-	Africa	-	-	AY330899/91
A. regularis	Ar5	Uganda	Kampala	-	-	AF220890/43
A. regularis	Ar6	Kenya	Lake Baringo	0.60923	36.01560	AF220889/43
A. regularis	410	Niger	Tapoua	12.47480	2.42760	HM769984/770002
A. regularis	411	Niger	Tapoua	12.47480	2.42760	HM769985/770003
A. regularis	417	Burkina Faso	Gourma	12.06033	0.36933	HM769986/770004
A. regularis	423	Burkina Faso	Gourma	12.06033	0.36933	HM769987/770005
A. regularis	424	Burkina Faso	Gourma	12.06033	0.36933	HM769988/770006
A. regularis	460	Mali	Kayes	14.50400	-11.09098	HM769989/770007
A. regularis	B1	Guinea-Bissau	Bissau	11.86031	-15.57870	HM769990/770008
A. regularis	B2	Guinea-Bissau	Bissau	11.86031	-15.57870	HM769991/770009
A. regularis	001	Cape Verde	S. Antão	17.11363	-25.16835	HM769992/770010
A. regularis	002	Cape Verde	S. Antão	17.11363	-25.16835	HM769993/770011
A. regularis	003	Cape Verde	S. Antão	17.13884	-25.07343	HM769994/770012
A. regularis	004	Cape Verde	S. Nicolau	16.66314	-24.36332	HM769995/770013
A. regularis	005	Cape Verde	S. Nicolau	16.65855	-24.34591	HM769996/770014
A. regularis	006	Cape Verde	S. Nicolau	16.64485	-24.32094	HM769997/770015
A. regularis	007	Cape Verde	S. Nicolau	16.66047	-24.31520	HM769998/770016
A. regularis	008	Cape Verde	Santiago	14.94691	-23.57285	HM769999/770017
A. regularis	009	Cape Verde	Santiago	15.08491	-23.60028	HM770000/770018
A. regularis	010	Cape Verde	Brava	14.83216	-24.73434	HM770001/770019

Network and population analysis

The genealogical relationships within the 23 sequences of *A. regularis* were assessed with haplotype networks constructed using statistical parsimony (Templeton *et al.* 1992). This analysis was implemented in the program TCS v1.21 (Clement *et al.* 2000) with a connection limit of 95% and deletions treated as a fifth state. Other sequences available on GenBank only for 12S or 16S were not included in this analysis: AY028486 from Ghana (Pramuk *et al.* 2001) and GQ183570 from Uganda, Rwenzori Mountains, Bundibuyo (Siow *et al.* in press), respectively.

Haplotype (*Hd*) and nucleotide diversity (π) values, number of haplotypes (*h*) and segregating sites (*S*) were calculated with DnaSP v.4 (Rozas *et al.* 2003). Estimates of average evolutionary divergence over sequence pairs within and between groups, using p-distances (*p*-dist), were calculated based on the number of base differences per site from averaging over all sequence pairs within each group and estimation of net average between groups of sequences, respectively. Analyses were conducted in MEGA 4.0.2 (Tamura *et al.* 2007). Standard error estimates were obtained by a bootstrap procedure (1,000 replicates).

RESULTS

In total, including outgroups, 30 individuals were analysed with the combined data set including 904 bp (397 bp from 12S and 507 bp from 16S rRNA), of which, 106 positions were variable and 73 parsimony-informative (27 and 19 for 12S and 79 and 54 for 16S rRNA, respectively).

The general time reversible model (GTR), with an estimate of invariable sites (I= 0.7795), was the most appropriate model of evolution for this dataset. A single tree (–ln= 2192.36412) was recovered from the ML analysis. Two MP trees were recovered (191 steps), the consensus of which differed from the ML tree only in some minor arrangements of taxa or individual samples. The Bayesian analysis recovered the same tree as the ML analysis. The results of the MP, ML and Bayesian analyses of the combined 12S+16S rRNA data are shown in Fig. A.I.2 and indicate that two lineages, western and eastern, exist within *A. regularis*. The genetic distance between these lineages is 1.4 ± 0.4% (Table A.I.2).

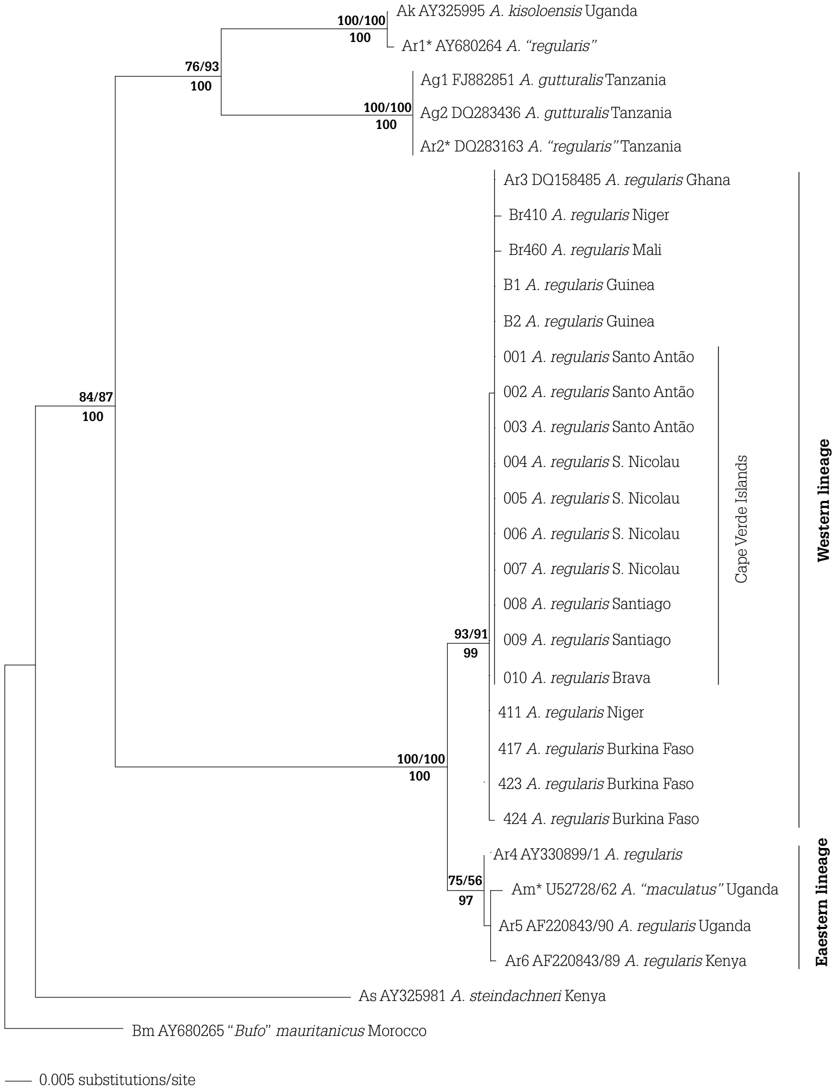


Figure A.I.2 Maximum likelihood (ML) tree inferred using the GTR+I model of sequence evolution showing relationships of *A. regularis* from different origins. The tree is rooted using *"Bufo" mauritanicus*. Bootstrap support values above 50% for the MP and ML analysis are shown above nodes, respectively and posterior probability values for the Bayesian analysis below nodes (see Materials and Methods). Sequences downloaded from GenBank are shown in the figure with their respective GenBank accession numbers for the 16S and 12S rRNA genes separated by a dash if the accession numbers differ. For locality data and GenBank accession numbers of the new (ranging from HM769984 to HM770019) and previously published sequences see Table A.I.1. For codes with an asterisk (*), refer to the Discussion section.

In addition, two sequences identified as *A. regularis* in previous studies, Ar1* and Ar2* (with GenBank codes AY680264 and DQ283163, respectively) cluster with *A. kisoloensis* and *A. gutturalis*, respectively, whereas one sequence assigned to *A. maculatus* (Am*, U52728/62) groups within the eastern lineage of *A. regularis* (Fig. A.I.2).

Table A.I.2. Mitochondrial 12S and 16S diversity of the western and eastern lineages of *A. regularis*. *n*, sample size; **π**, nucleotide diversity; *Hd*, haplotype diversity; *h*, number of haplotypes; *S*, segregating sites; evolutionary divergence within and between groups (*p*-dist ± standard error).

Lineage	***n***	π	***h***	***Hd***	***S***	***p*-dist**	***p*-dist**
Western	19	0.00095	7	0.574	4	0.2 ± 0.1%	1.4 ± 0.4%
Eastern	4	0.00194	4	1.000	3	0.1 ± 0.1%	

According to the network analyses, the western and eastern *A. regularis* lineages are 13 mutational steps apart (Fig. A.I.3). In the western lineage, all sequences from the four Cape Verde Islands are identical to each other and to the Guinea-Bissau sequences. On the contrary, sequences from individuals from Mali, Ghana, Burkina Faso and Niger are between one and three mutational steps apart from those (Fig. A.I.3). After preliminary analysis, the sample Ar4 (AY330899/91) of an unknown locality (Table A.I.1) was assumed to belong to the eastern lineage due to its affinities with this clade. As a result, in the eastern lineage, four closely connected haplotypes were recovered (Fig. A.I.3).

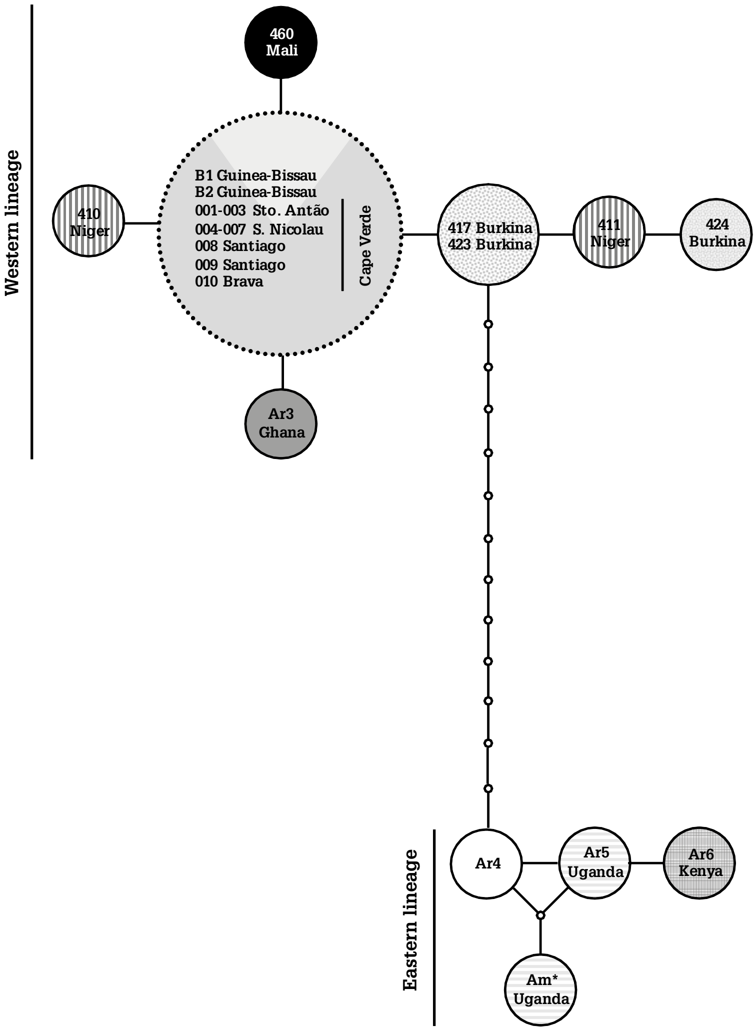


Figure A.I.3 Parsimony network corresponding to the 12S and 16S rRNA sequence variation in *A. regularis*. Lines represent a mutational step, circles haplotypes and dots missing haplotypes. The circle area is proportional to the number of individuals. The dotted circle represents the probable ancestral haplotype. Samples from the same country are indicated using the same pattern or grey scale. For correspondences of sample and location codes see Table A.I.1. For codes with an asterisk (*), refer to the Discussion section.

DISCUSSION

The phylogenetic analyses showed that two distinct mitochondrial lineages of *A. regularis* appear to exist, one in the western and another in the eastern part of Africa with a genetic divergence of 1.4% (1.5 % based only on 16S rRNA). Divergence levels between these western and eastern lineages could be explained by isolation through geographic distance alone or together with geographical barriers such as high mountains (Fig. A.I.1). Few anuran phylogeographic studies from Northern Africa exist and the ones using the same molecular markers, the Maghrebian *B. mauritanicus* and the sub-Saharan *A. xeros*, recovered very different patterns. The former presents minimal genetic variation within its range (Harris & Perera 2009) and the latter exhibits maximal divergence between samples from the same country (Froufe *et al.* 2009). However, an assessment of variation in the rodent *Mastomys erythroleucus* with the same geographical range as *A. regularis* recovered a similar pattern to the one presented here, although with two additional central-African lineages (Brouat *et al.* 2009). Thus, further sampling of *A. regularis* in Central Africa would be needed to define the ranges of the eastern and western lineages and to assess if additional lineages could be uncovered. Furthermore, it would be useful to sample isolated populations in the Sahara, such as in the Hoggar mountains of southern Algeria and in the oasis of south-western Libya (Schleich *et al.* 1996), to confirm its presence and determine if more variation exists.

