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# Investigating the origin of transoceanic distributions: mtDNA shows *Mabuya* lizards (Reptilia, Scincidae) crossed the Atlantic twice

**Abstract** Phylogenies with even a rough time scale can be used to investigate the history of non-volant taxa with disjunct distributions in widely separated land areas that were once connected. Basic methods for doing this are discussed. A partial phylogeny of *Mabuya* based on mtDNA (305 bp cytochrome *b*, 379 bp 12S rRNA and 388 bp 16S rRNA) is used to show that this genus invaded tropical America from Africa twice in the last 9 Myr, once reaching the American mainland and once the oceanic island of Fernando de Noronha, two journeys each of at least 3000 km. In general, phylogenetic evidence for multiple invasions is less equivocal than that suggesting a single invasion, which is more prone to sampling artefacts. Two alternative hypotheses explaining the presence of *Mabuya* in both Africa and tropical America are refuted on the basis of molecular clock considerations, namely that the occurrence of *Mabuya* in these continents pre-dated their separation over 100 My ago and that it was introduced from one continent to the other by human activities. Like several other lizard groups that have made successful long-distance transmarine colonizations, *Mabuya* has done this on many occasions. Phylogenetic results are also compatible with a SE Asian or Australasian origin of *Mabuya* followed by westward expansion.

**Key words** disjunct distribution, Fernando de Noronha, *Mabuya*, mtDNA, skinks, transmarine colonization.

## Introduction

Taxa incapable of aerial dispersal often occur in land areas that were previously connected but are now widely separated by sea. A number of questions arise in such situations. Do representatives of a taxon in the two geographical areas really form a clade? If so, why is it found in both areas? There are three possibilities here: (1) the taxon may have been widespread before the two areas separated; (2) presence in one area may result from natural transmarine migration by floating or dispersal on rafts of vegetation; (3) such presence may be due to very recent human introduction. At least, in cases 2 and 3, it is also possible to ask in which direction spread occurred and whether there was more than one dispersal event.

In fact, if the taxon was widespread before the two geographical areas parted, there are a number of possibilities. Representatives of the taxon in the two geographical areas may have diverged before these separated (Fig. 1a), or they may have diverged immediately following separation in a vicariance event (Fig. 1b). A third possibility is that the taxon had diversified in one geographical area and one or more of its lineages later extended into the second area so that these lineages alone were subjected to a vicariance event when separation took place (Fig. 1c). In this last case, subsequent differential extinction could convert the perceived phylogenetic pattern into either of those indicated in Fig. 1a and 1b.

### Approaches to investigation

Questions about disjunct distributions, involving previously connected land areas, may be answerable if a robust phylogeny with even an approximate time scale is available. This may determine whether a taxon really is a clade, and the age of the node or nodes at which subclades in the two areas diverge may distinguish between possibilities 1–3. Ages close to that of the separation of the land areas, or preceding them, would support geographical separation by this event. Extremely recent divergence or lack of it would be compatible with human introduction, while intermediate ages would favour natural

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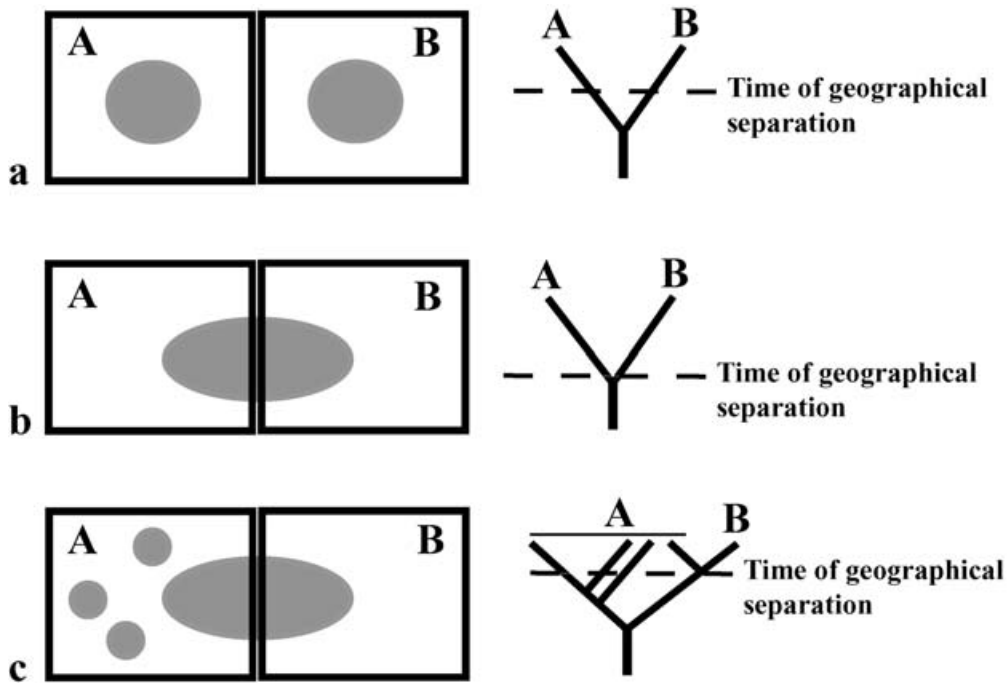


