Long-distance colonization and radiation in gekkonid lizards, *Tarentola* (Reptilia: Gekkonidae), revealed by mitochondrial DNA sequences

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Morphological systematics makes it clear that many non-volant animal groups have undergone extensive transmarine dispersal with subsequent radiation in new, often island, areas. However, details of such events are often lacking. Here we use partial DNA sequences derived from the mitochondrial cytochrome *b* and 12S rRNA genes (up to 684 and 320 bp, respectively) to trace migration and speciation in *Tarentola* geckos, a primarily North African clade which has invaded many of the warmer islands in the North Atlantic Ocean. There were four main invasions of archipelagos presumably by rafting. (i) The subgenus *Neotarentola* reached Cuba up to 23 million years (Myr) ago, apparently via the North Equatorial current, a journey of at least 6000 km. (ii) The subgenus *Tarentola* invaded the eastern Canary Islands relatively recently covering a minimum of 120 km. (iii) The subgenus *Makariogecko* got to Gran Canaria and the western Canary Islands 7–17.5 Myr ago, either directly from the mainland or via the Selvages or the archipelago of Madeira, an excursion of 200–1200 km. (iv) A single species of *Makariogecko* from Gomera or Tenerife in the western Canaries made the 1400 km journey to the Cape Verde Islands up to 7 Myr ago by way of the south-running Canary current. Many journeys have also occurred within archipelagos, a minimum of five taking place in the Canaries and perhaps 16 in the Cape Verde Islands. Occupation of the Cape Verde archipelago first involved an island in the northern group, perhaps São Nicolau, with subsequent spread to its close neighbours. The eastern and southern islands were colonized from these northern islands, at least two invasions widely separated in time being involved. While there are just three allopatric species of *Makariogecko* in the Canaries, the single invader of the Cape Verde Islands radiated into five, most of the islands being inhabited by two of these which differ in size. While size difference may possibly be a product of character displacement in the northern islands, taxa of different sizes reached the southern islands independently.

Keywords: *Tarentola*; 12S rRNA; cytochrome *b*; phylogeny; colonization; character displacement

1. INTRODUCTION

Many non-volant tetrapod groups have reached oceanic islands which have never been connected to other land masses. Such journeys involve floating or, more usually, rafting on buoyant vegetation, often over long distances. Colonizers arriving by such means frequently also then invade any nearby islands and may speciate repeatedly to produce adaptive radiations, for instance in the honey creepers and fruit flies of the Hawaiian archipelago (Carlquist 1974; Hollocher 1998). Although the general evidence for such events is strong, they have rarely been reconstructed in detail. Here we present such a historical analysis for the gekkonid lizards of the genus *Tarentola*.

Tarentola is a clade comprising around 20 species (Joger 1984*a,b,c*; Schleich 1984; Baha el Din 1997; Sprackland & Swinney 1998). Its members often climb, particularly on rocky surfaces in relatively dry areas and are active by night, although they often also bask during the day. The group is found across North Africa and on many of the islands which constitute Macaronesia including Madeira, the Selvages and the Canary and Cape Verde Islands (figure 1). An isolated species occurs in Cuba and the

Bahamas and another which is probably extinct has recently been described from Jamaica (Sprackland & Swinney 1998).

Tarentola is clearly related to some other African mainland geckos, in particular the large southern radiation including *Pachydactylus* (Russell 1976; Kluge & Nussbaum 1995), so the North Atlantic island taxa almost certainly came from the adjoining African mainland. As all the islands of Macaronesia are volcanic in origin without previous connections to other land masses (Schmincke 1976), *Tarentola* must have reached them by transmarine dispersal and the same is likely to be true for the West Indian species.

Although there is considerable variation in adult body size between species, *Tarentola* is anatomically quite uniform and no comprehensive estimate of phylogeny has been attempted using morphology. However, anatomical, biochemical (serum electrophoresis) and immunological (serum precipitin test) data have been employed to recognize groups of species which have been named as subgenera and to infer biogeography (Joger 1984*a,c*). The subgenera are *Sahelogecko* and *Saharogecko* in North Africa, *Tarentola sensu stricto* in North Africa, southern Europe and the eastern Canary Islands (Fuerteventura and Lanzarote), *Makariogecko* in the western Canaries (Gran Canaria, Tenerife, El Hierro, La Palma and La Gomera),
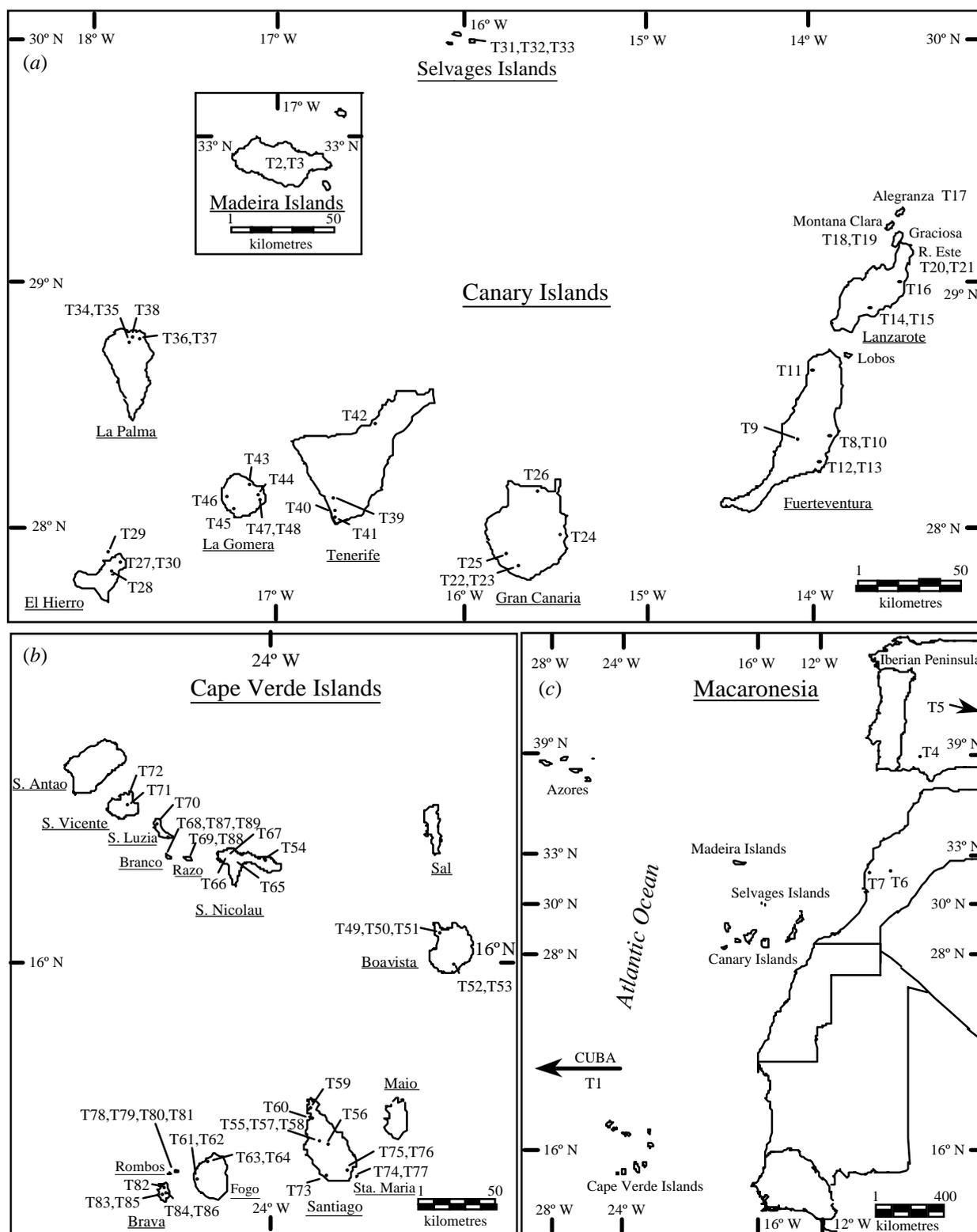
Figure 1. Localities of *Tarentola* samples (T); see table 1 for details. (*a*) Canary and Salvages Islands; (*b*) Cape Verde Islands; and (*c*) the position of the Selvages, Canary Islands and Cape Verde Islands within Macaronesia which lies *ca.* 15–40° N and 13–31° W.