Considering the Cape Verde Islands, it seems that this species is indeed introduced there and that a single introduction event occurred, as all individuals from the four islands where the species occurs have the same mitochondrial haplotype. Nevertheless, a scenario of multiple colonisations from the same source population is also possible and further SNPs or microsatellites analyses would be needed to distinguish with certainty between the two scenarios. The network analysis indicates Guinea-Bissau as the most likely source of the introduction of *A. regularis* in the Cape Verde Islands, given that samples from both regions share the same haplotype. This seems feasible as the Portuguese made regular trips during the 16th and 17th centuries from Guinea-Bissau to the previously uninhabited archipelago for colonizing it with a slave workforce and as a strategic stopping point of the slavery trade route between Guinea-Bissau and the American continent (Silva 1995). However, as samples from other West African areas are lacking and other sequences from different origins are only one to three mutational steps away from the Cape Verde sequences, an alternative origin for *A. regularis* found on the Cape Verde Islands cannot be ruled out. Since no other native amphibian exists on the islands, the presence of *A. regularis* probably does not raise any direct conservation issues, contrary to other accidentally introduced herpetofauna occurring in the Cape Verdes, such as *Hemidactylus angulatus*, *H. mabouia* (Arnold *et al.* 2008) and *Agama agama* (Vasconcelos *et al.* 2009). However, the impact that *A. regularis* might have on native invertebrates or indirectly on the vertebrate community dynamics is unknown. It is known to be abundant in Santiago, S. Nicolau and S. Antão (Hazevoet 1995) and it was considered invasive by López-Jurado *et al.* (2005) on the archipelago. This study reports it for the first time on Brava. Further studies are clearly warranted to assess its impact on this insular ecosystem.

Finally, as previously noted by Froufe *et al.* (2009), the Ar1* (AY680264; Pauly *et al.* 2004) and Am* sequences (U52728/62; Graybeal 1997) are probably morphological misidentifications rather than introgression, sequencing errors, contaminations or amplification of nuclear copies of the mtDNA. An additional sequence of *A. "regularis"*, Ar2* (DQ283163; Frost *et al.* 2006), appears identical to *A. gutturalis* specimens sequenced by Frost *et al.* (2006) and Van Bocxlaer *et al.* (2009). This study again emphasises the importance of using multiple individuals of the same species in phylogenetic analyses and of including sequences from GenBank with caution. Additionally, as some *Amietophrynus* are morphologically similar, with some individuals presenting ambiguous morphological characters used in identification keys (pers. obs.), future work with nuclear genes should be done to confirm the estimates of relationships based on mtDNA sequence data. Also additional morphological studies should be implemented in order to try to find clearly diagnostic characters.

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APPENDIX II
Em busca do gigante perdido

PARQUES PARKS AND

E VIDA SELVAGEM

Ano IX - N.º 27 - 21 de Março 2009 a 20 de Junho 2009

Report: Tornada Wetlands
Report: Arouca Geopark
Interview: Coast research

Reportagem
PAUL DE TORNADA
Reportagem
GEOPARQUE DE AROUCA
Entrevista
ESTUDOS COSTEIROS

ENTREVISTA 51

Em busca do **gigante perdido**

Ilha de Santo Antão

Apesar de extinto, há quem acalente a esperança de nalgum ilhéu cabo-verdiano ainda se conseguir ver o maior réptil do arquipélago, descrito por Bocage, o *Macroscincus coctei,* que chegava a atingir 60 centímetros de comprimento…

Alguns dos répteis endémicos de Cabo Verde têm as suas populações sob ameaça de extinção. Afirma-o uma investigadora portuguesa, Raquel Vasconcelos, do CIBIO da Universidade do Porto.

Na sequência da pesquisa que empreendeu diz que «já estamos perante a extinção de uma dessas espécies».

Como seria de esperar, «desde que foi declarado extinto em 1915, voltar a encontrar o lagarto *Macroscincus coctei* transformou-se no Santo Graal de muitos herpetologistas», palavra que agrupa os estudiosos dos répteis e anfíbios.

Dezenas de expedições galgaram terreno na ideia de poderem reencontrar sobreviventes e assim apagar este réptil da lista da biodiversidade perdida: «Eu própria fui à ilha de Santa Luzia, numa barca de pescadores com velas feitas de sacos de cereais, para procurar este sáurio especial», sobretudo depois de, em 2005, um investigador chamado Mateo garantir ter encontrado uma mandíbula de juvenil nas fezes de um gato».

Como se terá extinguido este escincídeo gigante?

As linhas de força estão à vista: «Os pescadores passam temporadas nos ilhéus, que não são habitados. Nas suas viagens, levaram para lá cães e gatos. Além disso, no passado comiam-nos e usavam a gordura de sáurios para fins medicinais. Isso pode ter ajudado à extinção». Mas, «mais grave, foi uma época de fome derivada de uma seca violenta ocorrida em 1833. Na altura, o Governo colonial português exilou prisioneiros para esses ilhéus e

O menino que venceu o mito das terríveis osgas...

Vulcão da ilha do Fogo: duas horas para subir, 10 minutos para descer

Parques e [illegible]**a Selvagem** Primavera 2009

Destino: ilha de Santa Luzia, vela feita de sacos de cereais

Raquel Vasconcelos percorreu 10% do território cabo-verdiano

decerto que, esfomeados, comeram lagartos» para sobreviverem.

Outra ajuda para a extinção deste réptil da família dos escincídeos deve ter sido dada «durante os séculos XVIII e XIX», altura em que «eram uma raridade zoológica. Se não é o maior, é o segundo maior escincídeo mabuiforme do mundo, e todos os museus da Europa queriam um!».

Os felinos também contribuíram para a extinção. Animais de companhia dos pescadores durante as suas campanhas, os gatos tornaram-se um novo e terrível predador, até hoje. Instinto mais aguçado que as garras, diante da gataria uma boa parcela de tudo o que mexe marcha do mundo dos vivos.

Clima duro

Raquel Vasconcelos esteve nas dez ilhas de Cabo Verde, onde as estradas, as poucas que existem, são complicadas.

O solo das ilhas é basáltico. A cor ocre é dada pelo óxido de ferro: «Algumas ilhas são tão antigas que tinham relevo e agora são planas devido à erosão».

A paisagem típica de diversas ilhas é território deserto, quase destituído de vegetação. Para isso contribuem os anos coxos do seu clima, com uma estação seca garantida e nem sempre uma estação das chuvas capaz de dar um ar de sua graça.

Os registos novecentistas indicam que «os espécimes recolhidos há séculos terão vindo dos ilhéus Raso e Branco, e das proximidades da ilha de Santa Luzia».

No século XIX este gigante foi descrito pelos franceses «depois das suas invasões pilharem os exemplares de museu, em Lisboa, conservados em formol. Mais tarde, em França, alegavam não saber de onde teria saído aquilo». Quando Bocage, o conhecido naturalista luso, foi visitar o museu francês, este investigador achou que eram muito parecidos com os dele: «Os invasores devem ter pilhado parcialmente a colecção». E assim redescreveu o género e resolveu o enigma da proveniência deste sáurio.

Diga catorze

Muito próximas do lagarto extinto ainda há duas outras espécies do grupo dos escincídeos, do tamanho do nosso lagarto-de-água, a que em Cabo Verde chamam lagartixas: o *Mabuya vaillanti* e o *Mabuya spinalis*.

Ao todo, contam-se neste momento 14 espécies de répteis no arquipélago de Cabo Verde.

Com vista a um maior conhecimento da localização dessas populações Raquel Vasconcelos empreendeu uma investigação iniciada em 2006 durante a qual acumulou conhecimentos fundamentais para a gestão de áreas protegidas em Cabo Verde.

Num percurso geológico, foram vulcões os responsáveis pelo surgimento do arquipélago, a cerca de 450 quilómetros da costa ocidental africana. Mesmo assim, sem que houvesse uma terra firme a ligá-lo ao continente em qualquer altura — «o que permitiria a passagem de fauna» —, Cabo Verde ostenta muitos endemismos de terra firme, reunidos em osgas — *Tarentolas* e *Hemidactylus* — e escincídeos *Mabuya*. Não há serpentes.

«Na Macaronésia — Açores, Madeira, Canárias — este arquipélago soma o maior número de taxa (não de espécies), se contarmos com as subespécies», sublinha a bióloga.

Impõe-se uma pergunta: Cabo Verde é já um destino para o turismo de natureza?

«Creio que sim», diz Raquel Vasconcelos e continua: «Este arquipélago oferece aos visitantes desde praias fantásticas, onde desovam tartarugas marinhas, um vulcão com cerca de 3 mil metros de altura, répteis gigantes, até caminhadas de montanha em Santo Antão e São Tiago...». Enfim, «acho que Cabo Verde tem um potencial imenso».

Calcorrear caminhos

Raquel torce para que «o turista descubra este país não apenas pelas praias da ilha do Sal, mas que explore outras ilhas».

Não havendo bela sem senão, conclui: «Se

Escincídeo: *Mabuya vaillanti*

Osga, *Hemidactylus lopezjuradoi*: uma espécie nova descoberta entretanto

Escincídeo: as dunas são um mundo em Cabo Verde

o turismo se tornar massificado destrói. São ecossistemas frágeis: «A pressão de cem turistas já faz uma diferença enorme, é preciso saber gerir isso».

Para Raquel Vasconcelos, cada período de trabalho de campo tinha um procedimento habitual: «Percorri 10% do território e recolhia amostras da cauda para fazer análises genéticas». Não é um problema para os animais: «a cauda volta a crescer». Para dizer quem é quem neste grupo de seres vivos não basta olhar: «Podem parecer uma mesma espécie e não o serem».

Foi assim que «o nosso grupo descobriu uma nova espécie em Cabo Verde, na ilha do Fogo: *Hemidactylus lopezjuradoi*».

Interessava um conhecimento geral: «Marcamos no GPS cada recolha e, com o sistema de informação geográfica, registamos o que existe e onde existe. Tirando a excepção do *Macroscincus coctei* não há quase estudos ecológicos».

Uma das metas da pesquisa empreendida consiste em apurar as razões que explicam a existência «desta e daquela espécie aqui e ali. Interessa-lhes depois estabelecer as coordenadas de como conservar».

Estes dados são vitais para a optimização da futura rede de 46 áreas protegidas, nem todas para protecção de fauna e flora», já que há inegáveis pontos de interesse geológico.

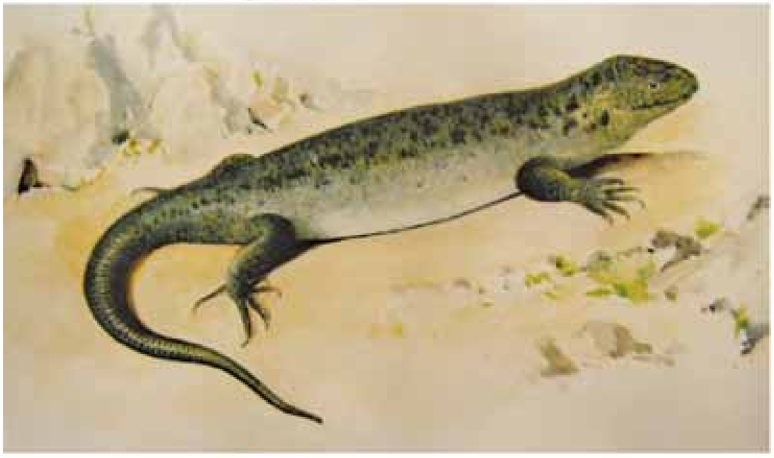
Estas espécies são únicas no mundo: «Algumas restringem-se a um ilhéu de 7 quilómetros quadrados», pelo que «valorizam o património cabo-verdiano e podem até promover o turismo de natureza». Pode ser uma fonte de riqueza e de biodiversidade.

«Todas as espécies nativas são endémicas em Cabo Verde mas, por mão do homem ou não, chegaram ali outras espécies, em especial duas outras osgas que são invasoras».

Um dado já se evidencia: «Na ilha da Boavista onde estão umas não estão outras». Isso quer dizer alguma coisa, até porque estas osgas exóticas «já extinguiram outras espécies noutros lugares do mundo».

Tais répteis, para além de poderem vir a ser «matéria-prima de algum medicamento, são matéria de estudos biomecânicos: as osgas conseguem subir vidro»! Quanto mais se estuda mais recursos se tornam disponíveis, «na engenharia, alta competição desportiva, etc. Daí podem resultar conhecimentos viáveis para aplicação em estruturas para uma bio-engenharia, feita pelo homem».

Macroscincus coctei em aguarela de Silva Lino



Sobre o apoio recebido os elogios abundam: «O povo cabo-verdiano foi fora de série. Pela simpatia e inclusive porque os meninos são caçadores natos». Ensinaram a Raquel técnicas para capturar répteis que desconhecia: «Por exemplo, há uma com um grão de catchupa, um prato tradicional à base de milho. Enlaçam o grão» como isco «e a fome é tanta que os escincídeos acabam por sair do muro em que se escondem».

Há outra, menos convencional, mas mais prática e de nenhuma maneira menos eficaz: «Também os capturam com cuspo. Cospem à saída dos buracos dos muros em que se escondem as lagartixas — como eles chamam aos *Mabuya* — e estes acabam por sair para beber».

Dos répteis que acabamos de referir «não sentem medo. Mas têm bastante repugnância das osgas! Dizem que se tocarmos numa osga podemos ficar pelados. Há vários mitos, diferentes em cada ilha».

Receiam tocar-lhes: «Quando os meninos me viam em trabalho de campo, fazia sempre questão de perder uns minutinhos a explicar-lhes que aquela espécie de réptil é exclusiva das suas ilhas, única no mundo, que era mais cabo-verdiana do que eles, que já estavam lá antes deles, que era preciso respeitar estes animais». Uma das coisas que fazia era tocar na osga e desafiá-los a fazer o mesmo.

Depois, «como sou menina, eles tinham de se mostrar valentes».

Num país com tão poucos recursos naturais como Cabo Verde, «vale a pena apostar na conservação do recurso mais valioso do arquipélago: a biodiversidade».