**Figure 1** Possible events when a taxon was present on a land mass which subsequently split into two parts, A and B. (a) Taxon divided into two sections before geographical separation; (b) Taxon divided into two parts by a vicariance event caused by geographical separation; (c) Taxon had long history of diversification in A, only one of its lineages divided into two parts by geographical separation.

transmarine dispersal. Obviously, given the limits of accuracy of any time scale, there will be instances where separation of land areas and natural transmarine dispersal cannot be distinguished, and recency alone does not guarantee human as opposed to natural dispersal, but some cases for vicariance and natural dispersal are likely to be robust. Phylogenetic topology may also suggest the direction of any movement, since the phylogeny of species in an area of origin is often likely to be paraphyletic with respect to subclades arising by invasion of the second area. The phylogeny may also provide information on the number of invasions that have taken place and give some idea of their timing. However, it must be borne in mind that preliminary evidence for a single invasion and for multiple invasions (two or more) may be differently affected by the addition of more species to the phylogeny. Evidence for a single invasion consists of the presence of a solitary clade in the invaded area that is derived from a paraphyletic assemblage in the source region. In contrast, a multiple invasion is characterized by more than one separate clade in the invaded area each of which has a different closest relative in the source region. In the case of an apparent single invasion that appears to have diversified subsequently, adding more taxa to the phylogeny from the area of origin may show that components of the supposedly single invading clade have different closest relatives in the source area, so revealing that invasion was actually multiple. Adding additional species from the source region to the phylogeny is unlikely to disturb a case for multiple introduction, although it might increase the number of occasions on which colonization occurred. More thorough initial sampling can limit the likelihood of erroneously assuming a single invasion but difficulties in obtaining material may restrict such a strategy. Also, there will always be a risk that taxa in the area of origin that would have revealed multiple invasion are unknown or extinct. A conclusion of multiple invasion is consequently often more secure than one of a single colonization.

Sampling can also affect estimated times of dispersal (Emmerson *et al*., 2000). The approximate age of the node at which an invading clade diverges from its nearest relative in the source region is often taken as the maximum time since dispersal, while the first divergence (if any) within the invading clade provides a minimum estimate. If the real nearest relative in the source region is absent from the sample of species investigated, an older, deeper node may be taken as indicating the maximum time since dispersal. For groups that are still extant in both widely separated geographical areas concerned, DNA sequence can often provide both the phylogeny and the rough clock required to explore such very disjunct terrestrial distributions. Fossils may supplement a timed phylogeny and detailed fossil records might even replace it for answering some questions, but for most taxonomic groups such evidence is not available. Where a timed phylogeny raises the possibility of human introduction, literature and archive records may provide corroborating evidence.

