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

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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 Myr 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.

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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 data sets 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 pratice 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 Myr old (Fig. 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 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,

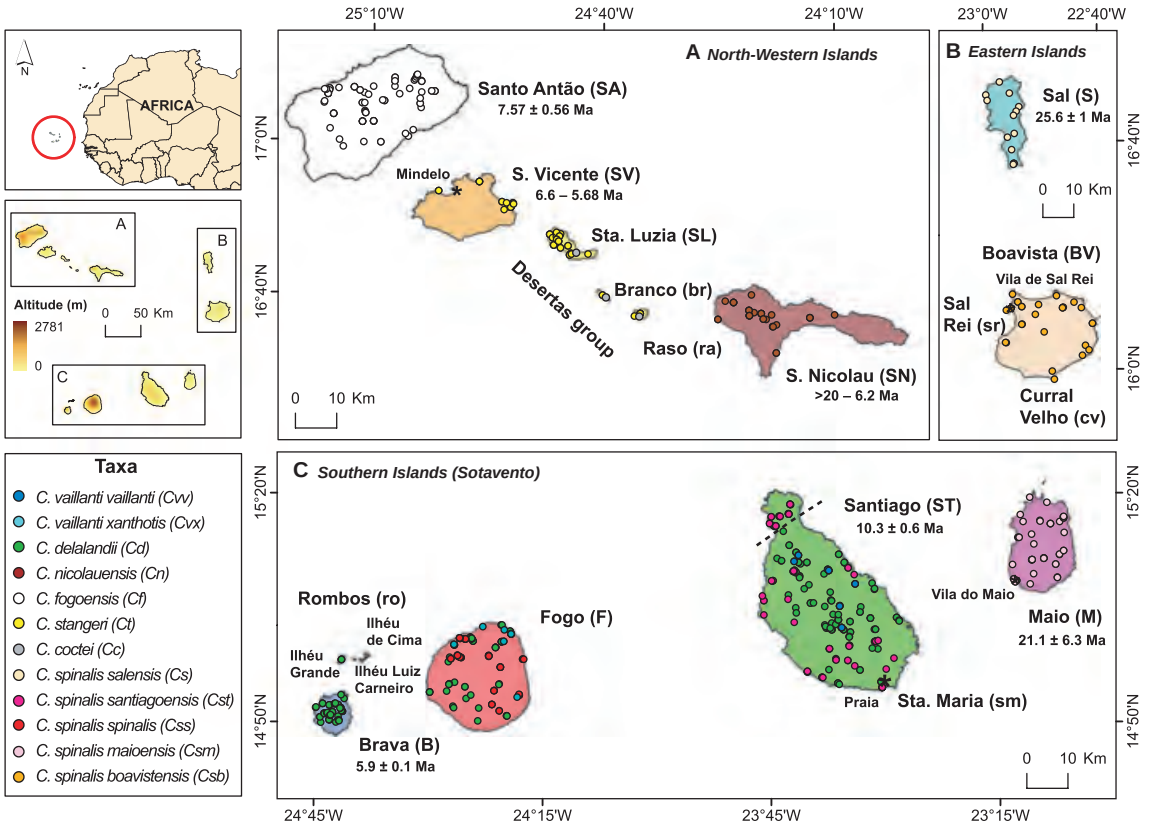


Fig. 1 Map of the Cape Verde Islands showing the geographic location (latitude and longitude in decimal degrees) and altitudes of the archipelago islands and the origins of the new *Chioninia* samples included in the molecular analyses (Geographic Coordinate System, Datum WGS 84). Island colours match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

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 S1.

The 275 voucher specimens examined for the morphological study (Appendix S2 and Fig. 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 S3).

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. 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+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 2×10^6 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 (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 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 Myr in the *Hemidactylus* geckos (Arnold *et al*. 2008) to 1.35% per lineage per Myr 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 Myr) 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 S1) 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 S1.

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 S4) 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 as 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. 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. 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 underestimate the number of species by being unable to detect cryptic or young species (false negative), whereas the IC is likely to overestimate 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. 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: *Euprepes coctei* Duméril & Bibron, 1839.

Charactodon Troschel, 1874: 225. Type species: *Euprepes 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 2A1,2, 3A1,2, 4A, 5A1,2 and 6A1,2)**

Diagnosis. Chioninia vaillanti is a relatively large species (adults between 87.5 and 123 mm snout-vent length, SVL; Table 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 2A1,2 and 4A). Number of transverse rows of dorsal scales from 77 to 95 (Table 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 Ma (see below molecular studies section and also Figs 3A1,2, 5A1,2 and 6A1,2, Table 2 and Appendix S5). The morphology of both populations has however significantly diverged in the number of ventral and dorsal scale rows along the body (Table 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. 4A). 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 particularly relevant 'taxonomic character'.

