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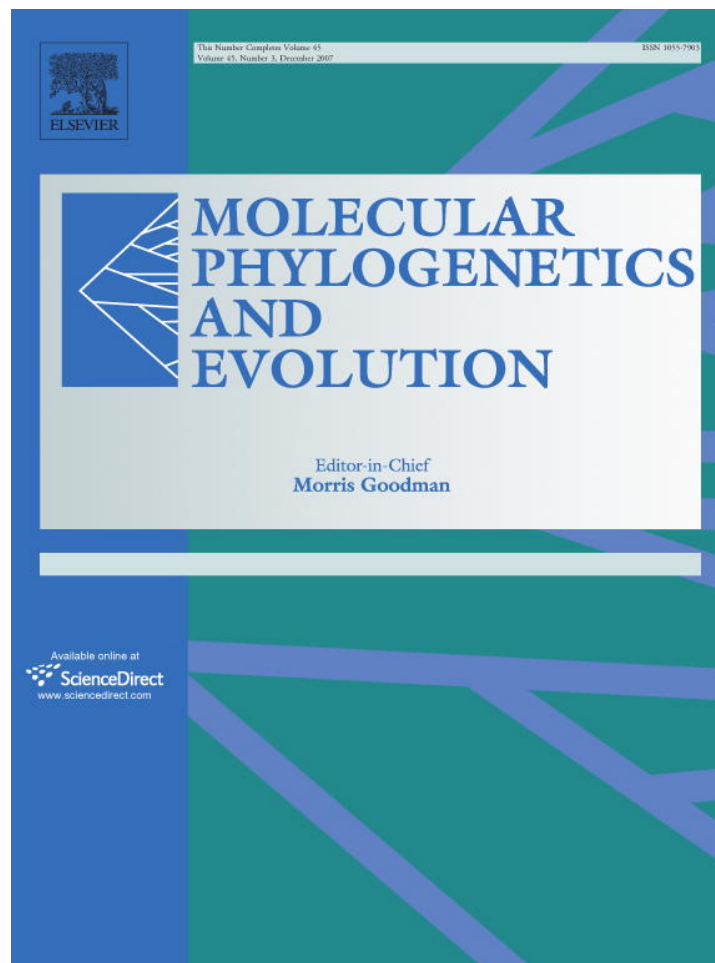
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Geographical patterns of deep mitochondrial differentiation in widespread Malagasy reptiles

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Abstract

Using sequences of the mitochondrial 16S rRNA gene, we reconstructed the phylogeography of six widely distributed Malagasy reptiles: two gekkonid lizard species, *Phelsuma lineata* and *Hemidactylus mercatorius*; two chameleons, the *Calumma brevicorne* complex, and *Furcifer lateralis*; and two skinks, *Trachylepis gravenhorstii* and *Trachylepis elegans*. Genetic differentiation among major haplotype lineages was high and in some cases indicates or confirms species status of the divergent populations. Maximum uncorrected sequence divergences were between 2.2% and 8.3% within the various species or species complexes. Haplotype lineages were exclusive to geographic regions, except in the commensal *H. mercatorius* where in three anthropogenic habitats coexistence of haplotype lineages was observed, possibly due to human translocation. The eastward flowing rivers Mangoro and Mananara may represent barriers to gene flow in the case of three species each. Some species sampled from humid eastern and arid western Madagascar showed no differentiation between populations from these two regions; instead the pattern observed was in several cases more concordant with a differentiation along a north-south axis.

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Keywords: Madagascar; Phylogeography; Squamata; *Calumma brevicorne*; *Calumma amber*; *Calumma crypticum*; *Furcifer lateralis*; *Phelsuma lineata*; *Hemidactylus mercatorius*; *Trachylepis gravenhorstii*; *Trachylepis elegans*

1. Introduction

The island of Madagascar is known for its particular geographic history and for the high level of endemism of its biota (e.g., Goodman and Benstead, 2003). Its biodiversity is not only extraordinarily distinctive and diverse, but also endangered, making its exploration an urgent matter. The knowledge of even its vertebrates is far from complete, and new species have been discovered and described at a vigorous pace in the last few years (Yoder et al., 2005).

Madagascar's bioclimatic zonation follows a primary east-west division. A central chain of mountains spaced

in north-south direction causes the humidity transported by eastern trade winds to rain down on the eastern escarpment where humid tropical rainforest occurs. Little rainfall reaches the west and especially the south, where dry deciduous forests and arid spiny forest (in the south-west) is the predominant type of vegetation.