the Cape Verde Islands, the Selvages and possibly Madeira, and *Neotarentola* which includes the West Indian *Tarentola americana*. More recently sequences of the cytochrome *b* and 12S rRNA mitochondrial genes have been used to elucidate the relationships of the Canary species (Nogales *et al.* 1998). These show there were two distinct

invasions of the Canary Islands. In order to investigate other colonizations in the North Atlantic and clarify the taxonomy of *Tarentola*, this work is extended here by including extensive material from the Cape Verde Islands as well as smaller samples from the rest of Macaronesia and from Cuba.

2. MATERIAL AND METHODS

(a) *Samples and localities*

A total of 89 individuals assigned to ten species and 17 subspecies of *Tarentola* were used in this study together with an individual each of *Pachydactylus* and *Hemidactylus* as outgroups. Their data are shown in table 1 and their localities in figure 1.

Total genomic DNA was extracted from 2–3 mm^3 of tail tissue following standard protocols described elsewhere (Harris *et al.* 1998; Carranza *et al.* 1999). The primers used in both amplification and sequencing were 12Sa and 12Sb for the 12S rRNA gene (Kocher *et al.* 1989) and cytochrome b_1, cytochrome b_2 (Kocher *et al.* 1989), the forward primer of cytochrome b_2 and CB3-3′ (Palumbi 1996) for the cytochrome *b* gene. Thermocycling consisted of an initial 90 s at 94 °C followed by 35 cycles of 30 s at 94 °C, 45 s at 45 °C and 1 min at 72 °C and then a single cycle of 10 min at 72 °C. Successful polymerase chain reaction (PCR) bands were cut out and purified using a silica-based method (Boyle & Lew 1995). The PCR products were sequenced using an ABI 377 automated sequencer (PE Biosystems, Warrington, UK), following the manufacturer's protocols.

(b) *Phylogenetic analysis*

The sequence data were aligned by hand with reference to the published secondary structure for 12S rRNA (Hickson *et al.* 1996) using an alignment editor (GDE; Smith *et al.* 1994). Alignment gaps were inserted to resolve length differences between sequences and those positions which could not be unambiguously aligned were excluded. For cytochrome *b* no ambiguous alignments were found and no gaps were postulated. All the cytochrome *b* sequences were translated into amino acids using the vertebrate mitochondrial code and no stop codons were detected, suggesting that all the sequences analysed were functional. The alignments are available from the authors on request.

Given that the various phylogenetic methods available often involve different assumptions about models of evolutionary change, the similarity of phylogenies produced by different methods increases confidence that the topologies involved are representative of the evolutionary history of the genes included. Therefore, two different methods (parsimony (MP) and neighbour joining (NJ)) were used in our phylogenetic analysis and the results compared. All analyses were performed using PAUP* (Swofford 1998) except where stated.

The parsimony analyses were heuristic searches involving tree bisection and reconnection (TBR) branch swapping and the MULTIPARS option with 100 random stepwise additions of taxa and gaps considered as a fifth state. Transversions were given the same weight as transitions in some analyses and four times the weight in others. The NJ (Saitou & Nei 1987) analyses were based on a maximum-likelihood (ML) model with HKY85 corrected distances (Hasegawa *et al.* 1985). The proportion of invariant sites, the shape parameter of the gamma (γ) distribution with eight rate categories and the transition:transversion (Ts:Tv) ratio were previously optimized onto an NJ tree under the JC model (Jukes & Cantor 1969). TrN-corrected (Tamura & Nei 1993) distance matrices using empirical Ts:Tv ratios and base frequencies were also employed in the distance analyses. The robustness of the inferred MP and NJ trees was tested by bootstrapping (Felsenstein 1985) (1000 heuristic pseudo-replications).

In order to assess the age of speciation events, molecular clock assumptions were incorporated. The likelihood ratio test (implemented in PUZZLE, v. 4.0) was used to test the statistical significance of the difference between the log likelihood of the trees calculated with and without the clock assumption.

The incongruence length difference (ILD) test (Mickevich & Farris 1981; Farris *et al.* 1994) was used to test for incongruence between the two genes used. For the ILD test, 10 000 heuristic searches with ten random addition replicates each were used and invariable characters were always removed before starting the analysis (Cunningham 1997).
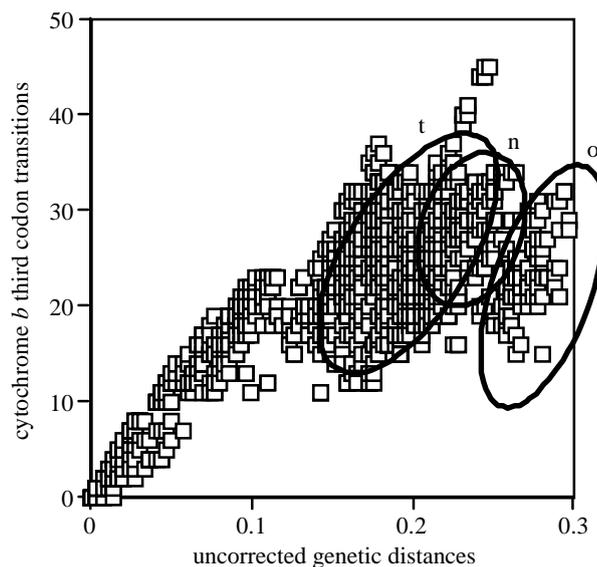

Figure 2. Observed number of transitions plotted against uncorrected distances for the cytochrome *b* third codon positions. The ringed transitions are those involved in the comparisons between the group in question and all other taxa included in the analysis. t, subgenus *Tarentola*; n, subgenus *Neotarentola*; o, outgroups.

3. RESULTS

(a) *Relationships of the main island assemblages*

A total of 623 bp for 91 individuals representing all the taxa concerned in this study were used to assess the relationships between the main species units. Out of these, 303 bp were derived from the cytochrome *b* gene (primers cytochrome b_1 and cytochrome b_2) and 320 bp from the 12S rRNA gene. Out of the 623 positions, 317 were variable and 258 parsimony informative. The ILD test showed that the two gene fragments were congruent (ILD $p > 0.45$) and could consequently be combined in a total evidence analysis. As evolutionary relationships may be obscured if sites have become saturated by multiple substitutions (Swofford *et al.* 1996), the 12S rRNA gene and each codon position of the cytochrome *b* gene were independently tested for saturation by plotting the observed proportions of transitions and transversions against the uncorrected sequence divergence. Only transitions of the third codon positions of the cytochrome *b* gene showed some degree of saturation in the deepest branches of the tree (figure 2). Therefore, subsequent phylogenetic analyses were performed both with and without third codon positions. When these positions (a total of 101 characters) were excluded, the number of variable and parsimony informative sites was reduced to 220 and 163, respectively. An overall Ts:Tv ratio of 3.8 was estimated for this data set.