Nevertheless, according to the presently selected protocol of integration (IPC), none of the two molecular lines of evidence (mtDNA and nDNA) clearly supports the differentiation of both island populations (see Figs 3, 5A1,2 and 6A1,2), 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. 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

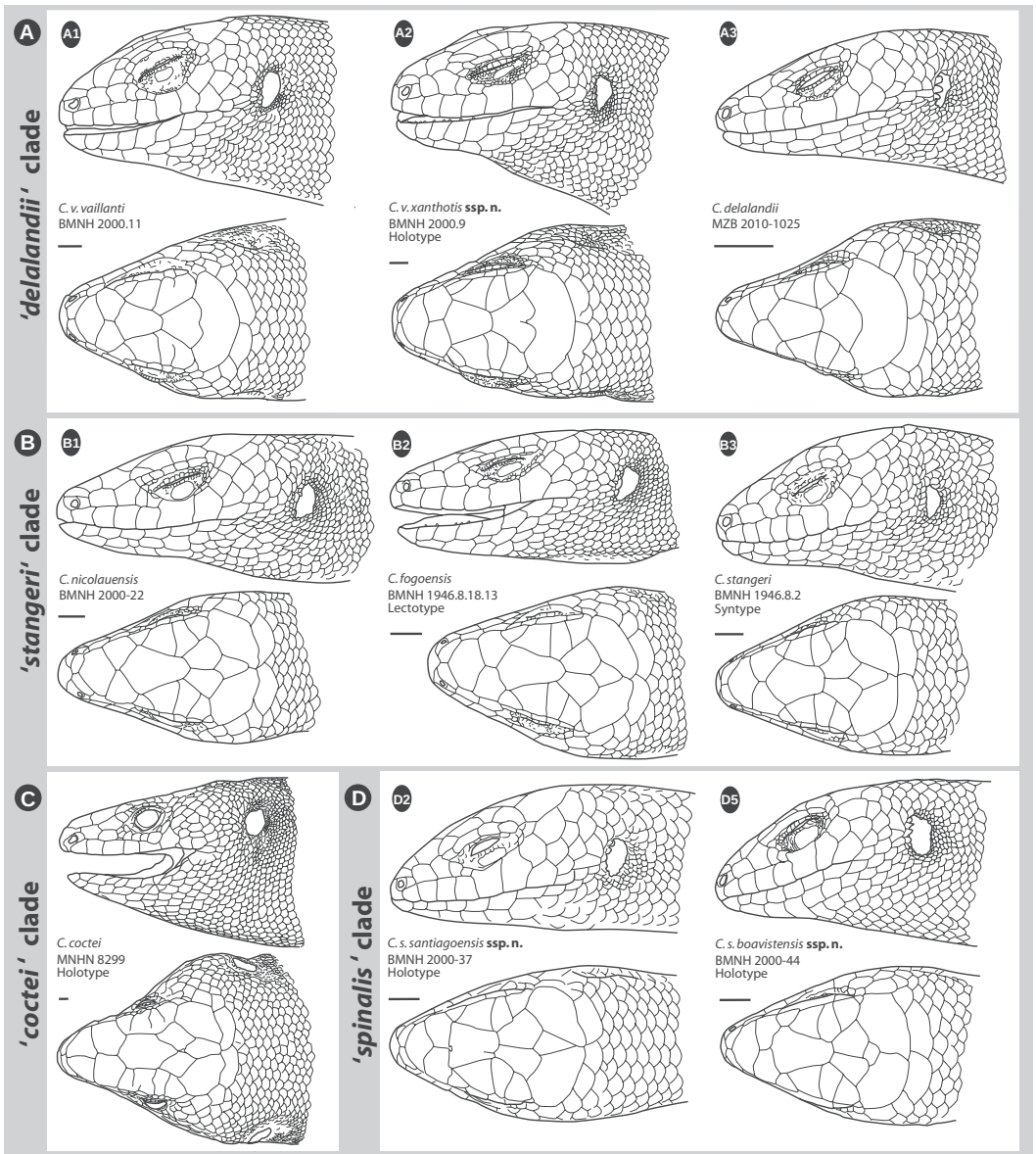
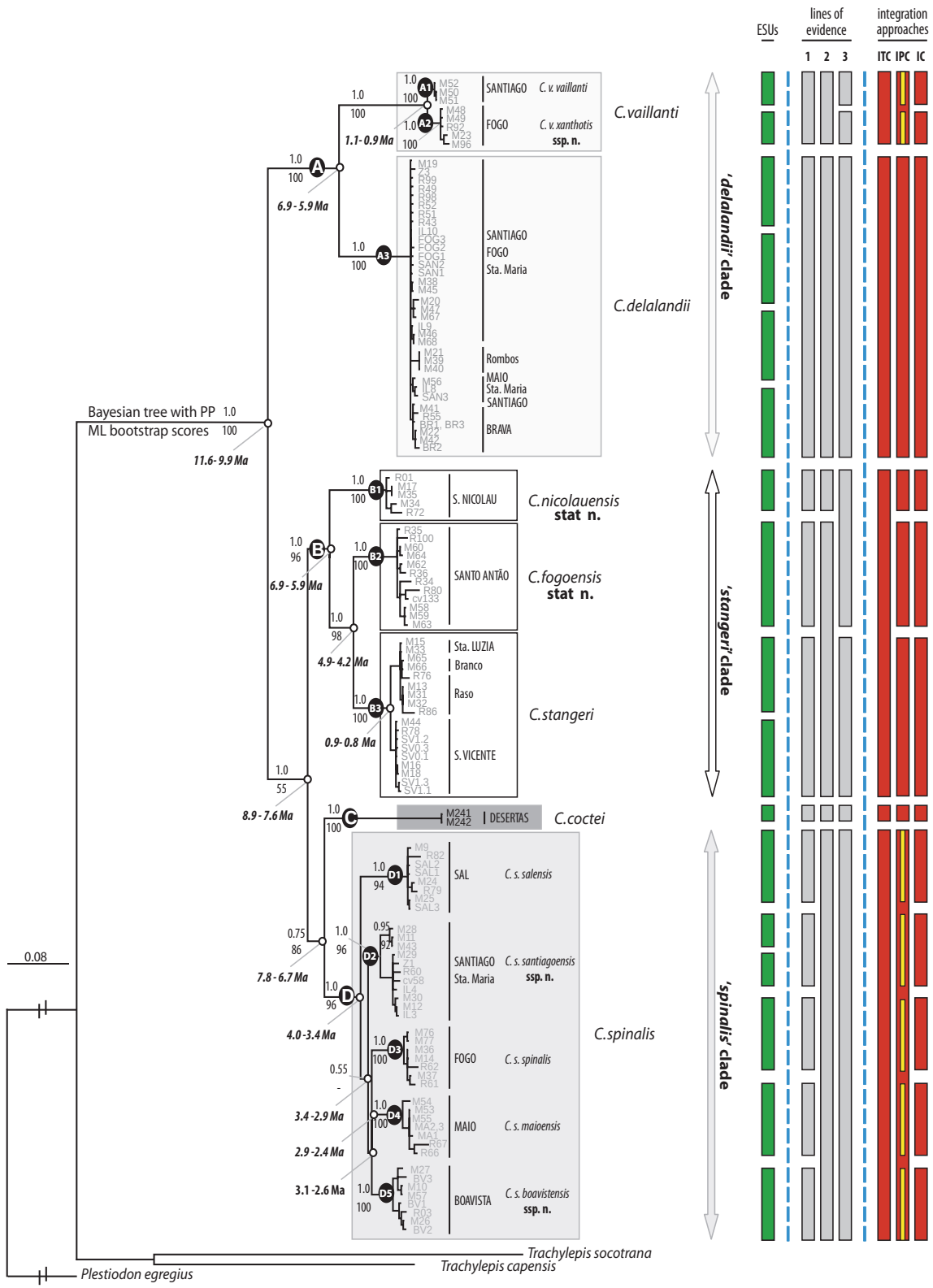