Fotos: **Raquel Vasconcelos** Texto: **Jorge Gomes**

Parques e Vida Selvagem Primavera 2009

APPENDIX III
Santa Luzia – uma Reserva Integralmente Em Perigo

Raquel Vasconcelos[1,2], Miguel Fonseca[1] e Samir Martins[3]

[1] CIBIO-UP – Centro de Investigação em Biodiversidade e Recursos Genéticos da Universidade do Porto

[2] UB – Universidade de Barcelona

[3] ISECMAR – Instituto Superior de Engenharias e Ciências do Mar de Cabo Verde

Entrevistámos uns pescadores amigos de Salamansa que costumam ir para a costa de Santa Luzia e constatámos que nesta Reserva Integral existe uma forte e preocupante expansão de uma população de predadores introduzidos - gatos.

Segundo as nossas fontes, que lá estão a pescar durante a semana, existem possivelmente 50 gatos na ilha! De facto inúmeros esqueletos e dejectos de gato são encontrados por toda a ilha, mesmo nos picos mais altos. Tudo terá começado com um par de gatos trazidos por um pastor para controlar a população de micromamíferos (fatos) e depois a situação descontrolou-se. Com alimento abundante, uma vez que os pescadores lhes deixam os restos do jantar, pois afeiçoaram-se a estas criaturas que os acompanham no silêncio das noites, e as (ainda) muitas aves e répteis endémicos para caçar, o número de gatos cresceu exponencialmente. De facto, estudos de Mateo *et al.* (2005) revelaram que dois terços da alimentação destes animais nocturnos são répteis! Podem até ser responsáveis pela extinção do endémico lagarto gigante de Cabo Verde (*Macroscincus cotei*), pois há evidências de predação pelos gatos sobre esta espécie, única a nível mundial. E pelo mesmo caminho podem ir as também endémicas osgas de Cabo Verde (*Hemidactylus bouvieri razoensis* - já em perigo crítico - e a *Tarentola caboverdiana raziana*) e ainda a lagartixa (*Mabuya strangeri*) (Schleich, 1996); já para não falar nas aves, como o guincho (*Pandion haliaetus* - Raro) (Hazevoet, 1996) que constrói os ninhos em pequenos cumes, tornando os ovos bastante acessível aos gatos.

Não basta classificar, há que fiscalizar e desenvolver um plano de gestão da biodiversidade e ecossistemas das áreas protegidas. Assim, é urgente a remoção rápida e total dos gatos em Santa Luzia de modo a garantir a salvaguarda dos restantes endemismos cabo-verdianos presentes nesta magnífica área natural protegida. Aproveitamos para sugerir aos estudantes dos Institutos, que possuem uma importante e delicada mão-de obra voluntária, um "djunta mon".

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APPENDIX IV
Environmental Impact Assessment of the S. Vicente Wind Farm on the *Tarentola caboverdiana substituta* gecko – Final report

R. Vasconcelos[1,2,3], S. Rocha[1,2,4] & D.J. Harris[1,2]

[1] CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos,
Campus Agrário de Vairão, 4485-661 Vairão, Portugal.

[2] Departamento de Zoologia e Antropologia, Faculdade de Ciências da Universidade do Porto,
Pr. Gomes Teixeira, 4099-002 Porto, Portugal.

[3] Institute of Evolutionary Biology (CSIC-UPF) CMIMA,
Passeig Marítim de la Barceloneta, 37-49 E-08003 Barcelona, Spain

[4] Departamento de Bioquímica, Genética e Inmunología Facultad de Biología,
Universitad de Vigo, Vigo, 36310, Spain.

Study supported by InfraCo

CONTENTS

ABSTRACT

Following the study conducted in 2009 for InfraCo it became evident that there is a need for evaluation of the population densities of the *Tarentola caboverdiana substituta* gecko in S. Vicente, essential for evaluation of population tendencies through the years, and to implement the correct management of the species. So, this study aimed to estimate the density of the species in number of individuals and in biomass in different habitats in S. Vicente and Santo Antão, where a different subspecies occurs; to study its distribution, identifying the habitats where it is found, calculating its extent of occurrence and area of occupancy and predicting its probability of occurrence in S. Vicente; and to provide an instrument to inform and educate in relation to the biodiversity of the Cape Verdes in general, including endemic reptiles like the targeted gecko.

Forty-five quadrates of 10x10m stratified by habitats were sampled and each observation was recorded with GPS. Using that data, a Geographic Information System, bibliographic records and a maximum entropy algorithm those objectives were fulfilled.

We found that the studied gecko, weights between one to eight grams, males being significantly heavier than females, which is another evidence of sexual dimorphism of the species. We also confirmed that the most common habitats on the island are very arid areas, occupying more than a half of the cover area of the island. Regarding the density study, in average 2.8±3.8 animals with a biomass of 12.8±21.1 g were found in each quadrate in S. Vicente. In Santo Antão, these values drop to 0.4±0.9 animals with a biomass of 2.3±3.5 g per 10 m^2. One reason that might explain this is that Santo Antão is much more mountainous and humid, habitat that the species seems to avoid, and with a more widespread sympatric skink than S. Vicente, that can compete with the same resources. Indeed, the highest densities and biomasses were registered on very arid habitats, which are also the most common habitats on the island. This explains the high values of extent of occurrence and area of occupancy observed. Thus, *Tarentola caboverdiana* has a high probability of occurrence all over S. Vicente Island. In this way, presently the species has no conservation concern with respect to the habitat. However, it is important to continually monitor the population tendencies of the species in the future to ensure the conservation of this endemic gecko.

Finally, we consider that the documentary possibly will be a valuable instrument on environmental education campaigns to inform the Cape Verdean citizens about its biodiversity, including reptiles.

INTRODUCTION

The Cape Verde wall gecko is a Cape Verdean endemic species with an endemic subspecies *Tarentola caboverdiana substituta* (Joger 1984) found in the island of São Vicente. It is classified as Data Deficient (DD) on the national red list, meaning that there is deficient information on this particular gecko (Schleich 1996). Following the study conducted in 2008 for InfraCo, for which information was collected concerning thermal biology, refuge selection (Vasconcelos *et al.* in preparation) and diet (Vasconcelos *et al.* 2009), it became evident that there is a need for evaluation of the population densities of the gecko in S. Vicente. Due to the fact that there is a complete lack of reference values prior to construction of the wind farm, it would only be possible to monitor the trends of the population along the years if this study was conducted.

It is known that islands generally present higher densities of reptiles than adjacent continental areas with comparable habitat, due to the reduced number of predators, lower levels of interspecific competition and higher productivity of insects (Soulé 1966; Case 1975), especially in remote insular areas. However, insular ecosystems are more fragile and its species are more vulnerable to extinction (Whittaker 2007). Thus, fundamental studies, such as estimating densities of endemic species, extent of occurrence and area of occupancy are essential for evaluation of population tendencies through the years, which is one of the IUCN criteria to evaluate the conservation status of species (IUCN SPWG 2008), and to implement the correct management of the species.

Although *Tarentola caboverdiana substituta* subspecies only occurs on S. Vicente, it is important to keep in mind that most of conservation studies and measures are applied at the species level because they are the recognisable units whose loss can be quantified, but more importantly because the public can relate to species in a more direct way (Pullin 2002). In this way, information regarding other *Tarentola caboverdiana* subspecies, as the one occurring in S. Antão, is essential to better understand the data deficient population of S. Vicente.

Objectives

Density study

This study aimed to count the number of *Tarentola caboverdiana substituta* individuals and their biomass per area in different sites. Based on these counts, the density of the species in S. Vicente's population was estimated and will be used as reference value for future monitoring studies of the population tendencies of the subspecies. The study also aimed to count geckos and measure their biomass in Santo Antão, and hence estimate the density of a different subspecies of the same species, *Tarentola caboverdiana caboverdiana*, occurring in a neighbour island. This sampling was important as conservation actions are generally implemented at species level. It allowed us, using the same methodology as for the target subspecies, on the same type of habitats that exist on S. Vicente, to obtain comparative figures for the density of the species in both islands. This allowed us to consider other factors (such as interspecific interactions, etc.) than the ones intrinsic to the species affecting the species. So, the research questions were:

Which are the densities (in number of individuals and biomass) of the species in S. Vicente?
Are these densities similar in Santo Antão areas with similar habitat types to S. Vicente?

Distribution study

This study was aimed at identifying the habitats where the target subspecies is found in order to predict the probability of occurrence of this gecko in S. Vicente. With this analysis it was possible to calculate the extent of occurrence and area of occupancy of the subspecies in the island. These figures were used to revaluate the conservation status that for now is considered Data Deficient. It also allowed us to identify the most important habitats and topographic condition to the species occurrence and to predict its occurrence. So, the research questions were:

In which habitats can we find *T. caboverdiana* in S. Vicente?
Which is its extent of occurrence and area of occupancy of the species in S. Vicente?
What is the probability of occurrence of the species in all S. Vicente?
Can we revaluate its conservation status with this data?

Documentary film

This film intended to inform and educate in relation to the environmental problems affecting endemic reptiles in Cape Verde, mainly in S. Vicente Island, and report the actions implemented to protect them. This film aimed to increase the awareness to the conservation of biodiversity, especially of children and adolescents. This documentary might be divulgated in schools and be used as an environmental education tool for teachers.

METHODOLOGY

Study Object

Tarentola caboverdiana substituta was almost always the only reptile present in the study area, as *Chioninia stangeri* is restricted to more humid and agricultured areas (Vasconcelos unpublished data). This is a flattened, robust gecko (Fig. A.IV.1) with a long tail and a delicate head with relatively long, sharpen snout, which attains 60 mm snout-vent length, SVL (see Joger 1984 for a full morphological description). Based on the measurements taken during the past study displaying a bimodal distribution, individuals smaller than 45 mm SVL were considered juveniles, as they also lacked sexual secondary characters (ovarian follicles seen by transparency in females, developed hemipeneal bags in males).

Figure A.IV.1 Dorsal (**A**) and lateral (**B**) view of the endemic gecko subspecies of S. Vicente Island, *Tarentola caboverdiana substituta.*

Study Area

The study area was all S. Vicente Island, and parts of S. Antão Island which present similar habitats to S. Vicente (Fig. A.IV.2). The São Vicente and Santo Antão Islands belong to the windward island group of Cape Verde Republic (Fig. A.III.2).

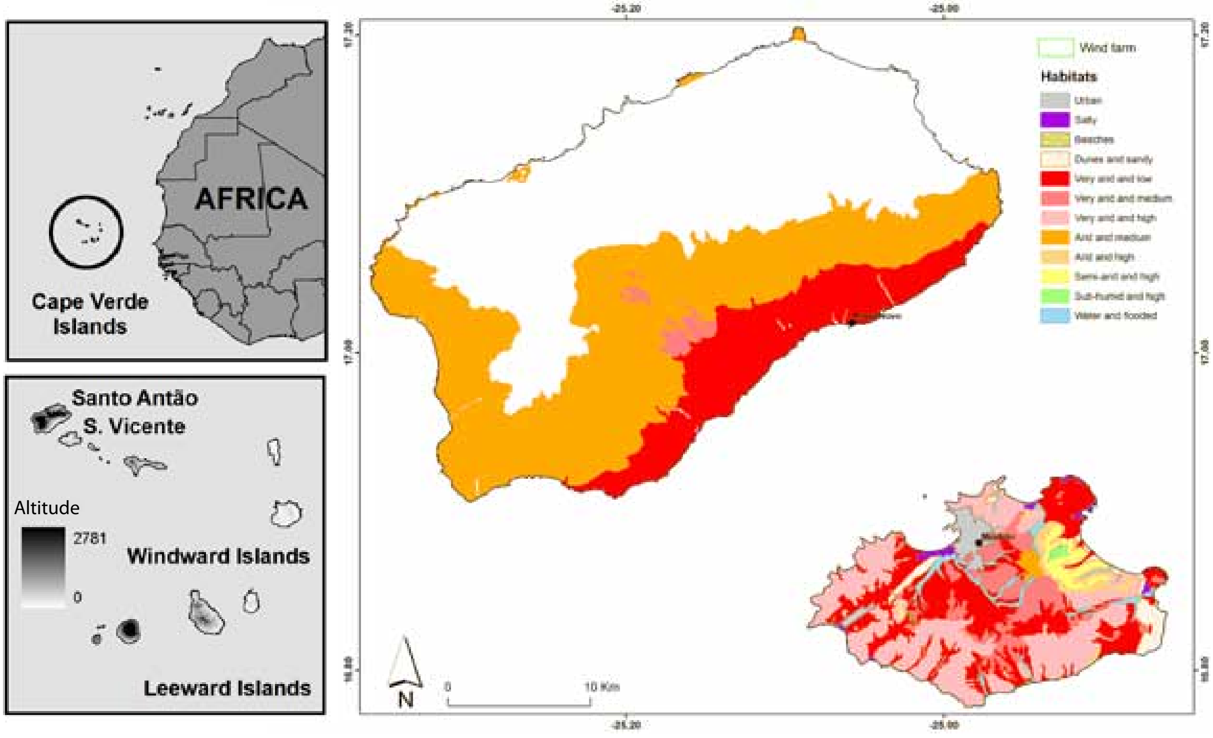

Figure A.IV.2 Location of the study area (in decimal degrees) with representation of the different habitats found on S. Vicente and the most similar ones to S. Vicente in Santo Antão.