Based on the opening of the Indian Ocean by the northward drift of India, and the correlated onset of the trade winds that reach Madagascar, Wells (2003) estimates the origin of the Malagasy eastern rainforests in the Eocene or Oligocene. In the northern fourth of Madagascar, the rainforests occupy much of the center and reach the north-western coast around the Sambirano estuary. Here they are formed by a special kind of monsoon rainforest of possibly younger Late Miocene or Pliocene age (Wells,

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2003). Schatz (1999) also divides Madagascar into a bioclimatic eastern and a western region, each of which are subdivided into several domains. Much of the northern fourth of Madagascar is included in the eastern region. A zoogeographical zonation proposed to explain the distribution of Madagascar's reptiles (Angel, 1942) is largely in agreement with this bioclimatic zonation (Glaw and Vences, 1994: 11–14), cf. Fig. 1. Several studies have supported east-west vicariance causing species formation in Madagascan vertebrates. Thus, in the context of recurrent climatic oscillations, this may well have been one of the triggers causing the large species diversity in Madagascar's fauna. The underlying process would be that the sharp ecological distinction between eastern and western habitats constitutes a barrier to gene flow, causing a basal split between eastern

and western clades in the phylogeography of species of initially wide distribution, eventually leading to speciation. Yoder and Heckman (2006) refer to this hypothesis as the 'ecogeographic constraint'.

In reptiles, the examples of east-west vicariance come from species pairs such as the geckos *Ebenavia inunguis* (east) and *Ebenavia maintimainty* (west), *Matoatoa spanringi* (east) and *Matoatoa brevipes* (west), and *Paragehyra gabriellae* (south-east) and *P. petiti* (west), and the boid snake subspecies *Sanzinia madagascariensis madagascariensis* (east) and *S. m. voluntany* (west) (Nussbaum and Raxworthy, 1998; Nussbaum et al., 1998; Vences and Glaw, 2003). Similar examples from the amphibians include the treefrogs *Boophis albilabris* (east) and *Boophis occidentalis* (west), and *Boophis tephraeomystax* (east) and *Boophis doulioti* (west) (Andreone et al., 2002; Glaw and Vences, 1994: 90; Vences and Glaw, 2002).

However, (Yoder and Heckman (2006)) have recently challenged this traditional perspective on Madagascar's biogeography. They show that in mouse lemurs of the genus *Microcebus* the primary phylogenetic split, instead of being between east and west, is between a northern and a southern clade. Each clade contains several species, spread over the diverse ecological habitats of east and west, without recurrent east-west vicariant patterns at shallower phylogeographic levels (Yoder and Heckman, 2006; Yoder et al., 2000). Deep interspecific north-south splits can also be found in the dwarf chameleons of the genus *Brookesia* (Raxworthy et al., 2002) and in the colubrid snake genus *Madagascarophis* (Nagy et al., in press); a vicariant north-south pattern of sister species pairs occurs in several reptile groups, e.g., the boids *Acrantophis madagascariensis* (north) and *Acrantophis dumerili* (south), the geckos *Uroplatus alluaudi* (north) and *Uroplatus malahelo* (south), and the chameleons *Brookesia lolontany* (north) and *Brookesia nasus* (south) (Nussbaum and Raxworthy, 1994; Raxworthy and Nussbaum, 1995; Vences and Glaw, 2003). Interestingly, there is no obvious biogeographic barrier which would explain this primary biogeographic division between north and south.

Early studies on lemur biogeography (Martin, 1972) have proposed a division of Madagascar that is largely congruent with the one of Angel (1942), reflecting the same climatic conditions that differentiate the central highlands, the east coast, and the West and South. Multi-species phylogeographic studies (Pastorini et al., 2003) have emphasized the importance of three large rivers as barriers in species distribution. Wilmé et al. (2006) postulate that river basins at intermediate altitude functioned as stable refugia during cold glacial periods. Climatic oscillations have caused forests to move up and down the slopes, enabling and severing gene flow and thereby promoting speciation (cf. Fig. 1).