Fig. 2 Drawings of the lateral and dorsal view of the head for all *Chioninia* species, including the holotype of the new subspecies presently described. Scale bar = 2 mm. Head lateral views in A1–3, C and D5 have been symetrically reversed, and thus represent the right side.

Fig. 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 S3. 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 5 and 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.


ESUs
lines of evidence
1 2 3
integration approaches
ITC IPC IC
Bayesian tree with PP 1.0
ML bootstrap scores 100
11.6-9.9 Ma
A1
A2
A3
1.1-0.9 Ma
6.9-5.9 Ma
SANTIAGO
C. v. vaillanti
FOGO
C. v. xanthotis
ssp. n.
C.vaillanti
SANTIAGO
FOGO
Sta. Maria
Rombos
MAIO
Sta. Maria
SANTIAGO
BRAVA
C.delalandii
'delalandii' clade
B1
B2
B3
6.9-5.9 Ma
4.9-4.2 Ma
0.9-0.8 Ma
S. NICOLAU
C.nicolauensis stat n.
SANTO ANTÃO
C.fogoensis stat n.
Sta. LUZIA
Branco
Raso
S. VICENTE
C.stangeri
'stangeri' clade
8.9-7.6 Ma
M241
M242
DESERTAS
C.coctei
7.8-6.7 Ma
4.0-3.4 Ma
3.4-2.9 Ma
2.9-2.4 Ma
3.1-2.6 Ma
D1
D2
D3
D4
D5
SAL
C. s. salensis
SANTIAGO
Sta. Maria
C. s. santiagoensis
ssp. n.
FOGO
C. s. spinalis
MAIO
C. s. maioensis
BOAVISTA
C. s. boavistensis
ssp. n.
C.spinalis
'spinalis' clade
0.08
Trachylepis socotrana
Trachylepis capensis
Plestiodon egregius

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).