Table 1. *Details of material and sequences used in the present study. Localities are shown in figure 1*

(BMNH prefixes the accession numbers of voucher specimens deposited in the Natural History Museum, London. DB-ULPGC-GG- prefixes the accession numbers of voucher specimens deposited in the Department of Biology, University of Gran Canaria, Canary Islands, Spain. LU indicates the specimens used by Nogales *et al.* (1998) and deposited in the Zoology Department, University of La Laguna, Tenerife, Canary Islands, Spain. Representatives of the reduced data set used for the molecular clock analysis.)

species	location on figure 1	locality	museum number	GenBank accession numbers 12S rRNA–cytochrome *b*
outgroups				
Hemidactylus (turcicus) parkeri[a]	—	Dhafra beach, near Ruwais, Abu Dhabi (UAE)	BMNH1996.169	AF186117–AF184989
Pachydactylus laevigatus[a]	—	Richtersveldt NW Cape Province, South Africa	—	AF186118–AF184990
genus *Tarentola*				
subgenus *Neotarentola*				
T. americana[a]	T1	Guantánamo, Cuba		AF186119–AF184991
subgenus *Tarentola s.* str.				
mainland				
T. mauritanica	T2	Funchal, Madeira[b]	—	—
T. mauritanica	T3	Ponta do Garajao, Madeira[b]	—	—
T. mauritanica	T4	Sevilla, Iberian Peninsula[b]	—	—
T. mauritanica	T5	Valéncia, Iberian Peninula[b]	—	—
T. mauritanica	T6	Marrakech, Morocco[b]	—	—
T. mauritanica	T7	Essaouira, Morocco[b]	—	—
Canary Islands				
T. angustimentalis	T8	Fuste, Fuerteventura	—	AF186121–AF184993
T. angustimentalis[a]	T9	Pájara, Fuerteventura	—	AF186122–AF184994
T. angustimentalis	T10	Fuste, Fuerteventura	—	AF186120–AF184992
T. angustimentalis	T11	Barranco Esquinzo, Fuerteventura[b]	—	—
T. angustimentalis	T12	Gran Tarajal, Fuerteventura[b]	—	—
T. angustimentalis	T13	Gran Tarajal, Fuerteventura[b]	—	—
T. angustimentalis	T14	Playa Quemada, Lanzarote[b]	—	—
T. angustimentalis	T15	Playa Quemada, Lanzarote[b]	—	—
T. angustimentalis	T16	Guatiza, Lanzarote[b]	LU	—
T. angustimentalis	T17	Alegranza[b]	—	—
T. angustimentalis	T18	Montana Clara[b]	—	—
T. angustimentalis	T19	Montana Clara[b]	—	—
T. angustimentalis	T20	Roque del Este[b]	—	—
T. angustimentalis	T21	Roque del Este[b]	—	—
subgenus *Makariogecko*				
Canary Islands and				
Selvages				
T. boettgeri boettgeri[a]	T22	Tauro, Gran Canaria	—	AF186123–AF184995
T. boettgeri boettgeri	T23	Tauro, Gran Canaria	—	AF186124–AF184996
T. boettgeri boettgeri	T24	Arinaga, Gran Canaria	—	AF186125–AF184997
T. boettgeri boettgeri	T25	Mogan, Gran Canaria[b]	—	—
T. boettgeri boettgeri	T26	Arucas, Gran Canaria[b]	—	—
T. boettgeri hierrensis[a]	T27	Tamaduste, El Hierro	—	AF186126–AF184998
T. boettgeri hierrensis	T28	Los Llanillos, El Hierro	—	AF186127–AF184999
T. boettgeri hierrensis	T29	Roque Grande de Salmor, Hierro[b]	LU	—
T. boettgeri hierrensis	T30	Tamaduste, Hierro[b]	—	—
T. bischoffi[a]	T31	Selvagem Grande, Selvages Islands	—	AF186128–AF185000
T. bischoffi	T32	Selvagem Grande, Selvages Islands[b]	—	—
T. bischoffi	T33	Selvagem Grande, Selvages Islands[b]	—	—
T. delalandii[a]	T34	Puntagorda, La Palma	—	AF186129–AF185001
T. delalandii	T35	Puntagorda, La Palma	—	AF186130–AF185002
T. delalandii	T36	San Andrés, La Palma[b]	—	—
T. delalandii	T37	San Andrés, La Palma[b]	—	—

(*Continued*)

Table 1. (*Cont.*)