In S. Vicente, total annual precipitation is between 63 and 274 mm (mean=113±41 mm), 0 mm in the driest month and 37 to 103 mm in the wettest month, (mean=57±14 mm). The annual mean temperature is between 20.0 and 24.5°C (mean=23.0±0.8°C), ranging only in 8.1 to 8.7°C (mean=8.3±1.0°C) throughout the year due to the moderating influence of the Atlantic Ocean, with temperatures on the warmest month ranging from 24.4 to 28.6°C (mean=27.2±0.8°C) and on the coolest from 15.7 to 20.4°C (mean=18.9±0.8°C) (Hijmans *et al.* 2005). It is a volcanic island with the landscape dominated by stony plains, sandy dunes and barren hills. Apart from the summit of "Monte Verde" (774 m), the island is very dry and with very scarce vegetation (Fig. A.IV.3), although in recent years, considerable areas have been afforested with exotic *Prosopis juliflora* trees.

Figure A.IV.3 General view of the study area showing dry and with very scarce vegetation.

Density study

Sampling in S. Vicente

Sampling sites were randomly chosen stratified by habitats, with 40 replicates all over the island, including around the construction site (Fig. A.IV.4). Quadrates of 10x10 meters were used to count all the geckos as well as small, medium and large rocks present (Fig. A.IV.5.A). Counts had variable limits of time and were terminated when all geckos' refuges were checked. All animals were put on tissue bags during counts to avoid double counts. All geckos were measured (Fig. A.IV.5.B), weighted, sexed and photographed. The individuals were manipulated for the least possible time period and freed in the same location that they were captured. In this way, necessary data for calculating mean densities per habitat (in frequency and biomass) of each class of geckos (juveniles, adult males and adult females) was collected.

Attainment of cross reference values in Santo Antão

The choice of five sampling sites in Santo Antão that have similar habitats as those existing in S. Vicente (see Fig. A.IV.2) was made based on agro-ecological and vegetation zoning maps (Diniz & Matos 1994, 1999). The same methodology as referred on section 2.3.1. was followed. Due to time constrains, sampling was less focused on this non-target subspecies.

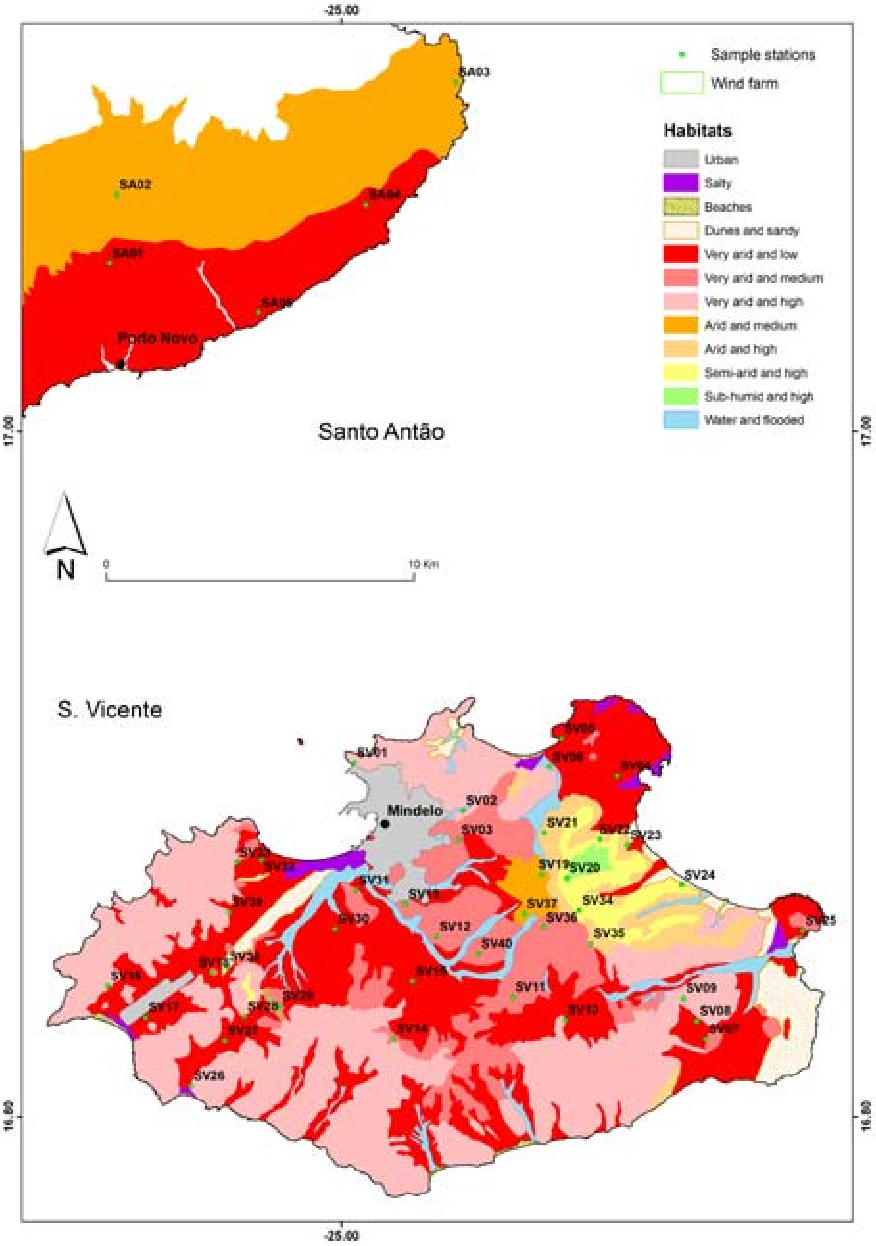

Figure A.IV.4 Location of the placement of the 10x10 meters quadrates used to calculate geckos densities.

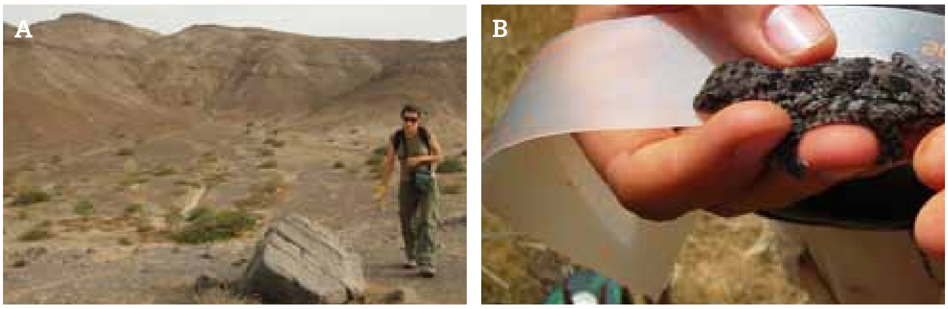

Figure A.IV.5 A) Sampling in S. Vicente. **B)** Measuring SVL of a gecko.

Distribution study

Habitats of occurrence

During counts referred to in point 2, the habitats in which the species occurs were noted by recording the GPS coordinates of each site in which they were observed. This information was overlapped with maps of habitats of S. Vicente in a Geographic Information System (GIS) software which allowed us to detect the habitats where occurrence was more frequently registered in the island. By comparing the mean densities of the geckos found on each habitat type with the total area of the habitat it was possible to determine in which extent each habitat is important for the occurrence of the subspecies.

Extent of occurrence and area of occupancy

Using the Arcmap 9.3 software and bibliographic records of the subspecies, including the ones recently published by our research team (Jesus *et al.* 2002; Vasconcelos *et al.* 2010), together with the records resulting from this study, the extent of occurrence, EOO, was calculated, using the minimum convex polygon method (EOO = imaginary boundary which encompass all the occurrences), and the area of occupancy, AOO (AOO = nr occupied cells × area of an individual cell, 1x1 Km^2) of this gecko in S. Vicente.

Ecological modelling

Based on the presence records resulting from this study and bibliographic records, together with several topographic and climatic variables (altitude, slope, distances to each habitat type) a probability map of occurrence of the subspecies in S. Vicente was obtained using the maximum entropy principle, implemented in Maxent software (Phillips *et al.* 2006). In this way, it was possible to identify areas of high and low probability of occurrence of the species in S. Vicente. The analyses were developed using a grid cell size of 225m. Models were trained using 36 observations (localities), collected from bibliographic data and data collected during the long term research on the island (from 2006 until the present). Model fit was assessed using nine independent observations and the area under the curve (AUC) of a receiver-operating characteristics curve (Liu *et al.* 2005).

Documentary film

Threats to the herpetofauna and implemented actions

Several interviews were conducted (Fig. A.IV.6) with representatives of different environmental government agencies, such as in Santiago to Sónia Araújo, responsible for the Biodiversity section on the General Direction of Environment (DGA); to the botanical engineer Samuel Gomes, the biologists Aline Rendall and Isildo Gomes from the National Institute for Agrarian Investigation and Development (INIDA); João Mascarenhas, Director of the 'Serra da Malagueta' Natural Park and, in S. Vicente, to the head of the program on conservation of turtles, Sandra Merino from the National Institute for Fishery Development (INDP).

Also, in S. Vicente a professor at the University of Cape Verde (UniCV), Rui Freitas and his student Evandro Lopes were interviewed. The interviews approached the major problems that affect endemic fauna, focusing also on reptiles, and the implemented actions currently underway aimed at protecting biodiversity.

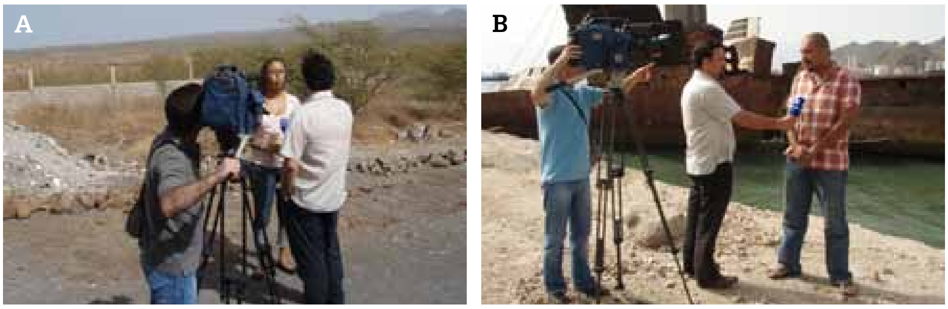

Figure A.IV.6 Interviews conducted to representatives of different environmental government agencies and members of the University of Cape Verde in Santiago and S. Vicente.

Research in Herpetology

The target species were filmed as well as the habitats in which it occurs. There was also an attempt at focusing on the sampling techniques and the research work being developed on the Cape Verdean endemic reptiles by interviewing the scientist that are currently studying them.

Local perspective

Testimonials from local people about biodiversity in general and reptiles in particular were gathered, including about fears and myths related with geckos.

RESULTS

Study Object

A total of 113 were observed, 110 geckos were collected (three animals were just seen and not measured). Of those, 75 were adults and 35 were non-adults (juveniles and sub adults), that will be referred to as juveniles hereinafter. The size of the animals (SVL) varied between 24 to 61mm, similarly to the variation on the latter report, and their weight between 1 and 8 grams (Table A.IV.1 and Fig. A.IV.7.A).

Table A.IV.1 Sample size (*n*), average, minimum, maximum, standard deviation (SD) of the snout-vent length and weight for adults and juvenile geckos.

	AGE	*n*	Average	Minimum	Maximum	SD
SVL (mm)	Adults	75	52.5	45.0	61.0	4.1
	Juveniles	35	28.4	24.0	44.0	4.6
Weight (g)	Adults	75	6.0	4.0	8.0	1.2
	Juveniles	35	2.0	1.0	4.0	0.5

There were significant differences between the biomass of juveniles and adults. Regarding to adults, males were significantly heavier than females, although their weight ranges were identical (Mann-Whitney Test, U= 374, *p*= 0.00045; Fig. A.IV.7.B).

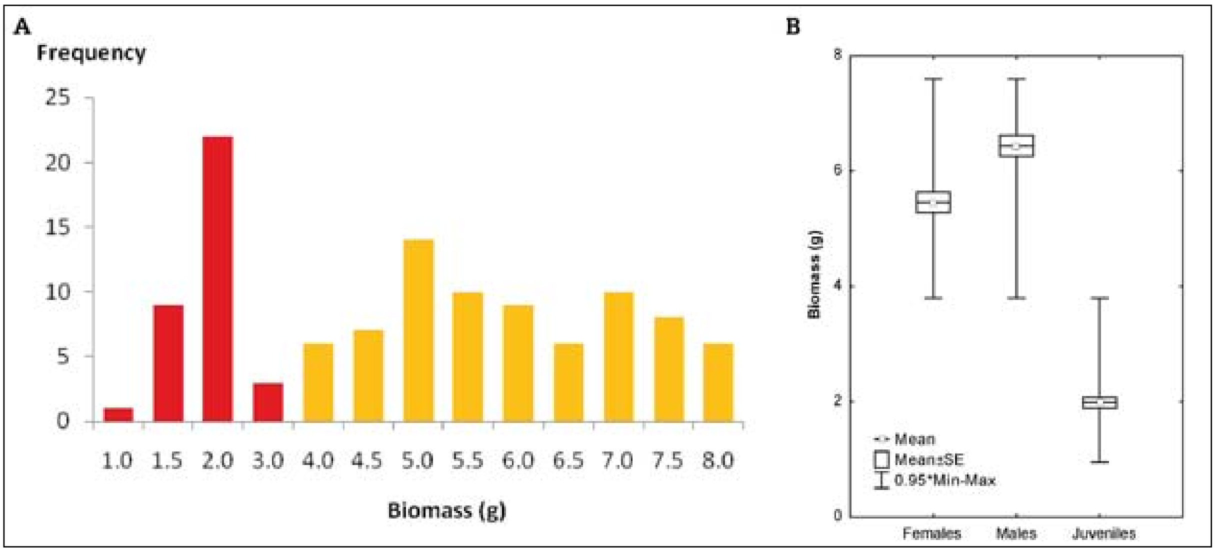

Figure A.IV.7 **A)** Frequencies for each weight class of adult (orange) and juvenile (red) geckos. **B)** Biomass differences between adult males, adult females and juveniles.