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

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 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. 4A); lower number of transversal scale rows along the body (47–52 and 77–87 rows of ventrals/dorsals respectively; Table 1).

Distribution (Fig. 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; this study).

***Chioninia vaillanti xanthotis* ssp. n. (Figs 2A2, 3A2, 4A, 5A2 and 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 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. 4A); a higher number of transversal scale rows along the body (53–58 and 84–95 rows of ventrals/dorsals respectively; Table 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 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

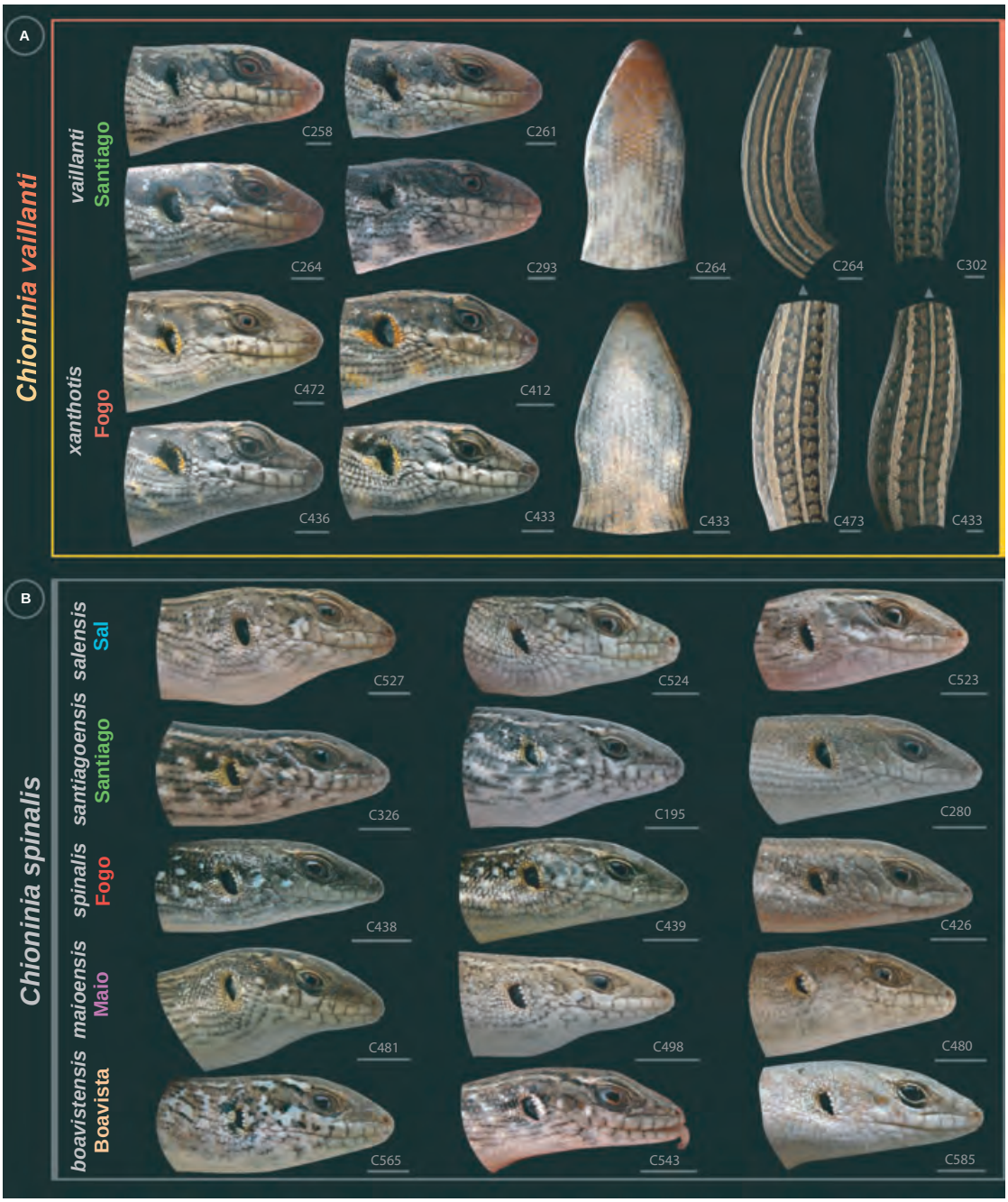


Fig. 4 Inter- and intra-subspecific phenotypic variation in (A) *Chioninia vaillanti* (lateral and ventral side of the head, and dorsal side of the body) and (B) *Chioninia spinalis* (lateral side of the head) illustrated by a selection of photographs of live specimens (see Appendix S1 for exact localities).