species	location on figure 1	locality	museum number	GenBank accession numbers 12S rRNA–cytochrome *b*
T. delalandii	T38	Los Sauces, La Palma[b]	LU	—
T. delalandii[a]	T39	Adeje, Tenerife	—	AF186131–AF185003
T. delalandii	T40	El Palmar, Tenerife[b]	—	—
T. delalandii	T41	Punta de Rasca, Tenerife[b]	—	—
T. delalandii	T42	El Sauzal, Tenerife[b]	—	—
T. gomerensis	T43	Playa Hermigua, La Gomera	—	AF186132–AF185004
T. gomerensis[a]	T44	El Molinito, La Gomera	—	AF186133–AF185005
T. gomerensis	T45	La Rajita, La Gomera	—	AF186134–AF185006
T. gomerensis	T46	Valle Gran Rey, La Gomera[b]	—	—
T. gomerensis	T47	San Sebastian, La Gomera[b]	—	—
T. gomerensis	T48	San Sebastian, La Gomera[b]	—	—
Cape Verde Islands				
T. rudis boavistensis	T49	Sal Rei, Boavista	DB-ULPGC-GG-1	AF186137–AF185009
T. rudis boavistensis	T50	Sal Rei, Boavista	BMNH 1998.342	AF186138–AF185010
T. rudis boavistensis	T51	Sal Rei, Boavista	BMNH 1998.343	AF186139–AF185011
T. rudis boavistensis[a]	T52	Curral Velho, Boavista	BMNH 1998.344	AF186135–AF185007
T. rudis boavistensis	T53	Curral Velho, Boavista	DB-ULPGC-GG-2	AF186136–AF185008
T. darwini[a]	T54	Juncalhino, S. Nicolau	BMNH 1998.346	AF186164–AF185036
T. darwini[a]	T55	Assomada, Santiago	DB-ULPGC-GG-3	AF186166–AF185038
T. darwini	T56	Rui Vaz, Santiago	BMNH 1998.348	AF186167–AF185039
T. darwini	T57	Assomada, Santiago	DB-ULPGC-GG-4	AF186168–AF185040
T. darwini	T58	Assomada, Santiago	BMNH 1998.350	AF186169–AF185041
T. darwini	T59	Tarrafal, Santiago	BMNH 1998.351	AF186170–AF185042
T. darwini	T60	Chao Bom, Santiago	DB-ULPGC-GG-5	AF186171–AF185043
T. darwini[a]	T61	S. Filipe, Fogo	DB-ULPGC-GG-6	AF186172–AF185044
T. darwini	T62	S. Filipe, Fogo	BMNH 1998.354	AF186173–AF185045
T. darwini	T64	Ribeira ilheu, Fogo	BMNH 1998.356	AF186175–AF185047
T. caboverdiana nicolauensis[a]	T65	Airport, S. Nicolau	DB-ULPGC-GG-8	AF186162–AF185034
T. caboverdiana nicolauensis	T66	Tarrafal, S. Nicolau	BMNH 1998.358	AF186163–AF185035
T. caboverdiana nicolauensis	T67	Tarrafal–Ribeira Brava, S. Nicolau	BMNH 1998.359	AF186165–AF185037
T. caboverdiana raziana[a]	T68	Branco	—	AF186157–AF185029
T. caboverdiana raziana	T69	Razo	DB-ULPGC-GG-9	AF186161–AF185033
T. caboverdiana raziana	T70	S. Luzia	BMNH 1998.362	AF186160–AF185032
T. caboverdiana substituta	T71	W. Monte Verde, S. Vicente	DB-ULPGC-GG-10	AF186158–AF185030
T. caboverdiana substituta	T72	Baia das Gatas, S. Vicente	BMNH 1998.364	AF186159–AF185031
T. rudis rudis[a]	T73	Cidade Velha, Santiago	BMNH 1998.365	AF186140–AF185012
T. rudis rudis	T74	S. Maria	DB-ULPGC-GG-11	AF186141–AF185013
T. rudis rudis	T75	Praia, Santiago	DB-ULPGC-GG-12	AF186142–AF185014
T. rudis rudis	T76	Praia, Santiago	BMNH 1998.368	AF186143–AF185015
T. rudis rudis	T77	S. Maria	BMNH 1998.369	AF186144–AF185016
T. rudis hartogi[a]	T78	Rombos	DB-ULPGC-GG-13	AF186148–AF185020
T. rudis hartogi	T79	Rombos	DB-ULPGC-GG-14	AF186149–AF185021
T. rudis hartogi	T80	Rombos	BMNH 1998.372	AF186150–AF185022
T. rudis hartogi	T81	Rombos	BMNH 1998.373	AF186151–AF185023
T. rudis protogigas	T82	Puerto de Furna, Brava	BMNH 1998.374	AF186152–AF185024
T. rudis protogigas	T83	Porto Anciâo, Brava	DB-ULPGC-GG-15	AF186153–AF185025
T. rudis protogigas	T84	Cachaço, Brava	BMNH 1998.376	AF186155–AF185027
T. rudis protogigas	T85	Porto Anciâo, Brava	BMNH 1998.377	AF186154–AF185026
T. rudis protogigas	T86	Cachaço, Brava	DB-ULPGC-GG-16	AF186156–AF185028
T. gigas brancoensis[a]	T87	Branco	—	AF186145–AF185017
T. gigas gigas	T88	Razo	—	AF186147–AF185019
T. gigas brancoensis	T89	Branco	—	AF186146–AF185018

[a] The 32 specimens used by Nogales *et al.* (1998) for which sequences were downloaded from GenBank and incorporated into the present study.
[b] Representatives of the reduced data set used for the molecular clock analysis.

NJ and MP analysis both produced the tree shown in figure 3. The subgenera *Tarentola* and *Makariogecko* appear as sister clades with *Tarentola* (*Neotarentola*) *americana* arising outside them. Within *Makariogecko*, the Cape Verde Islands' species form a clade which is sister to *Tarentola*

delalandii and *Tarentola gomerae* from Tenerife/La Palma and La Gomera, respectively.

With a view to calculating the approximate ages of origin of the three *Tarentola* subgenera considered here, the validity of the molecular clock was tested. An ML
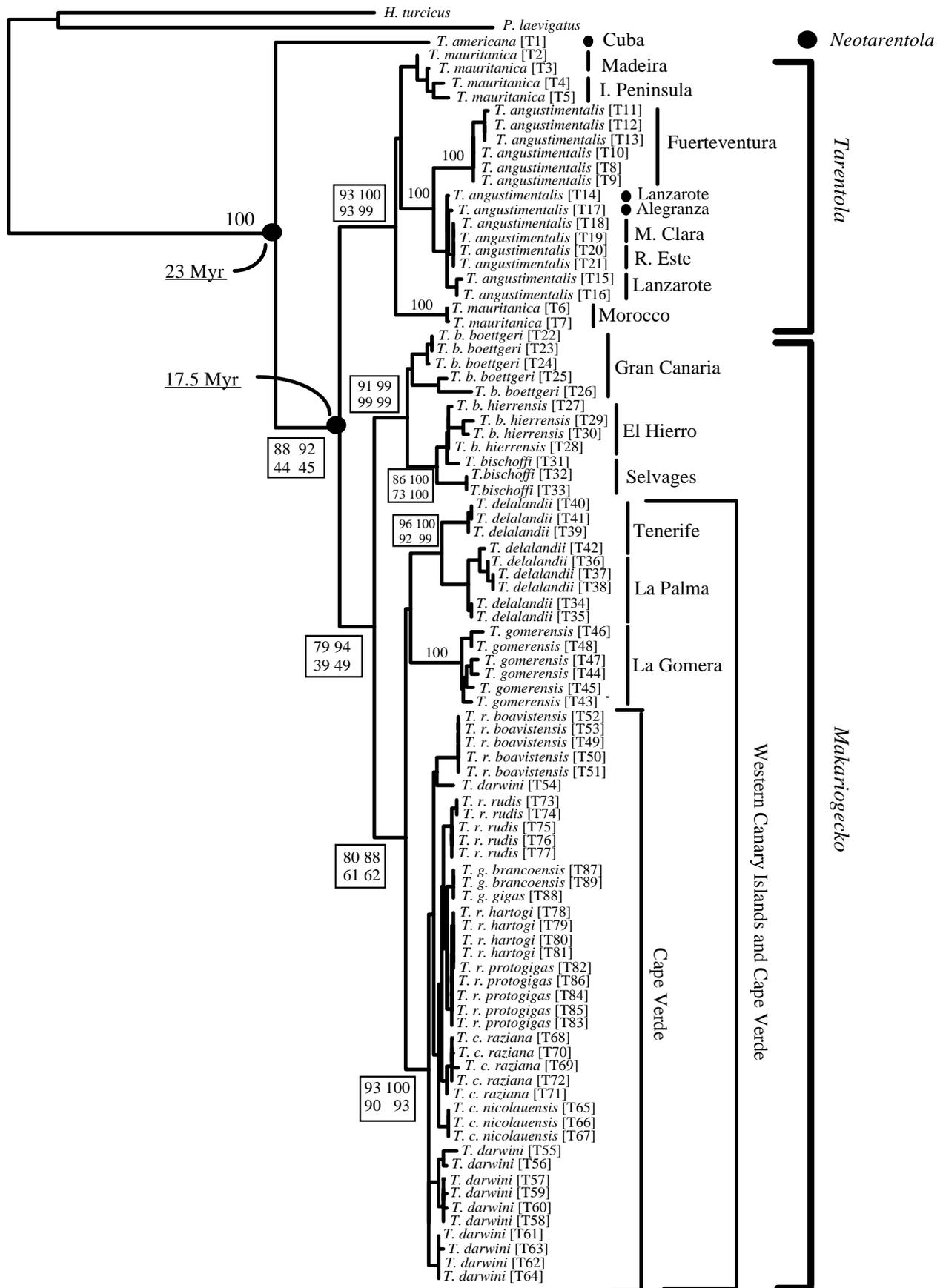
Table 2. *Pairwise comparisons of percentage differences between DNA sequences of Cape Verde* Tarentola

(Only clear monophyletic groups derived from figure 4 have been considered; genetic distances were corrected with the Kimura two-parameter model; SN, São Nicolau; Boa, Boavista; ST, Santiago; F, Fogo; Br, Branco; Ra, Razo; SL, Santa Luzia; SV, São Vicente; SM, Santa Maria; Ro, Rombos; Bra, Brava. The question mark denotes that only one specimen of *T. darwini* from São Nicolau was available so internal variability could not be calculated.)