## *Mabuya* in Africa and America

The genus *Mabuya* is widely distributed in most warmer parts of the world except Australasia and the Pacific. The group is related to other lygosomine skinks, an assemblage that originated in South-East Asia or Australasia (Greer, 1977; Honda *et al*., 2000). One interpretation of its range based on natural dispersal is that *Mabuya* first colonized the rest of southern Asia from this area, then the African plate including Arabia, and finally reached the Cape Verde islands (Carranza *et al*.,


**Figure 2** Main areas around the Atlantic Ocean where *Mabuya* occurs. Arrows show the direction of the main currents.

2001) and tropical America by rafting westwards across the Atlantic ocean (Greer, 1977). Alternatively *Mabuya* could have invaded America from Asia and then perhaps crossed the Atlantic eastwards to Africa. In contrast to these possibilities of active dispersal, *Mabuya* may have been present in Africa and South America for a long time and then split into two units when these continents separated approximately 119–105 My ago (McLoughlin, 2001). Recent intercontinental human introductions of *Mabuya* seem unlikely as species in the different continents are morphologically well differentiated from each other.

In the Neotropics *Mabuya* is represented by about 15 species. All but one occur on the mainland of America or in the West Indies and appear to form a clade (Greer *et al*., 1999). Among its apparent synapomorphies are absence of pterygoid teeth, elevated number of presacral vertebrae (average number 29 or more) and the production of fully formed young from extremely small eggs that are almost entirely nourished by placentation (Blackburn & Vitt, 1992). The remaining species, *M. atlantica* is confined to the oceanic archipelago of Fernando de Noronha, which lies in the Atlantic Ocean at 3°54′S and 32°25′W, 360 km off the coastal city of Natal (northeast Brazil) (Fig. 2). The archipelago forms the top of a submarine volcano surrounded by waters 4000 m deep, covers a land area of only 26 $km^2$ and its age is estimated as 3.3–1.7 My ago (Almeida, 2000). *M. atlantica* lacks the morphological synapomorphies of the other American species, having pterygoid teeth, only 26 presacral vertebrae and large-yolked, thick-shelled eggs, the primitive reproductive strategy in *Mabuya*. In any scenario involving westward dispersal across the Atlantic, there may have been a single invasion of the New World, in which case *M. atlantica* from Fernando de Noronha could be a relict primitive form that is sister to the more derived mainland clade. Alternatively, there may have been two invasions, one of the mainland and another directly of Fernando de Noronha.

The various hypotheses just outlined, about the origins of the present-day distribution of *Mabuya*, are tested here using a phylogeny based on fragments of three mitochondrial genes totalling 1072 bp. A rough time scale is provided by comparing molecular divergence rates in *Mabuya* to those in three other scleroglossan lizard groups in which rates have been calibrated against a geophysical event.

## Material and methods

A total of 46 individual skinks were used in this study (see Table 1). They included 38 individuals of 24 *Mabuya* species from Asia, Africa, Cape Verde archipelago, Fernando de Noronha, South America and the West Indies and eight outgroup taxa (four Lygosominae and four Chalcidinae). DNA extraction and amplification was carried out using methods described by Carranza *et al*. (2000, 2001). Primers employed in both amplification and sequencing were cytochrome *b*1 and cytochrome *b*2 (Kocher *et al*., 1989) for the cytochrome *b* gene, 12Sa and 12Sb for the 12S rRNA gene (Kocher *et al*., 1989) and 16SL1 (5′-CCG TGC AAA GGT AGC ATA ATC AC-3′; Carranza *et al*., 1999) and 16Sbr-3′ (Palumbi, 1996) for the 16S rRNA gene. DNA was extracted for five museum specimens of *M. atlantica* collected by H. N. Ridley during the 1887 Royal Society expedition to Fernando de Noronha, and subsequently kept in alcohol at the Natural History Museum, London. As with other old museum material used in recent studies of island lizards, special attention was paid to the extraction and amplification processes (Carranza *et al*., 1999, 2001). Despite all five *M. atlantica* specimens being more than 100 years old, DNA was not very degraded and therefore no extra primers were needed for the independent amplification of the three mitochondrial fragments.