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

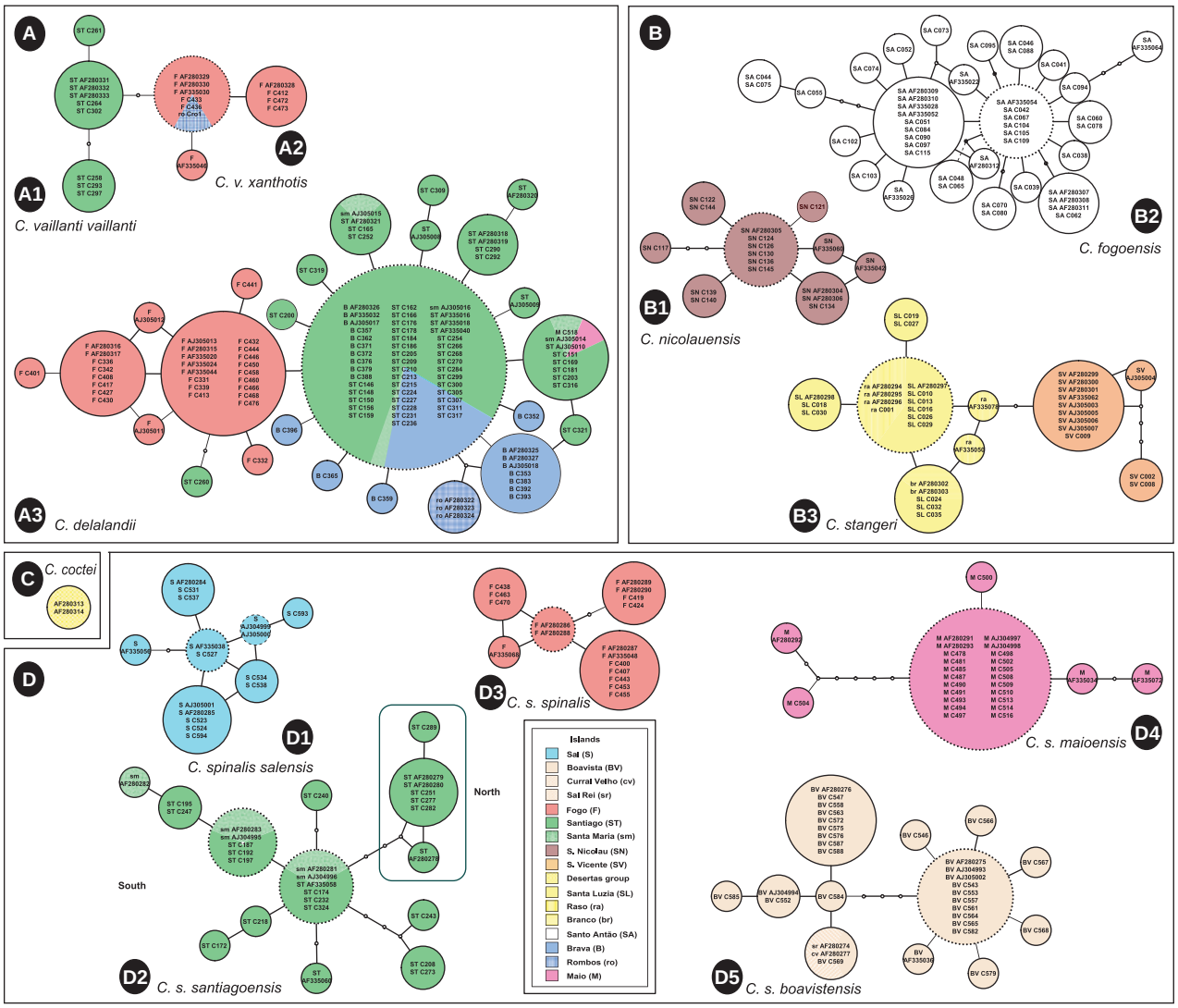


Fig. 5 Parsimony networks corresponding to cyt *b* sequence variation calculated with TCS with a connection limit of 95%. Lines represent a mutational step, dots missing haplotypes and circles haplotypes. The circle area is proportional to the number of individuals. Dashed lines represent probable ancestral haplotypes. For correspondences of sample locations and GenBank codes see Appendices S1 and S3. —A. '*delalandii*' clade. —B. '*stangeri*' clade. —C. *Chioninia coctei*. —D. '*spinalis*' clade.

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

Phylogenetic remarks (Figs 3A2, 5A2 and 6A2, Table 2 and Appendix S5). 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).