	1	2	3	4	5	6	7	8	9	internal variability
1 *T. darwini* (SN)	—	—	—	—	—	—	—	—	—	?
2 *T. r. boavistensis* (Boa)	7.81%	—	—	—	—	—	—	—	—	0.05%
3 *T. darwini* (ST)	7.80%	7.24%	—	—	—	—	—	—	—	1.66%
4 *T. darwini* (F)	7.55%	7.27%	6.39%	—	—	—	—	—	—	0.37%
5 *T. caboverdiana* (SN)	8.52%	8.50%	8.65%	7.41%	—	—	—	—	—	0.37%
6 *T. caboverdiana* (Br, Ra, SL, SV)	7.94%	7.19%	7.70%	6.87%	5.86%	—	—	—	—	0.83%
7 *T. r. rudis* (ST, SM)	7.85%	7.39%	8.33%	7.91%	5.16%	4.55%	—	—	—	0.35%
8 *T. r. hartogi / T. r. protogigas* (Ro, Bra)	8.70%	8.33%	9.06%	8.65%	6.26%	4.99%	3.40%	—	—	0.14%
9 *T. gigas* (Br, Ra)	8.30%	8.18%	8.44%	8.27%	5.90%	5.23%	3.16%	4.27%	—	0.38%

tree (HKY85 model with empirical Ts:Tv ratios and base composition and excluding the third codon positions of the cytochrome *b* gene) was calculated for a reduced data set (see table 1). This was compared with an ML tree constructed under molecular clock assumptions. The results show no significant difference between the likelihoods of the two trees (likelihood ratio test statistic $(-2\log\Lambda) = 19.95$ which approximates to a χ^2_{17} distribution under the null hypothesis; $p > 0.05$) and, therefore, the hypothesis that the sequences evolve in a clock-like way cannot be rejected. To calibrate the clock, a 0.6% genetic divergence per million years was used based on a previous analysis of the lacertid lizard *Gallotia* from the Canary Islands. This involved 12S rRNA and cytochrome *b* excluding third codon positions (S. Carranza and E. N. Arnold, personal observations). Using data from *Gallotia* to calibrate the molecular clock of *Tarentola* is appropriate as both genera are heterothermic and are relatively closely related in being non-iguanian squamates. If this calibration is accepted *T. (Neotarentola) americana* diverged from the rest of *Tarentola* around 23 Myr ago and the separation between the subgenus *Tarentola* and *Makariogecko* probably occurred *ca.* 17.5 Myr ago.

(b) *Relationships within* Makariogecko

To analyse the phylogenetic relationships within *Makariogecko*, a subset of 53 individuals was used including members of nearly all described taxa from the Selvages, Canary Islands and Cape Verde Islands and three indivi-

duals of *Tarentola angustimentalis* from Fuerteventura which were used as an outgroup. The amount of sequence was increased by adding 381 bp of cytochrome *b* (using primers cytochrome b_2 forward and CB3-3′). The new alignment consisted of 1076 positions (684 bp cytochrome *b* and 392 bp of 12S rRNA), 426 being variable and 397 parsimony informative. A saturation analysis of transitions and transversions was carried out for 12S rRNA and each codon position of the cytochrome *b* gene (see § 3(a)). In all cases there was no indication of saturation and, consequently, the third codon positions of cytochrome *b* were not eliminated from the analyses. An overall Ts:Tv ratio of 4.2 was estimated for this data set. An ILD test showed that the 12S rRNA and cytochrome *b* partial sequences were congruent with each other (ILD, $p > 0.70$) and could therefore be combined in a total evidence analysis.

The results of the phylogenetic analysis are shown in figure 4, with both the NJ and MP trees having the same general topology. The amount of genetic divergence between the sequences of different Cape Verde taxa is shown in table 2.

The Cape Verde taxa again constitute a monophyletic unit which is sister to a poorly supported clade consisting of the west Canary species *Tarentola delalandii* and *Tarentola gomerensis*. An ML ratio test of the molecular clock was performed for a data set including the sequences of all the Cape Verde individuals shown in figure 4 and using *T. delalandii* (T39) as an outgroup. The results showed