Although the complex topography of northern Madagascar may be seen as predictive of intensive speciation (Raxworthy and Nussbaum, 1995), none of these models provides a convincing explanation for the origin and main-

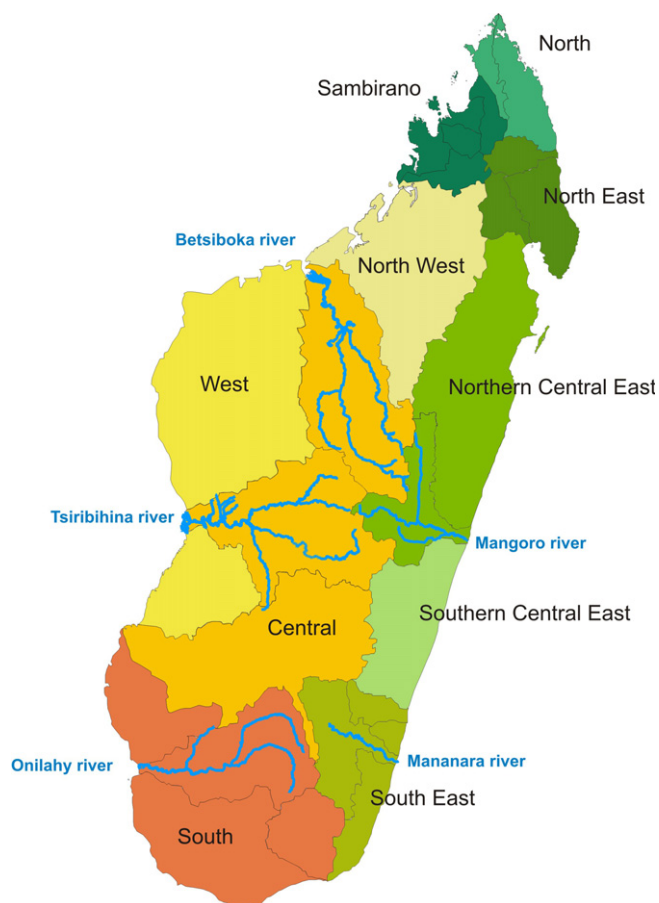


Fig. 1. Biogeographic regions of Madagascar as used in this paper. Lines delimit centers of endemism and refuges from the hypothesis laid out by Wilmé et al. (2006). Major rivers are depicted in blue. Different colors denote groups of these endemism centers and refuges that roughly fit the biogeographic regions as defined by Angel (1942) and Glaw and Vences (1994) for amphibians and reptiles. Pending future analyses, these regions as used here are not to be understood as an explicit hypothesis of a biogeographically meaningful zonation, but merely as definition to facilitate referring to particular areas of Madagascar in the text. Five major rivers (Mangoro, Mananara, Betsiboka, Tsiribihina and Onilahy) that may be relevant as barriers for gene flow in the species discussed herein are highlighted. (For interpretation of the references in color in this figure legend, the reader is referred to the web version of this article.)

tenance of basal splits between northern and southern populations of widespread species.

According to current classification, several taxa are widespread in Madagascar, occurring both across the north-south and the east-west biogeographic divisions. In this paper, we present a comparative phylogeographic analysis (Bermingham and Moritz, 1998) of six widespread Madagascan reptiles, based on samples spanning across most of their distribution areas. Our goal was to identify possibly concordant phylogeographic patterns and to provide a test of the hypotheses of basal west-east or north-south differentiation, in this case at the infraspecific level.

2. Materials and methods

2.1. Terminology for biogeographic regions

As summarized in Section 1, a variety of biogeographic zonation and definitions of areas of endemism and species formation have been proposed for Madagascar. In one of the most recent such proposals Wilmé et al. (2006) proposed a number of areas relevant as refugia and for speciation processes. We here overlaid these areas with the general biogeographic regions of Angel (1942) and Glaw and Vences (1994) in order to facilitate referring to particular areas of Madagascar in the text (Fig. 1). In the following, when referring to particular areas as defined in Fig. 1 these are capitalized, while for more general discussions we also subsume the areas of North, North-East and Sambirano as northern Madagascar, South-East and Southern Central East as south-eastern Madagascar, and North-West, West, and coastal parts of Central (Fig. 1) as western Madagascar.

2.2. Focal species

The six taxa selected for analysis were *Phelsuma lineata* and *Hemidactylus mercatorius* (Gekkonidae), the *Calumma brevicorne* complex and *Furcifer lateralis* (Chamaeleonidae), and *Trachylepis gravenhorstii* and *Trachylepis elegans* (Scincidae). These taxa are widespread and have different morphologies, life histories and habitat requirements, being adequate candidates for testing for shared phylogeographic patterns across the island.