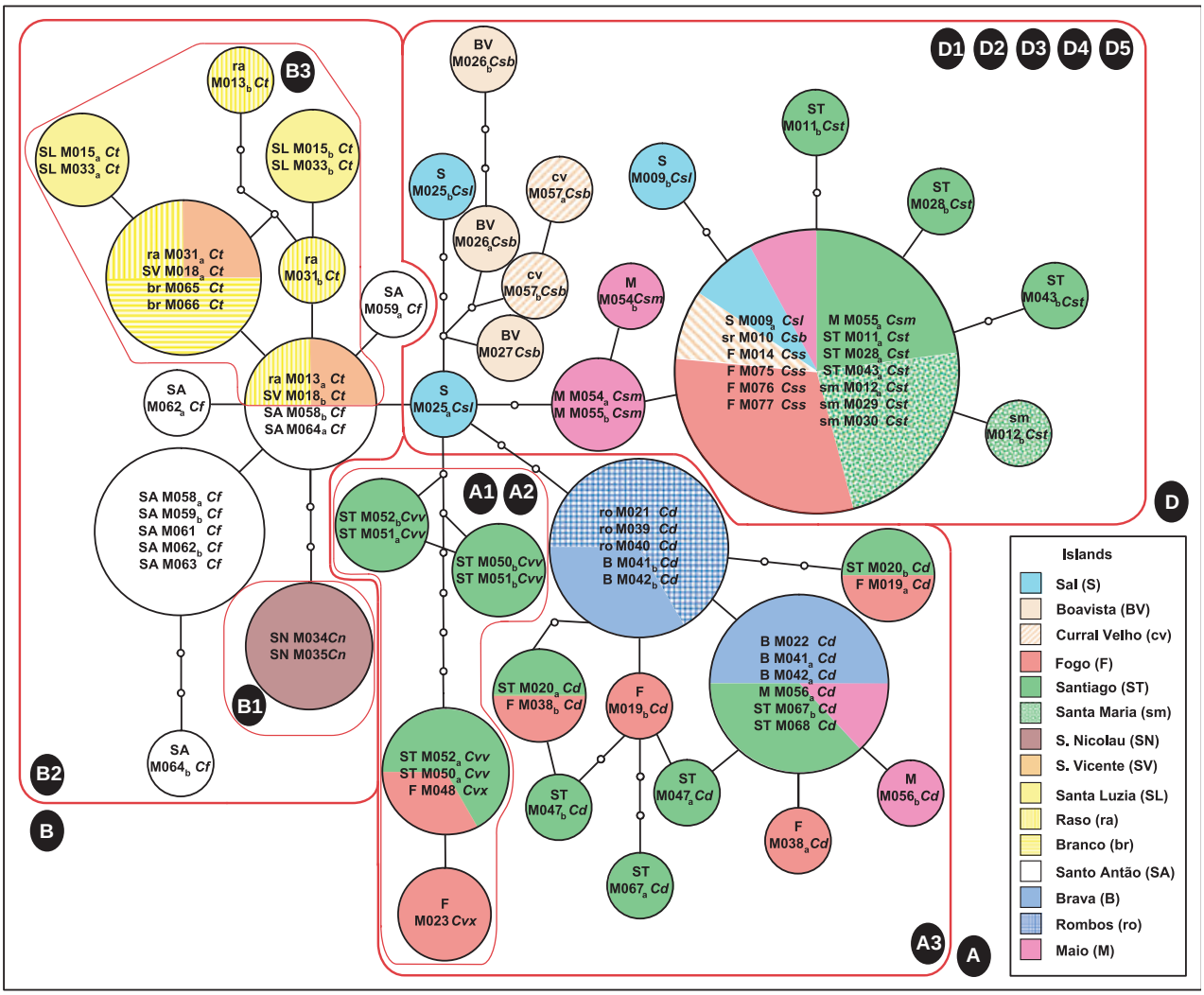


Fig. 6 Parsimony network corresponding to RAG2 sequence variation calculated with TCS with a connection limit of 95%. Lines represent a mutational step, dots missing haplotypes and circles haplotypes. The circle area is proportional to the number of haplotypes. For correspondences of sample locations and GenBank codes, see Appendix S1. —A. '*delalandii*' clade: (A1) *Chioninia vaillanti vaillanti* (*Cvv*), (A2) *Chioninia vaillanti xanthotis* (*Cvx*) and (A3) *Chioninia delalandii* (*Cd*). —B. '*stangeri*' clade: (B1) *Chioninia nicolauensis* (*Cn*), (B2) *Chioninia fogoensis* (*Cf*), (B3) *Chioninia stangeri* (*Ct*). —C. *Chioninia coctei* (*Cc*). —D. '*spinalis*' clade: *Chioninia spinalis salensis* (*Csl*), *Chioninia spinalis santiagoensis* (*Cst*), *Chioninia spinalis spinalis* (*Css*), *Chioninia spinalis maioensis* (*Csm*) and *Chioninia spinalis boavistensis* (*Csb*).