Figure 3. (*Opposite*) NJ tree for the 89 representatives of *Tarentola* plus two outgroup taxa based on an ML model: $-\ln$ likelihood $= 3270.18960$, Ts:Tv ratio $= 3.67$, proportion of invariable sites $= 0.013258$ and γ-shape parameter $= 0.28756$. Cytochrome *b* third codon positions were not included. Bootstrap support for particular nodes is shown in the boxes with the figures indicating the percentage support for different analyses. Upper left, bootstrap support derived by NJ using the ML model excluding the cytochrome *b* third codon positions. Upper right, bootstrap support derived by NJ under the TrN model and including the cytochrome *b* third codon positions. Lower left, bootstrap support derived by MP (Ts = Tv) and excluding the cytochrome *b* third codon positions. Lower right, bootstrap support derived by MP (Ts = Tv) and including cytochrome *b* third codon positions. When the difference between the four bootstrap support figures was < 5% only the average value is shown and no figures are given where none of the four exceed 50%. The underlined numbers indicate the age of the two oldest speciation events in the genus *Tarentola* considered here. The codes in brackets [T1, T2, etc. . . .] indicate the samples used, details of which can be found in table 1 and their localities in figure 1.
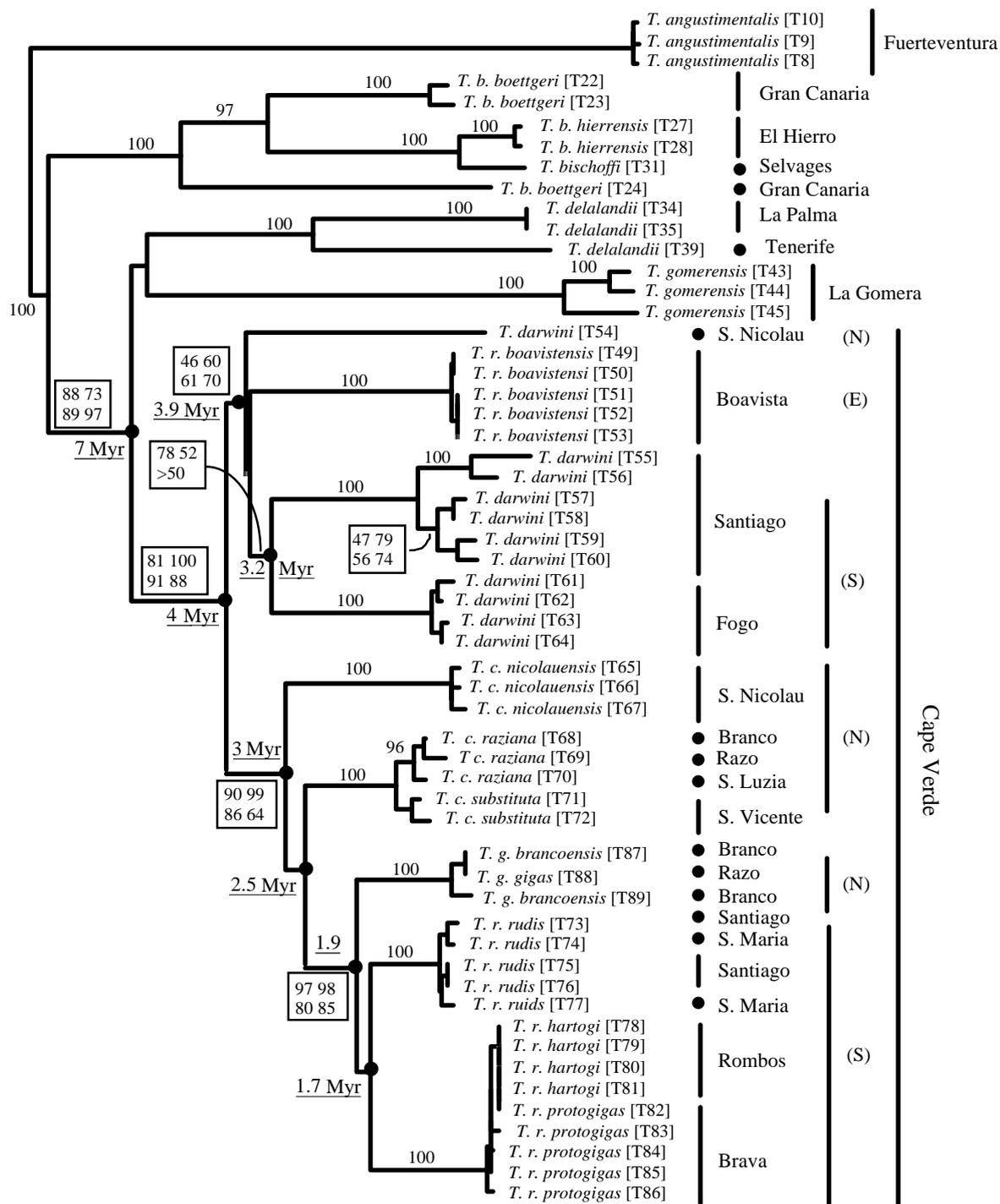
Figure 4. NJ tree for the 53 representatives of *Makariogecko* plus three *T. angustimentalis* used as an outgroup based on an ML model: ln likelihood = 6357.66426, Ts:Tv ratio = 4.2, proportion of invariable sites = 0.384 and γ-shape parameter = 0.6254. Cytochrome *b* third codon positions were included in the analysis. Bootstrap support for particular nodes is shown in boxes with the figures indicating the percentage support for different analyses. Upper left, bootstrap support derived by NJ using a specified ML model. Upper right, bootstrap support derived by NJ under the TrN model. Lower left, bootstrap support derived by MP (Ts = Tv). Lower right, bootstrap support derived by MP (Tv = 4 and Ts = 1). When the difference between the four bootstrap support figures was < 5% only the average value is shown and no figures are given when none of the four exceed 50%. The underlined numbers indicate the age of the speciation events. The codes in brackets [T22, T23, etc. . . .] indicate the samples used, details of which can be found in table 1 and their localities in figure 1. N, E and S, the northern, eastern and southern groups of the Cape Verde Islands.

that there is no significant evidence of a difference between the likelihoods of the two trees (likelihood ratio test statistic $(-2\log\Lambda) = 52.94$ which approximates to a χ^2_{40} distribution under the null hypothesis; $p > 0.05$) and, therefore, the hypothesis that the sequences evolve in a clock-like way cannot be rejected. To calibrate the clock, a 1.96% genetic divergence per million years was used, based on a previous analysis of the lacertid lizard *Gallotia*

from the Canary Islands. This involved 12S rRNA and cytochrome *b* including third codon positions (S. Carranza and E. N. Arnold, personal observations). The approximate dates were 7 Myr for the origin of the ancestor of all Cape Verde *Tarentola* and 4 Myr for the beginning of the radiation of species still extant in the archipelago.

Of the species currently recognized in the Cape Verde Islands our data suggest that only *Tarentola gigas* is monophyletic, although its two subspecies cannot be differentiated on molecular grounds.

Tarentola rudis is polyphyletic. The population from Boavista, which is known as *Tarentola rudis boavistensis*, is most closely related to populations assigned to *Tarentola darwini*, while *Tarentola rudis rudis* may possibly be sister to *Tarentola rudis protogigas* plus *Tarentola rudis hartogi* (which are molecularly nearly identical) and all three are closely related to *T. gigas*. The molecular similarity of *T. r. protogigas* and *T. r. hartogi* may reflect a very recent divergence of the two populations (Avise 1994).

Tarentola caboverdiana is related to *T. gigas* and associated *T. rudis* populations and the three subspecies represented each appear monophyletic. However, while *Tarentola caboverdiana raziana* and *Tarentola caboverdiana substituta* form a clade, *Tarentola caboverdiana nicolauensis* may constitute a separate lineage basal to all the above forms (except *T. 'rudis' boavistensis*), although bootstrap support for this is not strong.

As presently understood, *T. darwini* has three well-differentiated populations, those on Santiago and Fogo being sisters while another on São Nicolau forms an unresolved trichotomy with these and with *T. 'rudis' boavistensis*, the three constituting the sister group of all other Cape Verde *Tarentola*.

The extended analysis presented here corroborates the findings of Nogales *et al.* (1998) including the following: *Tarentola boettgeri hierrensis* of Hierro is more closely related to *Tarentola bischoffi* of the Selvages than to *Tarentola boettgeri boettgeri* of Gran Canaria. The latter form is paraphyletic with respect to the other subspecies of *T. boettgeri*, two animals from the south-west of Gran Canaria (T22 and T23) being more closely related to *T. b. hierrensis* and *T. bischoffi* than to an individual from the north-east of the island (T24) (see figure 4).

4. DISCUSSION

(a) *Patterns of colonization and speciation*

The tree in figure 3 clearly indicates that *T.* (*Neotarentola*) *americana* of the West Indies is not closely related to any of its congeners in either the Canary or Cape Verde Islands. There is consequently no evidence that it reached the West Indies via these archipelagos and it must represent an independent transmarine colonization, perhaps directly from the west coast of North Africa. It is likely that the colonizer was carried to the West Indies on rafting vegetation by the clockwise water circulation of the North Atlantic, first on the southward running Canary current and then on its eastward continuation, the North Equatorial current, which eventually passes close to the West Indies. Molecular clock considerations indicate that the *Neotarentola* lineage separated from the other *Tarentola* considered here around 23 Myr

ago. The colonization of the West Indies may have been as long ago as this, but if *Neotarentola* radiated in North Africa first (subsequently becoming extinct there), the colonization may have been more recent. Given that the position of the continents have not changed much since the Early Miocene (20 Myr ago) (Smith & Briden 1977; Adams 1981) the distance travelled by the ancestor of *T.* (*Neotarentola*) *americana* is likely to have been at least 6000 km. This is an exceptionally long transmarine journey for a non-flying organism, although some reptiles in Mauritius and the other Mascarene islands east of Madagascar apparently originated in tropical Australia over 4500 km away (E. N. Arnold and J. J. Austin, personal observations).