Study Area

After sampling 40 10x10 m quadrates for assessing the density and distribution patterns of *Tarentola caboverdiana*, we concluded that the presence of big loose rocks is very low along S. Vicente Island. Small rocks are much more abundant, covering most frequently more than 25 to 50% per m^2 of the soil (Table A.IV. 2).

Table A.IV.2 Refuge availability for geckos with average percentage of cover, minimum, maximum and standard deviation of smalls, medium and big rocks found along the 40 sampled 10x10 m quadrates.

REFUGE	Small rocks cover	Medium rocks	Big rocks
Average % cover per $10m^2$	25-50	13	2
Minimum	0-25	0	0
Maximum	75-100	48	6
SD		12	2

The habitats on S. Vicente presented very different areas and percentages of cover (Table A.IV.3) being the most common the very arid areas (see Fig. A.IV.4). Beaches and salty areas were not sampled based on bibliographic literature that mentions that geckos are absent from such habitats (Schleich 1987).

Density study

Regarding the density study, it seems that *T. caboverdiana* might be more abundant in S. Vicente than in Santo Antão, where only two individuals were found on five sampled stations. We discuss those potential differences in densities latter on.

Sampling in S. Vicente

A maximum of 21 animals and 118 grams of biomass were sampled per 10 m2 (Table A.IV.4), although densities per quadrate, measure either in terms of number of individual or in biomass, seem to follow an inverse exponential distribution (Fig. A.IV.8) and thus this high values are not frequent. We found similar numbers and weights of adult males, adult females and juveniles in total and per quadrate, although age classes present differences in biomass (Table A.IV.4).

Table A.IV.3 Total area (in squared meters) and percentage of cover of each habitat registered in S. Vicente Island. The grey coloured ones were not sampled (see above for details).

HABITAT	Area (km^2)	Cover %
Arid and hilly areas	2.5	1.1
Arid and mountain areas	8.9	4.0
Dunes and sandy areas	9.3	4.1
Semi-arid and mountain areas	6.7	3.0
Sub-humid and mountain areas	1.0	0.4
Very arid and hilly areas	29.9	13.2
Very arid and mountain areas	80.7	35.8
Very arid flat areas	72.3	32.1
Water lines and floodplains	11.2	5.0
Beaches	0.5	0.2
Salty areas	2.4	1.1
Total	225.4	100

Although we found many quadrates with no geckos (Fig. A.III.9), generally 3 animals were found in each quadrate, corresponding to around 13 grams of biomass (Table A.III.4).

Table A.III.4 Results of the average, maximum, minimum number (Nr) and biomass (g) of males, females, juveniles and total geckos found in the 40 quadrates in S. Vicente.

	Males		Females		Juveniles		Total	
	Nr	Biomass	Nr	Biomass	Nr	Biomass	Nr	Biomass
Average	2.2	14.4	2.3	13.0	1.8	3.4	2.8	12.8
Minimum	1.0	4.0	1.0	4.5	1.0	1.5	0.0	0.0
Maximum	10.0	66.5	9.0	47.5	7.0	13.5	21.0	118.0
SD	2.3	15.5	2.0	11.1	1.4	2.7	3.8	21.1
Total	38.0	244.5	36.0	195.5	37.0	71.5	111.0	511.5

Attainment of cross reference values in Santo Antão

Only two adult animals were observed on the five stations sampled, on an arid and hilly habitat. Only one female was captured, with SVL of 54 mm and 7.5 g of weight. The other individual was just seen and its weight was estimated based on the average weight of the species. In this way, Santo Antão presented in this preliminary study 0.4±0.9 animals with a biomass of 2.3±3.5 g per quadrate.

Distribution study

Habitats of occurrence

Animals were recorded on all sampled habitats except on sub-humid and mountain areas. The highest observed abundances and biomasses were recorded on very arid areas, on hilly and mountain areas for both adult and juveniles (Table A.IV.5).

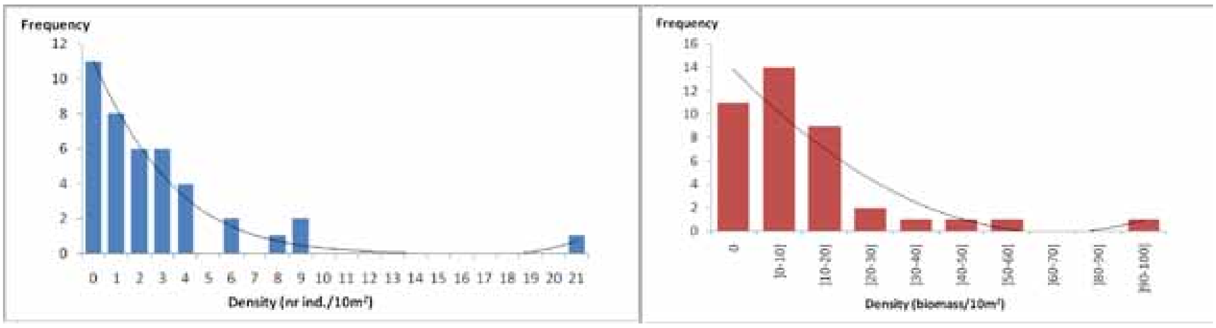

Figure A.IV.8 Frequency of densities of geckos found per sampling quadrate counted in number of individuals (nr ind.) and biomass (g) per quadrate (see methods for more details).

Extent of occurrence and area of occupancy

The calculated extent of occurrence (EOO) of *Tarentola caboverdiana substituta* in S. Vicente Island is 150.84 km^2 and the area of occupancy (AOO) 45 km^2. The area of the island is 225.4 km2, so its EOO and AOO is around 67% and 20% of S. Vicente's area, respectively.

Ecological modelling

The ecological models developed with Maxent were robust (mean AUC = 0.991 and 0.982 for the training and testing observations, respectively). The correct classification rate of all observations (N=45) was 82.3%, further suggesting a high model fit. Areas of high probability of occurrence for the species (Fig. A.IV.9) were widespread throughout the island with the exception of 'Monte Cara', the eastern (between 'Calhau' and 'Baía das Gatas') and south-eastern regions (around 'Palha Carga').

Documentary film

Seven themes approached about the biodiversity of Cape Verde and the actions taken by governmental agencies to protect it are available on the DVD attached to this document (Fig. A.IV.10). These focus on the reptiles, birds, marine turtles, flora, marine biology, costal fauna and protected areas.

CONCLUSIONS

The studied gecko, *Tarentola caboverdiana substituta*, presented weights between one to eight grams. As expected, differences in weight were observed between age classes mainly due to significant size differences. In addition, differences in weight between sexes in adults were also recorded, being males significantly heavier than females. This, together with differences in snout-vent lengths (Vasconcelos *et al.* 2009), is another evidence of sexual dimorphism of the species.

In relation to the study area we have concluded that, similarly to the wind farm area, the presence of big loose rocks is very low along S. Vicente Island and small rocks are much more abundant (Vasconcelos *et al.* 2009). This means that, based on the previous study, intra-specific competition for refuge is high all over the island, due to the high abundance of the species, as only medium rocks seem to have optimal thermal conditions (Vasconcelos *et al.* 2009).

Table A.IV.5 Relative average (avg), minimum (min), maximum (max) and sum of number (Nr) and biomass (g) of adult and juvenile geckos found on each habitat. *n*= number of sampled stations.

			HABITATS								
			Arid & hilly	Arid & mountain	Dunes & sandy	Semi-arid & mountain	Sub-humid & mountain	Very arid & hilly	Very arid & mountain	Very arid & flat	Water lines & flooded
		n	2	3	1	3	1	11	8	10	1
Adults	Avg	Nr	3	1	2	2	0	3	1	1	2
		Biomass	18.5	7.2	13.5	13.2	0	3.3	20.4	7.7	9.5
	Min	Nr	0	0	2	2	0	0	1	0	2
		Biomass	0	0	13.5	11.5	0	0	0	0	9.5
	Max	Nr	6	3	2	2	0	19	4	3	2
		Biomass	37	15	13.5	16.5	0	16.5	114	21	9.5
	Sum	Nr	6	4	2	6	0	38	11	6	2
		Biomass	37	21.5	13.5	39.5	0	33	225	61.5	9.5
Juveniles	Avg	Nr	0	1	1	1	0	1	1	1	2
		Biomass	0	2.7	1.5	1.2	0	1.9	2.1	1.6	4
	Min	Nr	0	0	1	1	0	0	1	0	2
		Biomass	0	0	1.5	0	0	0	0	0	4
	Max	Nr	0	2	1	1	0	3	2	7	2
		Biomass	0	4	1.5	2	0	13.5	6	4	4
	Sum	Nr	0	2	1	2	0	11	7	11	2
		Biomass	0.0	8.0	1.5	3.5	0.0	18.5	23.0	13.0	4.0
Total	Avg	Nr	3	2	3	3	0	4	2	2	4
		Biomass	18.5	9.8	15	14.3	0	5.2	22.5	9.3	13.5
	Min	Nr	0	1	3	3	0	0	2	0	4
		Biomass	0	4	15	13	0	0	0	0	13.5
	Max	Nr	6	3	3	3	0	21	6	9	4
		Biomass	37	19	15	16.5	0	26	118	23.5	13.5
	Sum	Nr	6	6	3	8	0	49	18	17	4
		g	37.0	29.5	15.0	43.0	0.0	51.5	247.5	74.5	13.5

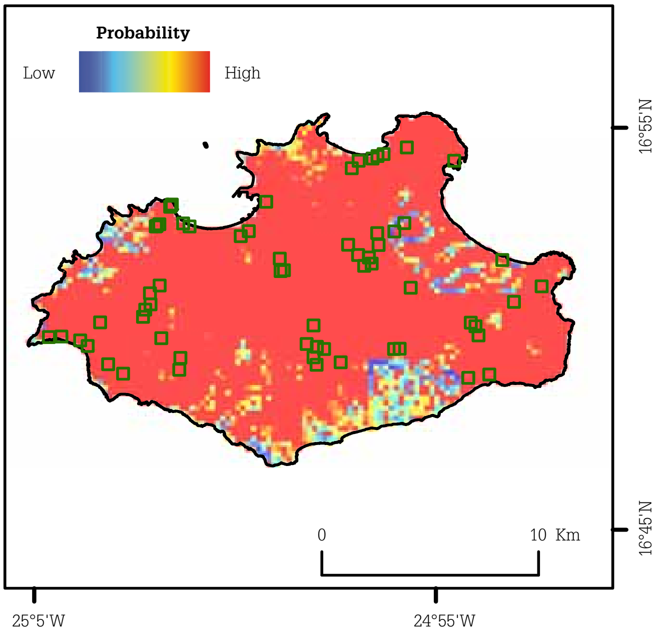

Figure A.IV.9 Map of probabilities of occurrence of *Tarentola caboverdiana substituta* in S. Vicente based on current and bibliographic data.

Figure A.IV.10 DVD cover of the documentary.

Furthermore, we can concluded that the most common habitats on the island are very arid areas, especially high and flat, occupying more than a third of the cover area of the island each.

Regarding the density study, in average 2.8±3.8 animals with a biomass of 12.8±21.1 g were found in each quadrate in S. Vicente. The number of animals per meter is high, as already suggested by other authors (Schleich 1987). These reference values are the first ones for the species and should be monitored intermittently in the future in order to detect fluctuations on population size to adequately protect this endemic species. These values could be underestimated since they were attained during the dry season. In Santo Antão, these values drop to 0.4±0.9 animals with a biomass of 2.3±3.5 g per quadrate. Nevertheless the small sample size of quadrates in this latter island, this value is an indicator that the density of the species might be lower on Santo Antão. However, further studies are needed, with bigger sampling, to assure this.

One reason that might explain why *T. caboverdiana* might be more abundant in S. Vicente than in all Santo Antão is that Santo Antão is much more mountainous and humid than S. Vicente as it is clear by the ecological model that the species avoids high altitude and humid areas. However, when sampled in similar habitat and topographical conditions, densities were also lower in Santo Antão. Thus, another factor involved can be inter-specific competition. In Santo Antão, the occurrence of sympatric skinks is widespread, whereas in S. Vicente it is restricted to the east side of the island, around 'Calhau' (Vasconcelos personal observation).

About the habitats of occurrence, animals were recorded on all sampled habitats except on sub-humid and mountain areas, indicating that the species might avoid this habitat. The highest densities and biomasses were registered on very arid habitats, especially in high and medium altitudes, that are also the most common habitats on the island. This explains the high values of extent of occurrence and area of occupancy observed, considering the area of the island. This indicates that the species is locally very abundant on a very wide area. Thus, the map obtain with ecological modeling shows that *Tarentola caboverdiana* has a high probability of occurrence all over S. Vicente Island with almost all habitats being favourable to the occurrence of the subspecies. The only exceptions are areas corresponding to high elevations, as "Monte Cara", "Palha Carga" and the east slope of "Monte Verde regions. It is interesting to notice that this latter region is also the only area of occurrence of the *Chioninia stangeri* skink (Vasconcelos, personal observation). This fact emphasizes again the probable importance of inter-specific competition explaining the distribution and abundance of the species.

In this way, we consider, based on its extent of occurrence, area of occupancy and estimated number of mature animals that the species has presently no conservation concern with respect to the habitat, following IUCN guidelines and criteria (IUCN SPWG 2008). However, it is important to continually monitor the population tendencies of the species in the future to ensure that these values keep favorable to the conservation of this endemic gecko in S. Vicente.

Finally, we consider that the documentary possibly will be a valuable instrument on environmental education campaigns to inform the Cape Verdean citizens about the threats to biodiversity, including reptiles, and which actions are currently being implemented. Its divulgation will certainly increase the awareness about this thematic in general and also about this endemic gecko.