DNA sequences were aligned using Clustal W (Thompson *et al*., 1994) with default parameters (gap extension penalty = 5, gap opening penalty = 10, delay divergent sequences = 40%). No gaps had to be postulated to align the cyt*b* sequences. These were translated into amino acids using the vertebrate mitochondrial code and no stop codons were observed, suggesting that all the sequences analysed were

| Species | Code | Locality | Museum number | GenBank accession numbers 12S rRNA/Cytochrome *b*/ 16S rRNA |
|---|---|---|---|---|
| Family Scincidae | | | | |
| Subfamily Chalcidinae | | | | |
| *Amphiglossus igneocaudatus* | — | Toliaria, Amboasary, Madagascar | | AF280114/AF280125/**AY151443** |
| *Pamelaescincus gardineri* | — | Silhouette, Seychelles | | AF280117/AF280128/**AY151446** |
| *Androngo trivittatus* | — | Toliaria, Amboasary, Madagascar | | AF280115/AF280126/**AY151444** |
| *Gongylomorphus fontenayi* | — | Mare Longue, SW Mauritius | | AF280121/AF280132/**AY151449** |
| Subfamily Lygosominae | | | | |
| *Cyclodomorphus casuarinae* | — | Tasmania | | AF280118/AF280129/**AY151447** |
| *Egernia whitii* | — | Tasmania | | AF280119/AF280130/**AY151448** |
| *Cryptoblepharus boutoni* | — | Gabriel Island, Mauritius | | AF280116/AF280127/**AY151445** |
| *Leiolopisma telfairi* | — | Round Island, Mauritius | | AF280122/AF280133/**AY151450** |
| Genus *Mabuya* | | | | |
| Tropical Asia | | | | |
| *M. multifasciata-1* | E111014 | Tropical Asia | | **AY151424/AY151496/AY151458** |
| *M. multifasciata-2* | E111015 | Cardamon Mountains, Cambodia | | **AY151425/AY151497/AY151459** |
| *M. multifasciata-3* | E111034 | Tropical Asia | | **AY151418/AY151490/AY151452** |
| *M. multifasciata-4* | E111035 | Tropical Asia | | **AY151419/AY151491/AY151453** |
| *M. multifasciata-5* | E111036 | Tropical Asia | | **AY151441/AY151513/AY151487** |
| Mainland Africa and Turkey | | | | |
| *M. macuilabris casuarinae* | M71 | Fogo I., Mozambique | | AF280138/AF280270/**AY151474** |
| *M. margaritifer* | M69 | Malema, Mozambique | | AF280136/AF280268/**AY151473** |
| *M. capensis* | M72 | Kouga Mts. E. Cape, South Africa | | AF280139/AF280271/**AY151475** |
| *M. sulcata* | E111037 | Kamanjab, Namibia | | **AY151420/AY151492/AY151454** |
| *M. perrotettii-1* | E111017 | Ghana, W. Africa | | **AY151417/AY151489/AY151451** |
| *M. perrotettii-2* | E111018 | Ghana, W. Africa | | **AY151439/AY151511/AY151485** |
| *M. perrotettii-3* | E111019 | Ghana, W. Africa | | **AY151440/AY151512/AY151486** |
| *M. vittata-1* | E111039 | Tozeur, Tunisia | | **AY151421/AY151493/AY151455** |
| *M. vittata-2* | E111040 | Tozeur, Tunisia | | **AY151442/AY151514/AY151488** |
| *M. vittata-3* | E111042 | Osmandere, Turkey | | **AY151422/AY151494/AY151456** |
| *M. vittata-4* | E111043 | Osmandere, Turkey | | **AY151423/AY151495/AY151457** |
| *M. aurata* | E11102 | Kisehir, Turkey | | **AY151435/AY151507/AY151469** |
| Seychelles | | | | |
| *M. wrightii* | M2 | Fregate Island, Seychelles | | AF280124/AF280135/**AY151472** |
| Socotra | | | | |
| *M. socotrana-1* | M73 | Socotra I., Yemen | | AF280140/AF280272/**AY151476** |
| *M. socotrana-2* | M74 | Socotra I., Yemen | | AF280141/AF280273/**AY151477** |
| Cape Verde archipelago | | | | |
| *M. vaillanti* | M49 | Feijoal, Fogo | BMNH 2000.9 | AF280198/AF280330/**AY151483** |
| *M. delalandii* | M45 | Chã das Caldeiras, Fogo | BMNH 2000.18 | AF280185/AF280317/**AY151482** |

**Table 1** Details of material and sequences used. Genbank accession numbers of new sequences obtained for this study are in bold; all the rest are from Carranza *et al.* (2001).