Neotarentola underwent at least some modest differentiation in the West Indies as two subspecies are recognized: *Tarentola a. americana* in Cuba and *Tarentola a. warreni* in the Bahamas (Schwartz & Henderson 1991). As noted, a second apparently West Indian species of *Tarentola*, *Tarentola albertschwartzi*, has recently been described (Sprackland & Swinney 1998). It is based on a single specimen deposited in the Royal Scottish Museum in Edinburgh in 1884, which is believed to have originated in Jamaica; if so, the population from which it comes may well be extinct. The largest known *Tarentola*, *T. albertschwartzi*, is morphologically distinct from *T. americana* and other species, but is superficially most similar to *Tarentola deserti* of Morocco and Algeria, a member of *Tarentola s. s.* If this reflects a real relationship and if its locality is valid, *T. albertschwartzi* may represent a second independent colonization of the West Indies.

The phylogeny of the Canary Islands *Tarentola* (figures 3 and 4) indicates two independent colonizations of this archipelago by *Tarentola*. The first, which may have occurred as long as 17 Myr ago, was by the ancestor of extant *Makariogecko* which is found on Gran Canaria and the western islands as well as the Selvages. The second involved a member of the continental *T. mauritanica* complex (*Tarentola s. s.*) that evolved to produce *T. angustimentalis*, which inhabits the eastern Canary Islands of Fuerteventura, Lanzarote and surrounding islets.

It is possible that *Makariogecko* also occurred in the archipelago of Madeira which lies *ca.* 350 km north of the Selvages. Only *T. mauritanica* is now known from Madeira and appears to represent an anthropogenic introduction, being apparently first recorded as late as 1988 (Báez & Biscoito 1993). Individuals from this island are very similar to animals from the Iberian Peninsula in the gene fragments examined here (figure 3) (Nogales *et al.* 1998). However, animals assigned to *T. bischoffi* but with some distinctive morphological features have also been recorded from Madeira in the past (Joger 1984*b*), although later opinion is that the locality is erroneous (Joger 1985, 1998; Nogales *et al.* 1998). This dismissal may be premature as three independent samples are known. These comprise one specimen in the Museum Alexander Koenig, Bonn (ZFMK 20552), another presented to the Natural History Museum, London by Andrew Smith in or before 1865 (BMNH 65.5.4.93) and seven specimens from P. B. Webb received by the same museum in the early 1840s or before (BMNH XXI.60a). Thus, a population morphologically similar but not identical to *T. bischoffi* may really have existed on Madeira into the 19th century.
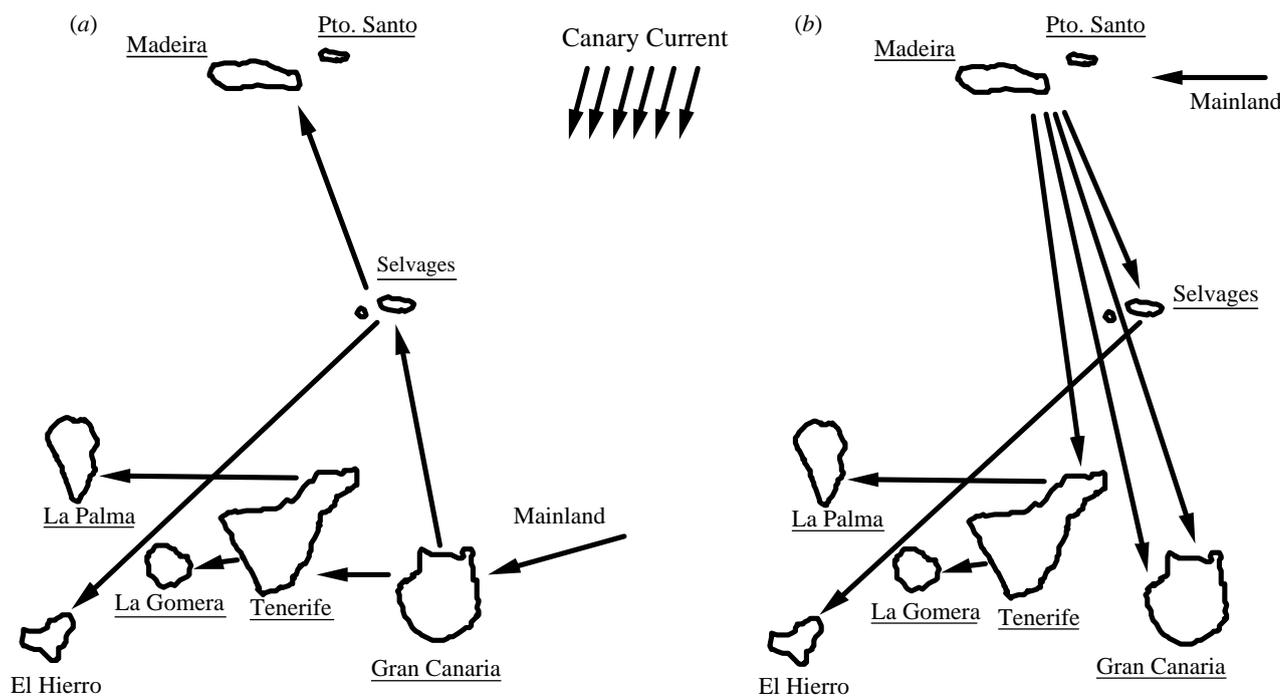
Figure 5. Two alternative hypotheses of colonization of the Selvages and central and west Canary Islands by *Makariogecko*:
(*a*) via Gran Canaria and (*b*) via the Madeira archipelago.

Within *Makariogecko* a parsimonious hypothesis of colonization of the Canary Islands from the mainland, in terms of the number and length of the journeys involved and in agreement with the phylogeny shown in figure 4, is that Gran Canaria was invaded first, with subsequent colonization of Tenerife to produce the ancestor of *T. delalandii* which later colonized Gomera resulting in *T. gomerensis*. At a later date *T. delalandii* invaded La Palma from Tenerife. The population remaining on Gran Canaria became *T. boettgeri* and, as it is apparently paraphyletic (figure 4), this could have been the source of *T. bischoffi* in the Selvages which in turn invaded Hierro to produce *T. b. hierrensis*. This putative pattern of colonization involves six journeys or seven if the presence of a population in the Madeira archipelago is accepted (figure 5*a*). Initial invasions of Tenerife or Gomera rather than Gran Canaria are equally parsimonious in terms of journey number, although they would require a longer first excursion. This may have happened in the case of the arthropod genera *Pimelia* and *Dysdera* which colonized Tenerife first and Gran Canaria later on (Juan *et al.* 1996, 1997; Arnedo 1998). An initial invasion of La Palma or Hierro by *Tarentola* is not a possibility, as these islands are too young being less than 2 Myr old compared with 7–17.5 Myr for the presence of the *Makariogecko* in the Canaries (see figures 3 and 4).