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APPENDIX V

High temperatures constrain microhabitat selection and activity patterns of the insular Cape Verde wall gecko

R. Vasconcelos[1,2,3], X. Santos[4], M.A. Carretero[1]

[1] CIBIO-UP, Centro de Investigação em Biodiversidade e Recursos Genéticos,
Campus Agrário de Vairão, R. Padre Armando Quintas, 7, 4485-661 Vairão, Portugal.

[2] Departamento de Biologia, Faculdade de Ciências da Universidade do Porto,
R. Campo Alegre, s/n, 4169-007 Porto, Portugal.

[3] Institute of Evolutionary Biology (CSIC-UPF),
Passeig Marítim de la Barceloneta 39-47; 08003 Barcelona, Spain.

[4] Departament de Biologia Animal, Universitat de Barcelona,
Av. Diagonal 645, E-08028 Barcelona, Spain.

ABSTRACT

The diel activity, microhabitat selection and thermobiology were investigated in *Tarentola caboverdiana substituta*, a gecko endemic to an arid Cape Verde island. Standardized 24-hour transects were performed recording the microhabitat availability and the body (Tb), soil, refuge, air temperatures, humidity, gecko category (juvenile/ adult male/ female) and activity status for each observation. Thermal conditions were monitored with data-loggers. The activity pattern was strictly nocturnal, as in deserts. All individuals selected rocks as diurnal refuges but adults used more medium-sized rocks (scarce) and juveniles small rocks (abundant). Such selection was mostly attributable to the refuges thermal properties: small rocks attained higher temperatures due to their lower thermal inertia. Geckos behaved as tigmotherms when active by night and as thermoconformers with the substrate by day. Nocturnal Tb did not differ between gecko categories or microhabitats. However, since juveniles selected small rocks, their diurnal Tb became higher, sometimes possibly risking overheating. Territoriality, scarcity of optimal refuges, high conspecific densities and lack of ground-predators may explain why juveniles use thermally suboptimal microhabitats. *Tarentola* sp. may be less adapted than other geckonids to arid conditions. However, ecological shifts (nocturnality, microhabitat selection) and lack of competitors allowed *T. caboverdiana substituta* to adapt to the archipelago's demanding conditions.

KEY WORDS

Activity, island, Macaronesia, microhabitat use, *Tarentola*, thermal biology

INTRODUCTION

As ectotherms, small lizards have their physiology constrained by the thermal environment, and behavioural thermoregulation is a response for ensuring maintenance and activity (Bartholomew 1982; Huey, 1982). Such responses usually consist of microhabitat selection but also basking and posturing (Huey and Slatkin 1976). Thermal requirements may, however, conflict with foraging, defence against predators/competitors, reproduction and social relationships (Huey 1982; Huey and Slatkin 1976). Hence, thermoregulatory patterns result from a trade-off between these forces. Cyclical environmental changes, together with variation in body condition and endogenous rhythms, promote temporal and ontogenic shifts in lizard thermoregulation (Underwood 1992).

Although most of the literature on these topics focuses on diurnal species, nocturnal lizards, especially geckonids (Kearney and Prevadec 2000), are gradually attracting more attention (Angilletta, Montgomery & Werner 1999; Angilletta & Werner, 1998; Autumn *et al.* 1999; Autumn, Ryan & Wake 2002; Brown 1996; Hitchcock & McBrayer 2006; Refinetti & Susalka 1997; Rock, Andrews & Cree 2000; Rock & Cree 2009; Rock, Cree & Andrews 2002). Compared to diurnal activity, nocturnality involves substantially different selective pressures, such as in locomotor performance (Autumn *et al.* 2002). In temperate climates, opportunities for heat gain during nocturnal activity are limited, and so availability of appropriate microhabitats plays a fundamental role for determining the activity period (Hitchcock & McBrayer 2006). On the other hand, selection of appropriate diurnal resting sites becomes equally crucial not only as shelters against predators but also as heat sources for the subsequent activity period (Angilletta *et al.* 1999; Huey *et al.* 1989a). In contrast, geckos inhabiting hot desserts may face opposite pressures, namely less thermal constraints during their nocturnal activity but extremely restrictive conditions for selecting a thermally safe site to survive inactive by day (Huey *et al.* 1989a).

Arid islands provide simple systems particularly useful for analysing relationships between microhabitat selection and thermal environment in geckos. In the absence of sympatric lizard species, scarcity of (terrestrial) predators, low but predictable food availability and structural simplicity of habitat (Brown 1996; Whittaker & Fernández--Palacios 2007), insular geckos are expected to select microhabitats mainly according to their thermal properties, excepting eventual intraspecific interactions (Downes & Shine 1998).

The São Vicente Island, (Cape Verde archipelago, NW Africa) is only inhabited by two endemic reptile species: a diurnal skink *Chioninia stangeri* (Gray, 1845), which is geographically restricted, and a nocturnal widespread gecko *Tarentola caboverdiana substituta* Joger, 1984. This gecko belongs to a specious genus, extensively distributed across North Africa and Southern Europe (Joger 1984a, 1984b; Joger & Bischoff 1983; Schleich, Kästle & Kabisch 1996), which has also colonised Cuba, the Bahamas and the Macaronesian archipelagos (Selvagens, Canaries and Cape Verdes) by means of transmarine dispersal (Carranza *et al.* 2000, 2002; Vasconcelos *et al.* 2010). According to phylogeographic studies, the relatively recent radiation of *Tarentola* in Cape Verde (7.73 My BP), in comparison to the origin of the genus (23 My), derives from a southwards colonisation from more temperate latitudes, the Canary Islands (Carranza *et al.* 2002; Vasconcelos *et al.* 2010).

Tarentola geckos, with their flattened bodies and adhesive pads, are excellent climbers on vertical surfaces and adapted to dry open habitats, including human-made structures (Arnold & Ovenden 2002). Although other species occur in Mediterranean and even in subtropical areas, those inhabiting Cape Verde have to face extremely high diurnal temperatures, irregular rainfalls and long drought periods characteristic of the Sahelian climate (Loban & Saucier 2007). Despite this, Cape Verdean *Tarentola* geckos are extremely abundant in comparison to their relatives in continental Africa and Europe (Schleich 1987).

Therefore, the aims of this study were 1) to identify patterns of activity and microhabitats selected by *Tarentola caboverdiana substituta*; 2) to infer to what extent such patterns are constrained by the thermal environment and 3) to discern if any of these patterns is affected by size or sex of the geckos.

MATERIALS AND METHODS

Study area

The São Vicente Island belongs to the windward island group of Cape Verde Republic (Fig. A.V.1.A). In S. Vicente, total annual precipitation is between 63 and 274 mm (mean±SE =113±41 mm), 0 mm in the driest month and 37 to 103 mm in the wettest month, (57±14 mm). The annual mean temperature is between 20.0 and 24.5°C (23.0±0.8°C), ranging only in 8.1 to 8.7°C (8.3±1.0°C) throughout the year due to the moderating influence of the Atlantic Ocean, with temperatures during the warmest month ranging from 24.4 to 28.6°C (27.2±0.8°C) and during the coolest from 15.7 to 20.4°C (18.9±0.8°C) (Hijmans *et al.*, 2005). The island is volcanic with the landscape dominated by stony plains, sandy dunes and barren hills. Apart from the summit of Monte Verde (774 m), the island is very dry with sparse vegetation (Fig. A.V.1.B), although in recent years, considerable areas have been planted with exotic *Prosopis juliflora* trees.

The study site (Fig. A.V.1.C) is located on the northwest side of the island, approximately 5km Northwest of Mindelo (coordinates in decimal degress: -25.03542 to -25.01225W; 16.83688 to 16.82780N, datum WGS 1984). It is a very dry area with two narrow valleys North-South and Northeast-Southwest orientated, surrounded by hills, with altitudes reaching 200 m. Dominant vegetation on the site is composed of sparse herbaceous species (*Cleome viscosa*, *Sclerocephalus arabicus* and *Zygophyllum simplex*; Diniz and Matos, 1994) and some *Calotropis procera* bushes.

Study species

The target species was the only reptile present in the study area, as *C. stangeri* is restricted to more humid and agricultured areas (Vasconcelos unpublished data). *Tarentola caboverdiana substituta* is a flattened, robust gecko with a long tail and a delicate head with relatively long, sharpened snout, which attains 60 mm snout-vent length, SVL (see Joger 1984a for a full morphological description). Based on the measurements taken during the present study, the population sampled displays a bimodal distribution, individuals smaller than 45 mm SVL were considered juveniles, as they also lacked secondary sexual characters (ovarian follicles seen by transparency in females, developed hemipeneal bags in males).

Activity patterns and refuge selection

The study was carried out in November 2008, after the wet season and out of the reproductive period of the species (Vasconcelos pers. obs.). During eight days, transects were performed in six-hour shifts by two observers. Forty-eight random transects were conducted in search of geckos (each 45 minutes, totaling 36 hours of sampling) in order to sample twice each hour-block throughout the diel cycle. For statistical analyses, observations were grouped into two periods of 12 hours each: day (06-18h) and night (18-06h). Total surveyed area was around 97,330 m2. Geckos detected along transects were classified as either active (with surface activity) or inactive (in refuge) and captured by hand. For each individual, the time of capture was recorded. Body (Tb, skin, <10s after capture or before touching the animal whenever possible), soil (Ts) and refuge (Tr) temperatures were recorded (in shade

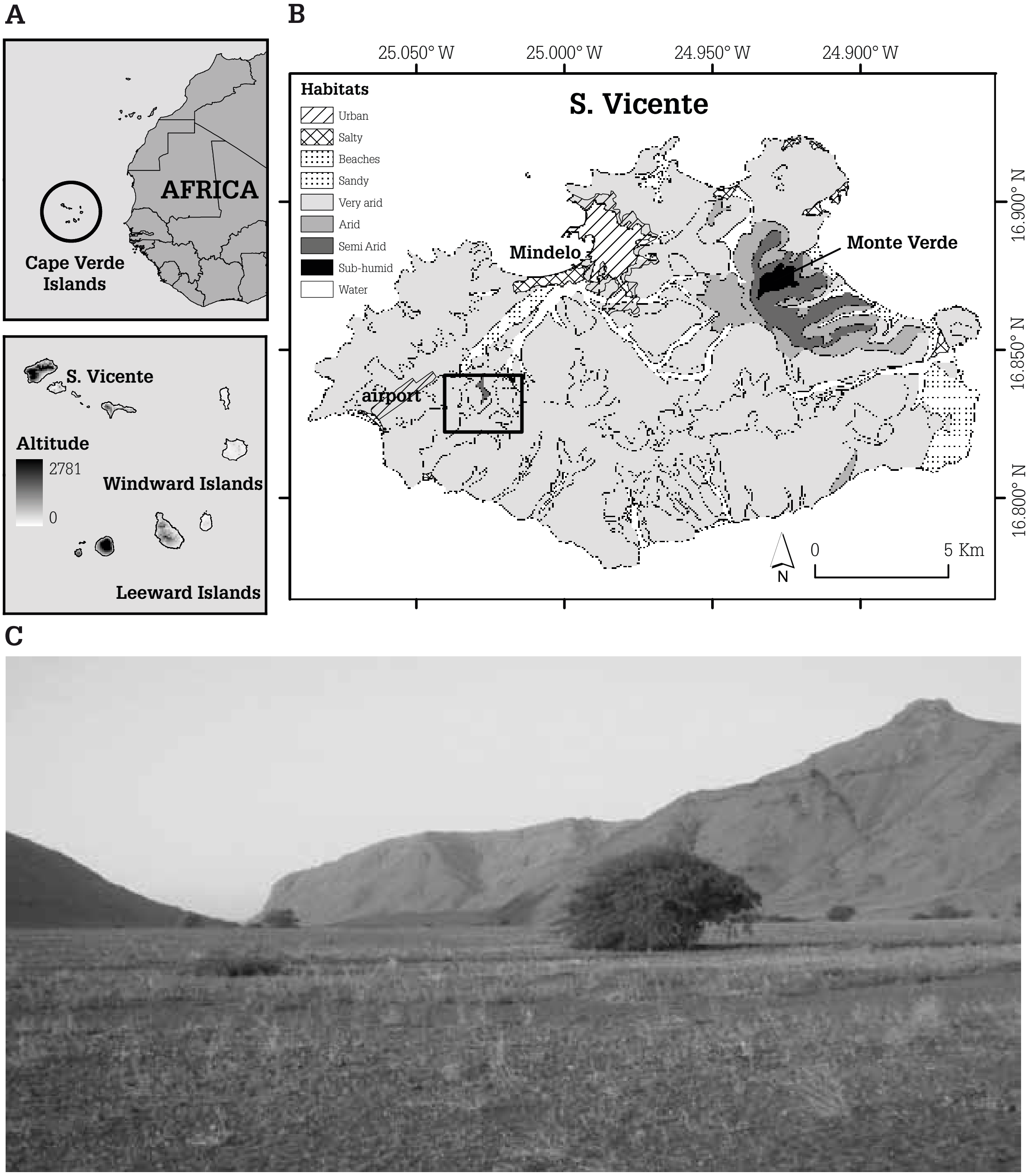

Figure A.V.1 Map of the Cape Verde Islands showing the archipelago location, its altitudes (**A**) and location of the study area in São Vicente Island (Geographic Coordinate System, Datum WGS 84) (**B**). Picture of the study site (**C**).

if by daylight) with a Fluke® 68 infrared thermometer. Air humidity (H; ±0.1%) and temperature (Ta; ±0.1°C) were also measured at 10cm from the ground using a Fluke® 971 temperature-humidity meter. For inactive animals, refuge type was categorised according to rock size due to its predictable effect on thermal environment (Huey *et al.* 1989b). Rock sizes were classified by a same observer as small (less than one hand span), medium-sized (between one and three hand spans) or big (more than three hand spans). Geckos were sexed, photographed (for assigning sex in case of doubt), measured (SVL) for establishing the age category, and released in the capture site.