| | | | | |
|---|---|---|---|---|
| *M. fogoensis nicolauensis* | M17 | Faro de Barril, Saõ Nicolau | DBULPGC-106 | AF280172/AF280304/**AY151481** |
| *M. fogoensis antaoensis* | M60 | Chã de Lagoa, Santo Antão | BMNH 2000.25 | AF280177/AF280309/**AY151480** |
| *M. stangeri* | M44 | Calhau, São Vicente | DBULPGC-109 | AF280167/AF280299/**AY151479** |
| *M. spinalis maioensis* | M53 | Morrinho, Maio | DBULPGC-113 | AF280159/AF280291/**AY151478** |
| America | | | | |
| Archipelago of Fernando de Noronha | | | | |
| *M. atlantica-1* | E11120 | Fernando de Noronha, Brazil | BMNH 1888.1.19.17 | **AY151429/AY151501/AY151463** |
| *M. atlantica-2* | E11121 | Fernando de Noronha, Brazil | BMNH 1888.1.19.18 | **AY151430/AY151502/AY151464** |
| *M. atlantica-3* | E11125 | Fernando de Noronha, Brazil | BMNH 1888.1.19.19 | **AY151431/AY151503/AY151465** |
| *M. atlantica-4* | E11127 | Fernando de Noronha, Brazil | BMNH 1888.1.19.20 | **AY151432/AY151504/AY151466** |
| *M. atlantica-5* | E11130 | Fernando de Noronha, Brazil | BMNH 1888.1.19.20a | **AY151433/AY151505 /AY151467** |
| Brazil | | | | |
| *M. frenata* | E11107 | Mato Grosso do Sul, SW Brazil | | **AY151427/AY151499/AY151461** |
| *M. agilis* | E11101 | Mato Grosso do Sul, SW Brazil | | **AY151434/AY151506/AY151468** |
| *M. dorsivittata* | E11106 | Brasilia, Central Brazil | | **AY151426/AY151498/AY151460** |
| *M. heathi* | E11108 | Exu, NE Brazil | | **AY151428/AY151500/AY151462** |
| Colombia | | | | |
| *M. nigropunctata* | E111016 | Puerto Inirida, Colombia | | **AY151438/AY151510/AY151484** |
| West Indies | | | | |
| *M. bistriata-1* | E11103 | Talparo, Trinidad | | **AY151436/AY151508/AY151470** |
| *M. bistriata-2* | E11104 | Talparo, Trinidad | | **AY151437/AY151509/AY151471** |

(*Note: BMNH – prefixes the accession numbers of voucher specimens deposited in the Natural History Museum, London. DBULPGC – prefixes the accession numbers of voucher specimens deposited in the Department of Biology, University of Gran Canaria, Canary Islands, Spain*.

**Table 1** *Continued...*

functional. The 12S rRNA sequences were adjusted manually with the help of an alignment editor (BioEdit v.5.0.6; Hall, 2001) and with reference to the published secondary structure for this gene (Hickson *et al*., 1996). Overall, only two small hypervariable regions (5–8 bp of the 12S rRNA and 28–42 bp of the 16S rRNA) could not be unambiguously aligned and were therefore excluded from further analysis because of their uncertain positional homology.

Three different methods of phylogenetic analysis were employed and their results compared. These were maximum likelihood (ML), Bayesian analysis, and parsimony (MP). Modeltest v. 3.06 (Posada & Crandall, 1998) was used to select the most appropriate model of sequence evolution under the Akike Information Criterion for the ML and Bayesian analyses. This was the General Time Reversible model (GTR) taking into account the number of invariable sites (I) and the shape of the gamma distribution (G). Both ML and MP analyses were performed in PAUP*4.0b10 (Swofford, 2002) and were heuristic searches involving tree bisection and reconnection (TBR) branch swapping. We used 1000 random stepwise additions of taxa with gaps considered as a fifth state in the MP analyses, and 10 random stepwise additions of taxa with gaps excluded for the ML analyses. In the MP analyses, transitions (ts), transversions (tv) and gaps were given the same weight. Robustness of the MP tree was assessed by bootstrap analysis (Felsenstein, 1985) and involved 1000 pseudo-replications. Due to computational limitations inherent in the ML method it was not possible to obtain bootstrap values for the ML (GTR+G+I) tree.