The above colonization hypothesis involves a journey of *ca.* 200 km to the Selvages and perhaps another of at least 350 km to the Madeira archipelago, both of which would have been more or less against the prevailing north-east trade winds and Canary current. An alternative hypothesis not involving journeys counter to prevailing dispersal agents involves initial colonization of the Madeira archipelago (Joger 1984*b*), with propagules

from this source successively invading Tenerife, Gran Canaria (twice) and the Selvages, the rest of the colonization sequence being the same as in the previous hypothesis (figure 5*b*). Such a version of events would not be much less parsimonious, involving eight instead of seven journeys and would be in equal agreement with the accepted phylogeny. Madeira itself is too young to have been the source area for the Canary *Makariogecko*, but the nearby island of Porto Santo, with an estimated age of 12–19 Myr (Féraud *et al.* 1981; Portugal Ferreira *et al.* 1988) is sufficiently old.

The larger of the Selvages Islands is thought to be several million years old (Portugal Ferreira *et al.* 1988), but apparently underwent a fairly recent period of submergence. Most of the present subaerial land is the result of volcanic activity in the Quaternary period (Bravo & Coello 1978). Consequently, if the present post-submergence *Makariogecko* populations of the Selvages came directly from Gran Canaria, it would be expected that the degree of differentiation in DNA sequence would be small. In fact it is substantial (> 7.8% of Kimura 2-parameter of genetic divergence, perhaps equivalent to a separation of *ca.* 3–4 Myr). On the other hand, this difference would be understandable if both islands were colonized at widely different times from the Madeira archipelago. Further support for this possibility is the presence of the Madeiran lacertid *Lacerta dugesi* on the Selvages but not in the Canaries.

Although it might be expected that the Cape Verde Islands were colonized by *Tarentola* from coastal West Africa just 500 km away to the east, they turn out to have been invaded from the western Canary Islands, probably either from Gomera or Tenerife. The propagule or propagules concerned presumably made the 1400 km journey

by rafting on the southward-flowing Canary current. It was already appreciated that the ancestor of some of the Cape Verde species arrived in this way (Joger 1984*b*, 1985; Guerrero *et al.* 1997) but the present investigation makes it clear that all Cape Verde forms constitute a clade and are likely to be descended from a single colonizing species from the Canaries which may have made the journey as long as 7 Myr ago.

The phylogeny presented in figure 4 indicates that the initial invasion of the Cape Verde archipelago was of the northern island group. It is uncertain which of the northern islands was colonized first, but it may have been São Nicolau as this is the only one to have populations more or less basal on both the branches formed by the initial dichotomy of Cape Verde *Tarentola*. If so, there were presumably subsequently modest movements through the closely spaced islands to the north-west of São Nicolau, as far as Santo Antão resulting in differentiation producing *T. gigas* and the subspecies of it and *Tarentola caboverdiana*.

It is most parsimonious to assume that the eastern and southern Cape Verde Islands were colonized from the northern group. Southward movement would have again been facilitated by the Canary current, which flows on through the Cape Verde archipelago. One or more invasions resulted in the origin of *T. 'r'. boavistensis* of Boavista and the distinctive *T. darwini* populations on Santiago and Fogo, something which is estimated to have occurred 3.2 Myr ago or longer. At least one later southward invasion, up to 1.9 Myr ago, produced the *T. rudis* populations on Santiago (*T. r. rudis*), Brava and Fogo (*T. r. protogigas*) and Rombos (*T. r. hartogi*).

It is known that the eastern Cape Verde Islands are the oldest in the archipelago, dating back to the Mesozoic period and that island age decreases in a westward direction, but no information about age of origin is available for several of the islands. Where it is (for instance Santiago 10.3 Myr and Brava 5.5 Myr; Mitchell-Thomé 1985) the ages are older than the estimated time of arrival of *Tarentola* on these islands.

(b) *Radiation and community structure*

Makariogecko in the Canaries forms a small radiation of three species one of which has three recognized subspecies. All the taxa are approximately the same body size and none exist in sympatry. In contrast, the Cape Verde Islands have a radiation of at least five species and 11 named subspecies and two species occur together on several of the main islands. Sal has apparently no *Tarentola* and Santo Antão, São Vicente, Santa Luzia, Boavista, Maio, Rombos and Brava have just a single species. In the northern islands there is very marked size difference between the sympatric forms, *T. caboverdiana* growing to *ca.* 60 mm from snout to vent, while *T. gigas* can exceed 125 mm. In the southern islands size difference is less marked, but on Santiago and Santa Maria *T. rudis* is markedly larger than *T. darwini* and the same is true of *T. r. protogigas* on Fogo. However, this is unlikely to be the result of character displacement. *Tarentola gigas* forms a clade with *T. rudis* so it is more parsimonious to assume the latter species was already quite large when it reached the southern islands. Nor is size necessarily maintained by the presence of another species, as the populations of

T. r. protogigas and *T. r. hartogi* which occur alone on Brava and Rombos, respectively, are still big.

(c) *Taxonomy*

The phylogenetic information presented here necessitates modification of the nomenclature applied to some Canary and Cape Verde *Tarentola*. The *Tarentola* population on the Selvages has recently been regarded as a full species, *T. bischoffi* (see Joger 1998), but this course makes *T. boettgeri* of Gran Canaria and Hierro paraphyletic since *T. bischoffi* is more closely related to the El Hierro population *T. b. hierrensis* than to *T. b. boettgeri* of Gran Canaria (Nogales *et al.* 1998). It therefore seems appropriate to regard all three forms as subspecies of *T. boettgeri*.

Although the taxonomy of *Tarentola* in the Cape Verde Islands has been substantially clarified (Joger 1984*a,b,c,* 1993; Schleich 1984, 1987, 1988; International Commission for Zoological Nomenclature 1990), mitochondrial DNA sequences make it clear that further revision is needed. Nine taxonomic or geographical units show a substantial divergence from each other of *ca.* 3–9% compared with a mean internal variability of less than 0.55% (see table 2). In this paper no changes to names are suggested and any modification of the nomenclature of the Cape Verde forms awaits more extensive molecular and morphological work on the group.

5. CONCLUDING REMARKS

Tarentola is clearly a persistent transmarine colonizer. Apart from at least four long-distance journeys to archipelagos, it has made many excursions within them: a minimum of five in the Canaries and islands to the north and quite possibly 16 in the Cape Verde archipelago. These geckos may be pre-adapted to transmarine dispersal by rafting. As well as the low food requirements typical of heterotherms, primitive occurrence in dry habitats probably means *Tarentola* are able to survive long periods without fresh water. Climbing ability and the possession of adhesive pads on the toes makes attachment to rafting vegetation more secure and the fact that *Tarentola* is often found on or near beaches increases the chances of being washed out to sea on such debris. Another predisposing factor is the pattern of water circulation in the North Atlantic which fortuitously tends to carry propagules from the north-west African coast and adjoining areas towards islands such as the Canaries and from there the Cape Verde archipelago and, eventually, the West Indies. Objects can be transported quite quickly by this means. The speed of the Equatorial currents in the mid-Atlantic may be almost $100 \, \text{km} \, \text{day}^{-1}$ and of the Canary current 14–$21 \, \text{km} \, \text{day}^{-1}$ (Guppy 1917). At the latter rate, a journey between the Canaries and the Cape Verde Islands could take just ten weeks.

Mitochondrial DNA reveals the diversity of the forms in the Cape Verde Islands, leading to a greater understanding of their systematics. Such knowledge of evolutionary units is essential for future conservation of this unique radiation. Some taxa are already very restricted, for instance *T. gigas* is now confined to the islets of Razo and Branco although recent fossils show it was more widely distributed in the past. The current economic

development in the Cape Verde Islands is likely to increase pressure on such taxa.

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