Temperature and microhabitat availability

To evaluate the local environmental temperature availability, two sets of four data-loggers (i-buttons TMEX-RTE®, accuracy of 0.1ºC) were placed in the different available habitats (under vegetation, a small, a medium-sized and a big rock) at two altitude classes (in a valley and a hilly slope). Data-loggers were programmed for recording temperatures every five minutes and moved to different sites within the same microhabitat and altitude class each three days in order to provide replicas.

Relative abundances of microhabitats available as refuge was evaluated by means of 16 random 200 m-transects. For each transect, the number of bushes, small, medium-sized and large rocks within 50cm from the transect line were counted. In this way, the abundance of bushes and of each rock type could be calculated in average number of each item found on the 16 transects/ 200 and percentages. The relative percentages of each item were compared to microhabitat use by geckos to determine if there was selection in relation to specific refuges and what this selection consisted of.

Statistical procedures

Normality (Liliefors tests, $P>0.05$) and homoscedasticity (Levene tests, $P>0.05$) of Tb, Ta, Ts and Tr were tested for each group (gecko category, time period, activity status and refuge type) prior to the analyses. Thermal relations were analysed by means of partial correlations between temperatures, least-squares regression and General Linear Models (GLM). Because slopes between Tb and environmental temperatures were always homogeneous among groups (parallelism tests, $P>0.05$), common slope ANCOVA design was employed. Values of Tb were compared between category of geckos (adult males, adult females, juveniles), time period (day, night), activity status (active, inactive) and refuge type (small, medium-sized and big rocks or outside refuge) with GLM using only those environmental temperatures displaying significant partial correlations with Tb, as continuous predictors (=covariates).
Log-linear analyses were used to test differences in the use of refuges by the three categories of geckos and to test for differences in activity patterns between day and night periods. This statistical procedure tests for association between several categorical variables in a multidimensional contingency table. The variables used were again: category of geckos, time period, activity status and refuge type. The algorithm used generates several models to test interactions between all variables and selects the least complex model that fits the data. Results were interpreted by checking odds-ratio scores among categories in expected values of partial and marginal association tests (see Jobson 1992).

RESULTS

A total of 261 geckos (80 adult males, 87 adult females and 94 juveniles) were observed. Adults males were significantly larger than females (mean SVL±SE, males: 52.19±0.41 mm; females: 51.07±0.38 mm; $T_{165}=2.00$, $P=0.047$). Log-linear models provided an excellent adjustment (final model: Maximum Likelihood ratio $\chi^2=14.63$, df=27, $P=0.97$) and showed significant interactions among the four variables analysed. Significant partial associations in the interactions between variables are discussed below in detail.

Activity patterns

Tarentola caboverdiana substituta was exclusively nocturnal, with active geckos recorded only at night (between 19h00 and 06h12 the following morning), although inactive individuals could be found at any time (Fig. A.V.2.A).

The ratio between active and inactive animals found during transects was around 1:4 throughout the day-cycle. Log-linear models showed that category of geckos was not associated to time period or activity status variables; in other words, juveniles, adult males and females did not exhibit differences in their activity patterns throughout a diel cycle (Table A.V.1). On the other hand, it indicated significant interactions between time period and activity status, confirming the observation that geckos are commonly inactive by day (Table A.V.1).

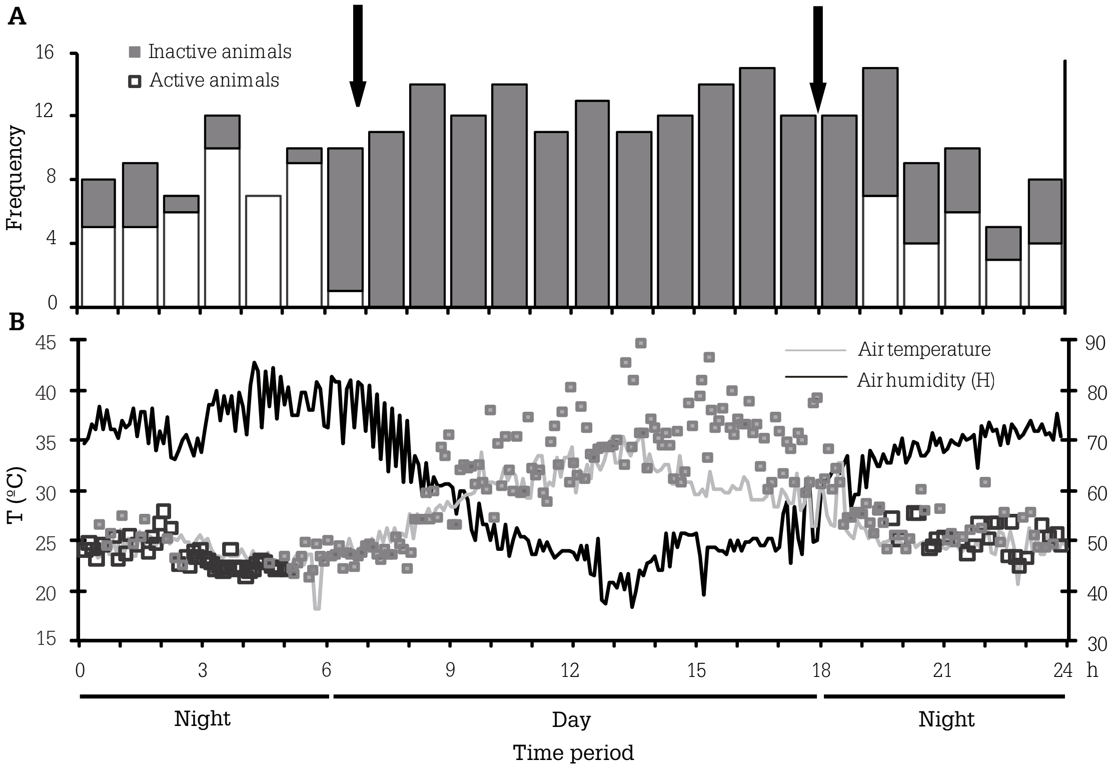

Figure A.V.2 Number of active and inactive geckos (total *n*=261) captured each hour over a 24-hour period (**A**). Air humidity (H), air temperature and body temperature (T) of active and inactive geckos, recorded at the capture site during the time period (**B**). Arrows indicate the sunrise (06:48) and sunset times (18:04). See Activity patterns and refuge selection section on Material and Methods for further details.

Table A.V.1 Results of the log-linear analysis indicating the values of the partial and marginal association tests (Jobson 1992) between the four variables. df stands for degrees of freedom. The informative results come from the interactions between environmental variables and gecko categories.

	df	Partial $\chi 2$	P		Marginal $\chi 2$	P	
Period of day (P)	1	1.01	0.31		1.01	0.31	
Activity status (A)	1	58.63	<0.001	***	58.63	<0.001	***
Refuge type (R)	3	59.37	<0.001	***	59.37	<0.001	***
Categories of geckos (C)	2	1.03	0.6		1.03	0.60	
P x A	1	25.94	<0.001	***	101.31	<0.001	***
P x R	3	12.00	<0.01	**	84.43	<0.001	***
P x C	2	3.60	0.17		1.44	0.49	
A x R	3	89.68	<0.001	***	164.62	<0.001	***
A x C	2	0.12	0.94		0.46	0.79	
R x C	6	32.23	<0.001	***	29.63	<0.001	***
P x A x R	3	0.41	0.94		0.28	0.96	
P x A x C	2	0.38	0.83		0.36	0.84	
P x R x C	6	2.69	0.85		4.11	0.66	
A x R x C	6	3.92	0.69		4.92	0.55	

Table A.V.2 Average number and percentage (%) of refuges found on refuge availability transects as well as percentages of male, female and juvenile geckos found on each refuge type. SE stands for standard error and N for sample size.

Refuge types		**Refuge availability**		**Refuge selection by geckos categories (%)**			
		mean±SE	% (*n*=2678)	Males (*n*=58)	Females (*n*=67)	Juveniles (*n*=69)	Total (*n*=194)
Vegetation (*n*=276)	Bushes	17.3±01.7	0.0	0.0	0.0	0.0	
Rocks (*n*=2402)	Small	129.1±21.1	77.1/ 86.0	20.7	17.9	57.9	32.6
	Medium-sized	19.6±04.0	11.7/ 13.0	69.0	67.2	35.3	56.5
	Large	1.4±00.7	0.86/ 0.96	10.3	14.9	7.4	10.9

Animals were most active at the time when humidity (H) was highest (active: H=72.87±0.59%, *n*=67; inactive: H=59.44±0.87%, *n*=194; T_{259}=8.79, *P*<0.001) and Ta was lowest (active: Ta=24.10±0.11°C, *n*=67; inactive: Ta= 28.19±0.26°C, *n*=194; T_{259}=9.26, *P*<0.001; Fig. A.V.2.B).

Microhabitat availability and refuge selection

Refuge availability (estimated from random transects) indicated that bushes and medium-sized rocks are not abundant on the sampled surface area and that the presence of big loose rocks is very low (<1% of total rocks and all refuges types). The more abundant microhabitats found on the sampled surface area were small rocks, which is also by far the most common rock type (Table A.V.2).

All inactive animals (*n*=194) were found under rocks and almost all of the 67 active animals were found on the ground (*n*=64; 95.5%), very few on rocks (*n*=3, 4.5%) and none under vegetation. Excluding the vegetation, neither each of the three gecko categories, nor geckos as a whole, used microhabitats according to availability (males: χ^2_2=124.42, *P*<0.001; females: χ^2_2=262.80, *P*<0.001; juveniles: χ^2_2=54.26, *P*<0.001; pooled χ^2_2=364.73, *P*<0.001). Specifically, geckos as a whole used large rocks more than expected. Log-linear analyses (Table A.V.1) provided statistical support to these results. Significant interactions were detected between refuge type and category of geckos, showing that juveniles were more frequently found under small rocks than adults whereas adult males and females were more commonly found under medium-sized and large rocks than juveniles (see Table A.V.2). Significant interactions were also found between refuge type and time period, making clear that geckos were outside of the refuge by night (see Table A.V.3).

Thermal biology

Records of the data loggers indicated that temperatures under vegetation increased faster (steepest slopes) and higher (maximum temperature=44.0°C) than in remaining habitats (Fig. A.V.3.A). Among the rocks, the temperature variation throughout a diel cycle was similar for all sizes (Fig. A.V.3.A). However, the temperature range was narrower in medium-sized and large rocks than in small ones (Fig. A.V.3.A), which attained the highest values (repeated measures ANOVA hour $F_{24,8023}$=1169.46, *P*<0.001, microhabitat (R) $F_{3,840}$9=2173.48, *P*<0.001, hour * microhabitat (R) $F_{69,8009}$=118.42, *P* <0.001, Scheffé post-hoc tests *P* <0.05).

The Tb of geckos ranged from 21.4 to 44.6°C with differences in maximum and minimum temperatures according to the category of geckos, time period and activity status (Table A.V.3). The most obvious difference was that geckos achieved higher Tb by day than by night, with the male, female and juvenile geckos following the same pattern (two-way ANOVA, time period: $F_{1,255}$=208.01, *P*<0.001; category of geckos: $F_{2,255}$=0.29, *P*=0.75; time period * category of geckos: $F_{2,255}$=1.14, *P*=0.32). By night, inactive geckos (in refuge) of all categories attained significantly

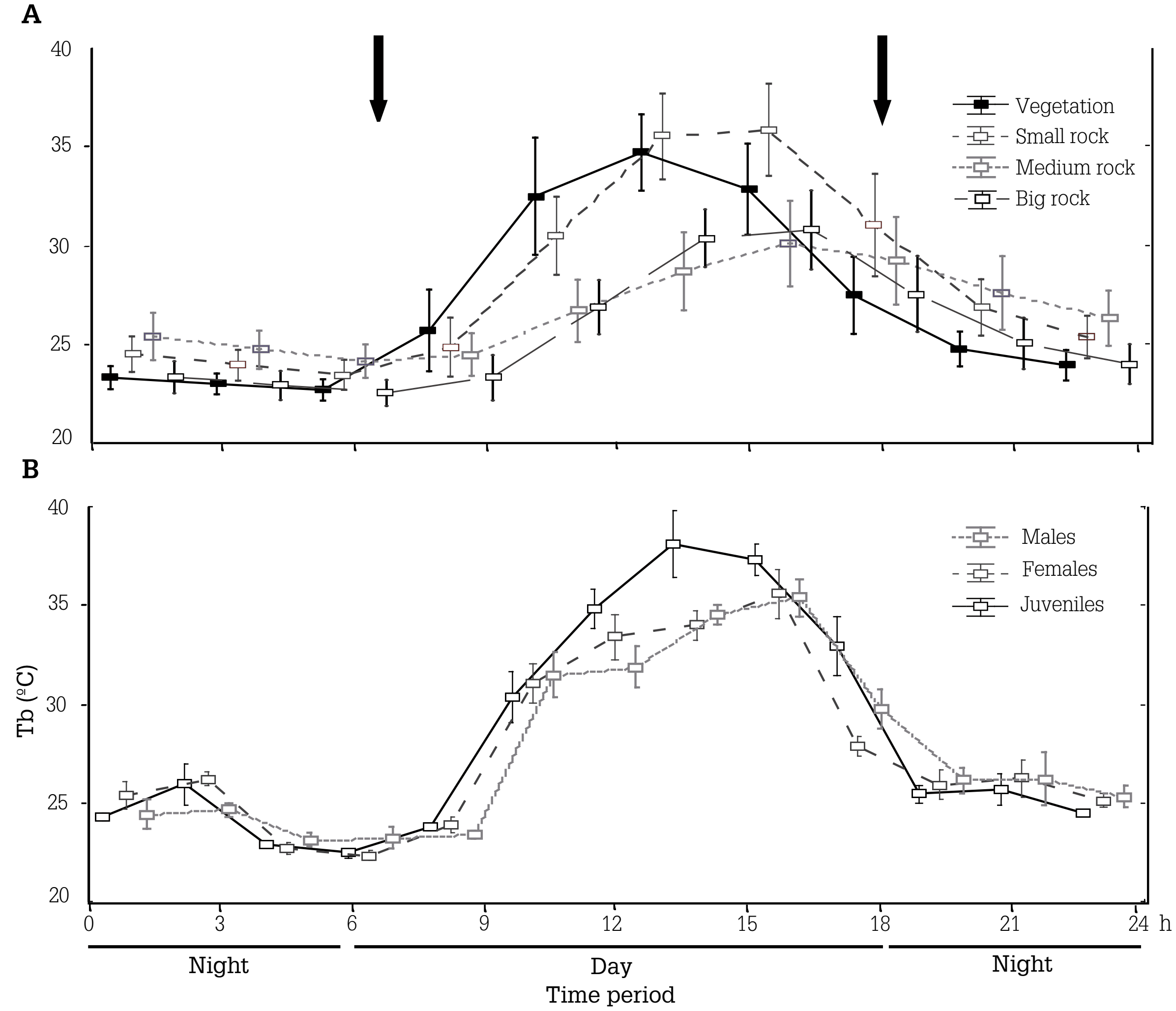

Figure A.V.3 Diel variation of refuge temperatures (average Tr, recorded with data loggers) (**A**) and body temperatures (Tb) of male, female and juvenile geckos (**B**) recorded during the study period (eight days).