Bayesian phylogenetic analyses (Rannala & Yang, 1996; Mau *et al*., 1999) were performed with MRBAYES v. 2.01 (Huelsenbeck & Ronquist, 2001) using the GTR+I+G model (Lanave *et al*., 1984; Yang, 1996) with parameters estimated as part of the analysis and four incrementally heated Markov chains with the default heating values. All analyses started with randomly generated trees and ran for $1.5 \times 10^6$ generations, with sampling at intervals of 100 generations that produced 15000 sampled trees. To ensure that our analyses were not trapped on local optima the data set was run independently four times, each occasion beginning with different starting trees. After the four runs, the log-likelihood values of sample points

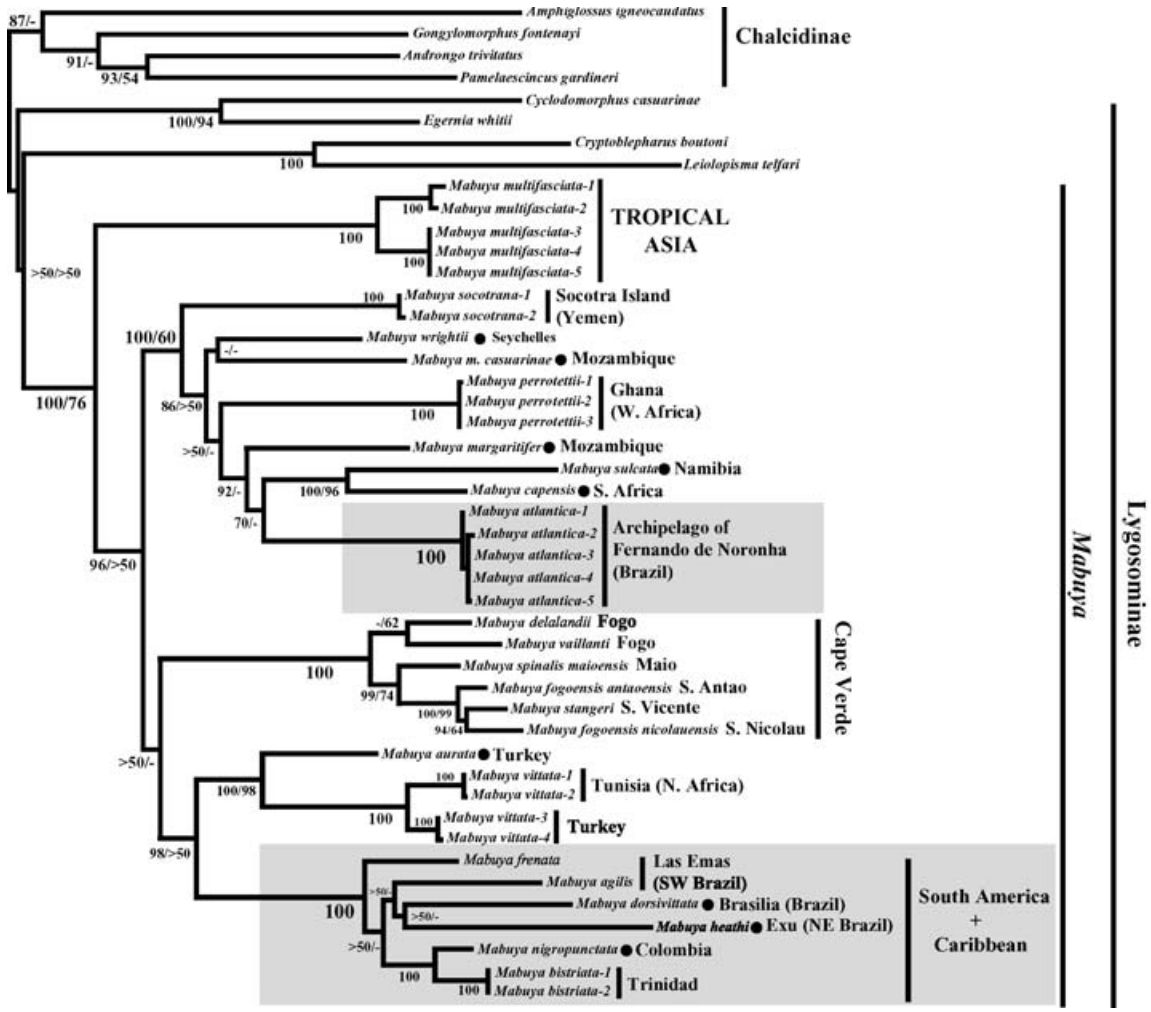


**Figure 3** ML phylogenetic tree of *Mabuya* (GTR+I+G; -log likelihood: 10200.87208) based on mitochondrial cytochrome *b*, 12S rRNA and 16S rRNA partial sequences. Numbers adjacent to the nodes indicate, from left to right, the posterior probability for the Bayesian analysis and the bootstrap support for the MP analysis (two most parsimonious trees of 2040 steps). The - symbol indicates that a particular node has not been recovered. Where only a single number is shown posterior probabilities and bootstrap values are identical.

were plotted against the generation time and all the trees prior to reaching stationarity were discarded making sure that we did not retain burn-in samples. A 50% majority rule consensus tree was generated combining the last 5000 sampled trees of each one of the four independent analyses. The frequency of any particular clade of the consensus tree represents the posterior probability of that clade (Huelsenbeck & Ronquist, 2001); only values above 95% were considered to indicate that nodes were significantly supported.

Where appropriate, topological constraints were generated using MacClade v.4.0 (Maddison & Maddison, 1992) and compared to our optimal topologies using the Shimodaira-Hasegawa (SH) (Shimodaira & Hasegawa, 1999) test implemented in PAUP*4.0b10 (Swofford, 2002).