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

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.

Table 1 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/P, 'scales separated or barely in point contact'; SVL, snout-vent length; *Cvv*, *Chioninia vaillanti vaillanti*; *Cvx*, *Chioninia vaillanti xanthotis*; *Csl*, *Chioninia spinalis salensis*; *Cst*, *Chioninia spinalis santiagoensis*; *Css*, *Chioninia spinalis spinalis*, *Csm*, *Chioninia spinalis maioensis*; *Csb*, *Chioninia spinalis boavistensis*

		(A) '*delalandii*' clade			(B) '*stangeri*' clade				(C)	(D) '*spinalis*' clade				
	Species clades	*C. vaillanti*		*C. delalandii*	*C. nicolauensis*	*C. fogoensis*		*C. stangeri*	*C. coctei* [1,2]	*C. spinalis*				
		A1	A2	A3	B1	B2		B3	C	D1	D2	D3	D4	D5
Scales	Variation	*Cvv* (Santiago)	*Cvx* (Fogo)	(Sotavento Islands)	(S. Nicolau)	(Santo Antão)	'Fogo' types	(Desertas, S. Vicente)	(Desertas)	*Csl* (Sal)	*Cst* (Santiago)	*Css* (Fogo)	*Csm* (Maio)	*Csb* (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/F[3]	C				73.70%	8.30%	25.00%	8.70%						
	S/P	–	–	–	26.30%	91.70%	75.00%	91.30%	–	–	–	–	–	–
	n sides				(19)	(24)	(16)	(46)						
Supraciliaries	2	–	–	–	–	–	–	–	–	–	–	2.80%	–	8.30%
	3	–	–	–	–	–	–	–	–	88.90%	15.20%	38.90%	75.00%	70.80%
	4	5.50%	–	5.80%	44.40%	–	12.50%	6.40%	–	11.10%	82.60%	55.50%	25.00%	8.30%
	5	44.40%	16.70%	91.00%	50.00%	100%	75.00%	85.40%	10.00%	–	2.2%	2.80%	–	12.5%
	6	44.40%	66.60%	3.20%	5.60%	–	12.50%	8.20%	45.00%	–	–	–	–	–
	7	5.50%	16.70%	–	–	–	–	–	45.00%	–	–	–	–	–
	n sides	(18[a])	(12[a])	(156)	(18)	(22)	(16)	(110)	(20)	(27)	(46)	(36)	(16)	(24)
Lamellae	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
under	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
4th finger	*n* sides	(11)	(4)	(122)	(17)	(21)	(14)	(106)	(17)	(35)	(43)	(27)	(16)	(23)
Lamellae	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
under	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
4th toe	*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 identify reliably 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 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 1, 5 and 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* ST_{North}	D2	*Cst* ST_{South}	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**

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 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. 2A3). Number of transverse rows of dorsal scales from 68 to 91 (Table 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 2A3, 3A3, 5A3 and 6A3, Table 2 and Appendix S5). 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. 3). However, they are isolated and with significant *Snn* values for cyt *b* and are hence considered as ESUs.

Distribution (Fig. 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; 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 2B1, 3B1, 5B1 and 6B1)**

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 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. 2B1). Number of transverse rows of dorsal scales from 84 to 93 (Table 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. 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 2B2, 3B2 and 5B2)**

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 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 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. 2B2). Number of transverse rows of dorsal scales from 87 to 95 (Table 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. 3B). 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. 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 (1955) 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 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. 2B2) 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 3, 5 and 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 genetic differences were noticed. The *C. geisthardti* holotype was also studied and its morphological characters fell within *C. fogoensis* variation (Joger 1993).

Distribution (Fig. 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 2B3, 3B3, 5B3 and 6B3)**

Euprepis Stangeri Gray, 1845: 112. Four syntypes: BMNH 1946.8.1 to 1946.8.4, collected during the Niger Expedition. Type locality: '*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 Hopffferi 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 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. 2B3). Number of transverse rows of dorsal scales from 52 to 69 (Table 1).

Phylogenetic remarks (Figs 2B3, 3B3, 5B3 and 6B3, Table 2 and Appendix S5). 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. 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 2C, 3C and 5C)**

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 > 200 mm, 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. 2C). 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 1). Teeth with five cuspids (see figure in Bocage 1873b; Greer 1976; Mateo *et al.* 2005 and MorphoBank 52288).