higher Tb than active ones (two-way ANOVA, activity: $F_{1,116}$=21.92, *P*<0.001; category of geckos: $F_{2,116}$=0.57, *P*=0.57; activity * category of geckos: $F_{2,166}$=0.20, *P*=0.82).

Significant positive partial correlations between Tb against Ta, Ts and Tr were found for all categories of geckos, although for males significant correlations were only found for active animals (Table A.V.3). For active geckos observed by night, Tb was highly correlated to Ts and Ts in all categories (Beta>0.75, *P*<0.01). In contrast, for geckos found by day in refuges, Tb was more correlated with Tr (Table A.V.3)Considering all the observations, the GLMs failed to detect differences in Tb between the category of geckos and the time period once the effects of Ts and Tr were statistically removed (GLM [Ts, Tr covariates] time period: $F_{1,189}$=0.41, *P*=0.52; category of geckos: $F_{2,189}$=0.04, *P*=0.96; time period * category of geckos: $F_{2,189}$=0.01, *P*=0.99). When restricted to the diurnal observations (all inactive geckos), the absence of differences in Tb between category of geckos remained (GLM [Tr covariate]: $F_{2,134}$=0.18, *P*=0.84). Finally, if only the nocturnal observations were taken into account, no differences either between category of geckos or activity status were detected (GLM [Ts, Tr covariates], activity status: $F_{1,54}$=0.01, *P*=0.92; category of geckos: $F_{2,54}$=0.03, *P*=0.97; activity status * category of geckos: $F_{2,54}$=0.07, *P*=0.93). Subsequently, the Tb of geckos were then analysed also considering the different refuge types. By night, either active or inactive geckos did not display different Tb in regard to refuge type (two-way ANOVA, activity status:

Table A.V.3 Mean, minimum and maximum body temperature (Tb) and partial correlations (ρ) between Tb and air, soil and rock temperatures (Ta, Ts and Tr, respectively) of males (M), females (F) and juvenile (J) geckos recorded during the day (inactive) or at night (either inactive or active) (*P<0.05, ** P <0.01, *** P <0.001). SE stands for standard error and *n* for sample size.

		Day-inactive (*n*=38M, 48F, 53J)					**Night-inactive (*n*=20M, 19F, 16J)**					**Night active (*n*=22M, 20F, 25J)**				
		Mean±SE	Range	Beta	ρ	*P*	Mean±SE	Range	Beta	ρ	*P*	Mean±SE	Range	Beta	ρ	*P*
Males	Tb	32.38±0.68	22.9-38.7	0.16			25.75±0.51	22.1-30.8				24.32±0.33	21.9-27.2			
	Ta	30.02±0.46	23.3-35.4	0.40	0.28	0.10	24.33±0.39	18.2-26.3	0.28	0.30	0.21	24.55±0.20	23.1-26.1	0.23	0.45	0.04 *
	Ts	31.03±0.63	23.3-38.2	0.40	0.30	0.08	26.52±0.48	22.9-30.0	0.11	0.08	0.74	24.42±0.41	21.4-27.8	0.77	0.86	<0.001 ***
	Tr	33.50±0.89	23.0-43.8	0.23	0.30	0.08	26.34±0.71	20.7-31.9	0.42	0.28	0.25	24.3	-			
Females	Tb	31.36±0.69	22.2-41.0	0.02			25.85±0.51	21.4-30.1				24.37±0.38	22.0-26.9			
	Ta	29.57±0.41	23.7-35.2	0.70	0.35	0.02 *	24.42±0.40	18.2-26.3	0.43	0.48	0.04 *	23.84±0.25	20.6-26.1	0.29	0.50	0.04 *
	Ts	30.14±0.62	23.3-40.5	0.19	0.02	0.91	27.25±0.52	22.9-31.8	-0.35	-0.26	0.29	24.10±0.38	21.9-27.4	0.82	0.85	<0.001 ***
	Tr	31.73±0.77	22.0-42.2	0.21	0.57	<0.001 ***	26.88±0.72	20.7-33.7	0.76	0.50	0.03 *	26.10±0.76	24.7-27.3			
Juveniles	Tb	32.56±0.84	22.4-44.6	0.55			25.64±0.47	22.3-27.9				23.73±0.33	21.4-27.8			
	Ta	29.49±0.46	23.5-35.8	0.20	0.28	0.05 *	24.76±0.32	22.0-27.0	0.24	0.29	0.29	23.92±0.12	22.8-24.8	0.29	0.50	0.04 *
	Ts	31.95±0.81	22.9-43.8	0.17	0.16	0.27	27.13±0.47	23.6-29.5	0.71	0.54	0.04 *	23.82±0.33	21.3-27.3	0.82	0.85	<0.001 ***
	Tr	33.65±1.00	21.2-45.7	0.59	0.36	0.01 *	26.44±0.53	23.0-29.4	-0.06	-0.07	0.81	24.67±1.00	22.8-26.2			
Total	Tb	32.10±0.44	22.2-44.6				25.75±0.28	21.4-30.8				24.11±0.20	21.4-27.8			
	Ta	29.66±0.26	23.3-35.8	0.20	0.31	<0.001 ***	24.49±0.22	18.2-27.0	0.35	0.38	<0.01 **	24.10±0.11	20.6-26.1	0.19	0.31	0.01 *
	Ts	31.07±0.41	22.9-43.8	0.17	0.15	0.09	26.95±0.28	22.9-31.8	0.09	0.06	0.64	24.11±0.22	21.3-27.8	0.76	0.80	<0.001 ***
	Tr	32.95±0.53	21.2-45.7	0.59	0.44	<0.001 ***	26.56±0.39	20.7-33.7	0.41	0.30	0.02 *	25.23±0.57	22.8-27.3			

$F_{1,62}$=0.92, *P*=0.34; type of refuge: $F_{2,62}$=1.10, *P*=0.34; activity status * type of refuge: $F_{2,62}$=1.47, *P*=2.24) and such results persisted when removing the effect of the environmental temperatures, Ta, Ts and Tr (GLM [Ts, Tr covariate], activity status: $F_{1,50}$=0.002, *P*=0.96; type of refuge: $F_{2,50}$=0.04, *P*=0.96; activity status * type of refuge: $F_{4,121}$=0.15, *P*=0.86). In contrast, by day, geckos (all inactive) were hotter under small rocks than under medium-sized and big rocks (two-way ANOVA, type of refuge: $F_{2,130}$=120.47, *P*=0.01; category of gecko: $F_{2,130}$=1.11, *P*=0.97; type of refuge * category of geckos: $F_{4,130}$=0.07, *P*=0.93), such difference disappearing when removing the effect of the Tr (GLM [Tr covariate], type of refuge: $F_{2,121}$=0.30, *P*=0.73; category of geckos: $F_{2,121}$=0.41, *P*=0.67; activity status * category of geckos: $F_{4,121}$=0.83, *P*=0.51).

The Tb of geckos, both active (ANOVA, hour: $F_{11,55}$=12.81, *P*<0.001) and inactive (ANOVA, hour: $F_{22,171}$=34.42, *P*<0.001), displayed strong diel variation tracking environmental temperatures. The three categories of geckos followed a similar variation in Tb throughout the 24-hour period and reached the highest scores in the 12:00-17:00 interval (Fig. A.V.3.B). However, during this specific period, juveniles attained higher Tb than adult females and males (ANOVA, category of geckos: $F_{2,73}$=4.90, *p*=0.01; Scheffé tests, juveniles-males: *P*<0.05, juveniles-females: *P*<0.05, males-females: *P*>0.05).

DISCUSSION

Despite the Palaearctic origin of the genus, it becomes evident that *Tarentola caboverdiana substituta* behaves more as a desert gecko than most members of its congeneric species living under more temperate regimes.

First, its diel activity pattern is strictly nocturnal when virtually all *Tarentola* species are at least partially diurnal (Schleich *et al.* 1996), even those also living in islands, as *T. mauritanica* in Corsica (Capula & Luiselli 1994; Delaugerre 1984). Only *T. neglecta*, inhabitant of deep Sahara desert, have been described as strictly nocturnal (Schleich *et al.* 1996). Whereas such activity interruption is sharp and involving all categories of individuals, no other pattern than a general correlation with environmental temperature arose when only nocturnal observations are considered. This suggests an environmental release by night when temperatures were lower and humidity higher. In fact, it was already suggested that the thermal physiology of nocturnal geckos was more constrained by the high body temperatures reached during the day rather than to the low body temperatures maintained by night when foraging, particularly if cold diurnal refuges are unavailable (Huey *et al.* 1989b) and opportunities for behavioural regulation are severely limited (Porter & Gates 1969), as is the case. Further research based on physiological experiments will be able to test this hypothesis in *Tarentola caboverdiana substituta*.

Second, this gecko carefully selects diurnal retreat sites. All individuals were found under rocks, most small and medium-sized, and none under vegetation, which was the refuge reaching the highest temperatures. Still, other factors besides temperature variation could explain the absence of geckos from this refuge type. Considering rock refuges, adults tended to use more medium-sized rocks, which were not the most abundant refuge. Juveniles clearly differ from them in using small rocks more frequently but still less than expected based on availability alone. Such microhabitat choosiness, partially attributable to the thermal properties of refuges (see below), disappeared after sunset when most geckos were active moving outside of their shelters and those still in refuges did not display such bias in refuge use.

Third, from the thermal point of view, all geckos regardless of size or sex behave as tigmotherms when active by night, as thermoconformers with the substrate when in their diurnal refuges (Huey & Slatkin 1976) and in intermediate way (depending less on the refuge and more on the substrate) when inactive by night. By night, environmental temperatures decrease and most geckos abandon their refuges. Also those geckos remaining in refuges undergo similar thermal regimes even if different microhabitats were selected, as seen in Fig. A.V.3. As a consequence, nocturnal temperatures of geckos did not differ either between categories or microhabitats. In contrast, diurnal retreats greatly differ in their thermal properties: small rocks attaining higher diurnal temperatures due to their lower thermal inertia (Stevenson 1985) than larger ones. Thus, since juveniles use this type of refuge more often than adults and their bodies with smaller masses heat faster, their body temperature becomes higher.

So, why are juvenile geckos then found in such extremely hot diurnal microhabitats? Since selected temperatures could not be estimated in the study area due to logistic constraints, explanations must be tentative. Maximal temperatures in the hottest microhabitats measured are much higher (by 10-15ºC) than temperatures selected by other *Tarentola* species in a thermal gradient (Brown 1996; Carretero 2008; Gil *et al.* 1994). This suggests that at least some juvenile geckos using small rocks as diurnal retreats might be risking overheating (Arad *et al.* 1997). Territoriality for retreat sites and aggressiveness as demonstrated in other *Tarentola* species (Downes & Shine 1998; Picariell *et al.* 1989) combined with scarcity of optimal refuges, extremely high densities of conspecifics (authors unpublished data), and lack of native terrestrial predators may explain why juvenile geckos use this thermally suboptimal microhabitat. Nevertheless, in temperate species, as *T. mauritanica*, small individuals selected for higher temperatures (Carretero 2008) and recorded diel variation in selected temperatures (Arad *et al.* 1997; Carretero 2008; Gil *et al.* 1994) hence indicating some ontogenic and temporal plasticity in thermal physiology that partially compensate for such risk.

Apart from physiological adaptations such as eggs better adapted to desiccation (Picariello *et al.* 1989), *Tarentola* sp. may be less adapted than other specialised geckonid genera to hot and arid conditions as those prevailing in São Vicente. This island is almost devoid of vegetation that could provide some shade and has no running water that would cool the substrate (the minimum temperature registered by data loggers was 21.5ºC). However, some ecological shifts, (nocturnality, microhabitat selection) and the lack of continental competitors have allowed *T. caboverdiana substituta* and other Cape Verdean species of the genus to successfully adapt to the ecologically demanding conditions of the archipelago.

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