In order to infer approximate dates for the colonization events, Kimura 2-parameters genetic distances were calculated for all possible pairwise comparisons including only the cyt*b* and 12S rRNA genes. The 16S rRNA gene was excluded from the distance analysis, so that the results could be compared with other lizard divergence rates calculated for the same regions of the cyt*b* and 12S rRNA genes with the Kimura 2-parameters correction. The divergence rates were calibrated using an estimated age of 1.1 My for El Hierro island in the Canary archipelago (Guillou *et al*., 1996), and were similar in all three available cases, ranging from 1.96% per My for *Gallotia* lacertids (Carranza *et al*., 2000) to 2.4% per My for *Tarentola* gekkonids (Carranza *et al*., 2002), with the *Chalcides* scincids evolving at approximately 2.1% per My (Carranza & Arnold, pers. obs.).

## Results

The analyses included 305 bp of cytochrome *b*, 379 bp of 12S rRNA and 388 bp of the 16S rRNA gene. Of the 1072 positions in the combined data, 452 were variable and 377 parsimony-informative. The results of the phylogenetic analyses are summarized in Fig. 3. ML and Bayesian analysis produced almost identical topologies, which differed only slightly from the MP strict consensus of the two most-parsimonious trees found. All three methods clearly indicate independent origins for *M. atlantica* of Fernando de Noronha and for the mainland American clade, the two units having different closest

| Tree | - Log likelihood | Δ - Log likelihood | SH *p* |
|---|---|---|---|
| *Unconstrained ML tree (Fig. 3)* | 10200.87208 | (best) | |
| *All American* Mabuya *monophyletic* | 10230.06156 | 29.18949 | 0.039* |

SH, Shimodaira–Hasegawa test; *indicates $p < 0.05$ and suggests that the constrained and unconstrained trees are significantly different.

**Table 2** Statistical support for alternative hypotheses of phylogenetic relationships of Mabuya.

relatives in the Old World and being separated by eight nodes on the phylogeny (Fig. 3). This result was associated with high posterior probability values.