Distribution (Fig. 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, 1873b, 1896, 1897, 1902; Vaillant 1882; Peracca 1891; Angel 1937; Mertens 1955; Greer 1976; Schleich 1982, 1987, 1996; Hutchinson 1989; Andreone & Gavetti 1998; Andreone 2000; Carranza *et al.* 2001; Andreone & Guarino 2003; 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 2D, 3D, 4B, 5D and 6D)**

Diagnosis. Chioninia spinalis is a medium-sized species (adults between 52 and 82.5 mm SVL; Table 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. 2D). Number of transverse rows of dorsal scales from 52 to 73 (Table 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. 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*, *Mabuya stangeri spinalis* and *Mabuya stangeri 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 3, 5 and 6; Table 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. 3D 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 3 and 6D) 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 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. 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 3D1, 4B, 5D1 and 6D)**

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. 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; this study).

***Chioninia spinalis santiagoensis* ssp. n. (Figs 2D2, 3D2, 4B, 5D2 and 6D)**

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 2D2 and 4B; Table 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 (33–36 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 1 and also Fig. 4B for an overview of the high intraspecific variability of meristic and mensural characters and colour patterns respectively.

Phylogenetic remarks (Figs 3D2, 5D2, 6D, Table 2 and Appendix S5). 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. 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; this study).

***Chioninia spinalis spinalis* (Boulenger, 1906) (Figs 3D3, 4B, 5D3, 6D and Appendix S4)**

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. 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 3D4, 4B, 5D4 and 6D)**

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. 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 2D5, 3D5, 4B, 5D5 and 6D)**

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 2D5, 4B, Table 1 and MorphoBank M52289–M52294). Despite the relatively high mtDNA genetic divergences (Appendix S5) and subtle differences of colouration (Fig. 4B), 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 1 and also Fig. 4B for an overview of the high intraspecific variability of meristic and mensural characters and colour patterns respectively.

Phylogenetic remarks (Figs 3D2, 5D2 and 6D, Table 2 and Appendix S5). 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. 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. 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. 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 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. 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. 5A1,2), two subunits are visible, one including the population from Fogo and another one from Santiago, two mutational steps apart. In *C. stangeri* (Fig. 5B3), 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. 5A3), 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. 5B1,2 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. 5D1–5 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. 6). This network shows two different bifurcations corresponding to the *C. vaillanti* and *C. delalandii* samples (Fig. 6A1-2 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. 6B1) and *C. stangeri* samples (Fig. 6B3), although in this last case, the central haplotype is shared also with some *C. fogoensis* samples (Fig. 6B2). 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. 6D). However, various haplotypes were unique to specific islands, including Maio, Sal and Boavista.

Population analyses. The significant *Snn* comparisons tests (Table 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 2). Therefore, these 17 ESUs were regarded as independent units in the demographic analyses (Table 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. 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. 5, presented significantly negative Fu's F_s values, that is an indicator that these populations could

Table 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 Figs 1, 5 and 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	−17.675**	0.037295	0.001744	2.686	0.000	99999
B3	*Ct* Desertas	22	0.0033	6	0.7446	4	−1.3570	0.030160	0.00831	3.387	0.005	5.353
B3	*Ct* SV	12	0.0025	3	0.4394	3	0.1805	0.258264	0.28696**	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* ST_{North}	7	0.0019	3	0.5238	2	−0.9218	0.185941	0.022031	0.732	0.000	99999
D3	*Cst* ST_{South}	21	0.0083	10	0.8714	13	−3.281*	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

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 test (F_s), the sum of squared deviation statistic (SSD) and other relevant demographic parameters are given in Table 3.

Morphological studies

A synthetic table showing the quantitative results obtained in the morphological study is presented in Table 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. 2 and Appendix S4):

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). 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 5 and 6, Appendix S5), and population statistics (Table 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. 5B3 and by *Snn* tests (Table 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. 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 Ma) and S. Nicolau (0.1 Ma) (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 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 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. 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. 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 Ma vs. 6.2 Ma, 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. 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 Myr, Maio 21.1 ± 6.3 Myr, Santiago 10.3 ± 0.6 Myr, Santo Antão and Brava about 7.56 ± 0.56 and 5.9 ± 0.1 Myr, respectively, and S. Vicente about 6.6–5.68 Myr (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 Myr, being the easternmost and thus the oldest island of the north-western group (see Fig. 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 Ma, giving rise to the ancestor of the '*delalandii*' clade, which split about 6.9–5.9 Ma 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. 3), especially in *C. delalandii*, despite its large distribution range across all the southern islands (Fig. 1) as suggested by its very recent population expansion (Table 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 Ma 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 Ma, and finishing with the colonization of Santo Antão approximately 4.9–4.2 Ma. 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 Myr 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. 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 ventrolateral 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

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Details of material used in the network and population studies.

Appendix S2. Voucher specimens used on the morphological study (n = 275). See Materials and methods section for museum acronyms.

Appendix S3. 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.

Appendix S4. Terminology used for head scales.

Appendix S5. 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 bp) and RAG2 (834 bp) respectively. The analyses were conducted in MEGA4. Island and taxa codes as in Figs 1, 5 and 6.

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