*M. atlantica* from Fernando de Noronha forms a clade with the seven Afrotropical forms included in the analysis, while the six other American and Caribbean *Mabuya* form a very well supported monophyletic group that is sister to a clade comprising *M. aurata* and *M. vittata*, from Turkey and North Africa. The Cape Verde species of *Mabuya* also constitute a well supported monophyletic group (Carranza *et al*., 2000). All three methods of analysis additionally support, with high posterior probability, the basal position of *M. multifasciata*, the one tropical Asian form included in the analysis, and the monophyly of the genus *Mabuya*. In order to further test the apparent polyphyly of the American *Mabuya*, the ML tree from Fig. 3 was constrained so that all American species formed a monophyletic group. The constrained tree was then compared with the unconstrained one (Fig. 3) using the SH test. The results show that both trees are significantly different (Table 2) and, therefore, the hypothesis of monophyly of all American *Mabuya* included in the analysis is rejected. The maximum genetic distance observed within the non-Asian *Mabuya* clade is 18%, suggesting a maximum age of 7–9 My for the origins of the two American units.

## Discussion

The estimated ages of the two American lineages indicate that their separation from African *Mabuya* could not result from continental splitting approximately 119–105 My ago (McLoughlin, 2001). This would only be possible if the rate of sequence divergence was more than ten times slower than in three other scleroglossan lizard groups, which is extremely unlikely. Conversely, recent human introduction across the Atlantic would involve unbelievably fast divergence rates as people have only crossed the ocean in the last thousand years or so. The maximum ages of the Fernando de Noronha and American mainland lineages indicates that they arose when Africa and South America were already widely separated by the Atlantic Ocean, the distance between them being very similar to that at the present time. So the ancestors of these lineages must have made very long transmarine journeys, presumably on natural rafts of vegetation. The distance involved is likely to be in excess of 3000 km.

The well supported phylogenetic topology, in which Old World *Mabuya* are paraphyletic with respect to American ones, indicates that movement across the Atlantic was westwards from Africa to the New World. Topology and the SH test also strongly indicate that there were two independent crossings, one to Fernando de Noronha and one to the American mainland. As noted in the Introduction, this is likely to be a more robust conclusion than if a single origin of American *Mabuya* was suggested. A westward transmarine journey is also favoured by prevailing currents and winds: the South Equatorial Current runs from the Gulf of Guinea to tropical South America (Fig. 2) and winds here are also westerly (Guppy, 1917). The restricted sampling of African species means that it is impossible to be confident that the actual sister taxa of *M. atlantica* and of the American mainland clade of *Mabuya* are included. This prevents more accurate dates for the invasions of the New World being inferred at the present time.

That *Mabuya* has crossed the Atlantic twice is not totally surprising, as the genus has apparently spread from Africa to Socotra, the Seychelles, Aldabra (Arnold, 1976), the Comores, Madagascar (twice – Mausfeld *et al*., 2000) and the Cape Verde archipelago within which it has made at least 17 inter-island journeys (Carranza *et al*., 2001). The phylogeny indicates that both trans-Atlantic colonizations were independent of the invasion of the Cape Verde islands. It is also in agreement with an Asian origin of *Mabuya* followed by westward spread into Africa and then America, rather than eastward movement to America and then perhaps Africa.

Other detailed phylogenies based on DNA sequence corroborate the evidence provided here that lizards have often made very long transmarine journeys. Such voyages sometimes resulted in the colonization of distant archipelagos and, more rarely, continents. Chameleons apparently made a number of journeys between Africa and Madagascar and perhaps elsewhere (Raxworthy *et al*., 2002). The Mascarene islands in the southwest Indian Ocean received reptile colonists not only from Madagascar 600 km to the west (Austin & Arnold, 2001), but also from South-East Asia 6000 km away (Arnold, 2000; Austin & Arnold, pers. obs.). *Tarentola* geckos travelled about the same distance across the Atlantic Ocean from north Africa to the West Indies (Carranza *et al*., 2000) and *Hemidactylus* geckos traversed the southern Atlantic to South America (Carranza & Arnold, pers. obs.).

Some lizard groups are much more prone to transmarine journeys than others. Such voyages are generally much commoner in geckos and skinks than in agamids, lacertids and teiids. Variation also occurs within geckos and skinks with particular groups making repeated journeys while others from the same source areas fail to do so. This suggests colonization across oceans is not a random process and the proclivities of

the organisms concerned are important in determining whether it takes place. Such proclivities include frequent occurrence on marine beaches, tolerance of salt water and desiccation, and ability to maintain position on natural rafts.

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