The diurnal gecko *P. lineata* is found mainly in humid areas in eastern and northern Madagascar. While being a forest species, *P. lineata* is also adapted to human disturbance and occurs in relatively high densities near houses, in secondary forest and banana plantations (Glaw and Vences, 1994: 292, 294). Five subspecies have been described which are distinguished by differences in size and coloration. *P. l. lineata* and *P. l. elanthana* have distributions covering most of the Northern Central East, Southern Central East, and South East; *P. l. dorsivittata* seems to be restricted to the North (Montagne d'Ambre); *P. l. punctulata* is reported only from Tsaratantana in the Sambirano region and *P. l. bombetokensis* lives in the

relatively arid climate of the North-West (Glaw and Vences, 1994: 294–295).

The nocturnal gecko *H. mercatorius* occurs all over Madagascar, on the Comoro islands and on islands in the Gulf of Guinea (Rocha et al., 2005; Vences et al., 2004b). The phylogenetic relationships with *H. mercatorius* and *Hemidactylus mabouia* populations on the East African mainland and in the Neotropics are in need of study. *H. mercatorius* is a commensal species that also lives in natural habitats in Madagascar (Glaw and Vences, 1994: 278).

The chameleon *C. brevicorne* was historically thought to be a widespread forest dweller occurring throughout the humid rainforests of Sambirano, North East, Northern Central East, Southern Central East and South East even in montane areas, and has long been hypothesized to constitute a species complex (Glaw and Vences, 1994: 245–246; Vences and Glaw, 1996). Raxworthy and Nussbaum (2006) have recently described six new species of occipital-lobed chameleons from Madagascar. Some of their new species include populations that previously had been considered as *C. brevicorne*, and which doubtless are closely related to these, especially *Calumma amber*, *Calumma jevy*, and *Calumma crypticum*. We included all samples from this species complex available to us in the analysis, and especially focused on the differentiation among samples of *C. crypticum* for which our sampling is most geographically comprehensive.

Furcifer lateralis is a chameleon adapted to a wide range of climatic conditions. It inhabits wet savannahs and both dry and humid forests as well as agricultural lands. It is widely distributed in the humid coastal areas in the South, South East, and Southern Central East in the cold highlands of Central Madagascar and even in the arid regions of the South and West (Glaw and Vences, 1994: 241, 254).

For the skinks, we follow Mausfeld et al.'s (2002) partitioning of the genus *Mabuya*, and the nomenclature of Bauer (2003). Skinks of the genus *Trachylepis* are typical inhabitants of savannah-like and deforested habitats. Two of the endemic Malagasy *Trachylepis* species, *T. gravenhorstii* and *T. elegans*, are very widespread (Glaw and Vences, 1994: 308–309). These two plus a third species, *Trachylepis madagascariensis* from woodless montane areas in Central Madagascar are closely related to each other (Whiting et al., 2006).

2.3. Samples and DNA sequencing

Collections were carried out during fieldwork throughout Madagascar in the period 2000–2005. Specimens were anesthetized and killed by injection of chlorobutanol, fixed in 5% formalin or 95% ethanol, and preserved in 70% ethanol. They were deposited in the herpetological collections of the Université d'Antananarivo, Département de Biologie Animale (UADBA), Zoologisches Forschungsmuseum A. Koenig (ZFMK), Zoological Museum Amsterdam (ZMA), and Zoologische Staatssammlung München

(ZSM). Muscle tissue samples were taken from freshly killed specimens in the field and preserved in 98% ethanol. Voucher specimens and their collecting localities are listed in Appendix A.

DNA was extracted from tissue samples using a standard salt extraction method (Bruford et al., 1992). A fragment of 500–550 base pairs of the mitochondrial gene 16S was amplified via the polymerase chain reaction (PCR) with the primers 16Sar-L and 16Sbr-H (Palumbi et al., 1991). Fragment length varied among taxa due to (1) missing nucleotides at the beginning of the sequences and (2) different length of variable regions corresponding to loops in the secondary structure of the 16S rRNA molecule. PCRs were performed using the following conditions: an initial denaturation at 94 °C for 1:30 min; 33 cycles at 95 °C for 0:55 min, annealing at 45 °C for 0:45 min, extension at 72 °C for 1:30 min; and final extension of 5:00 min at 72 °C. PCR products were loaded onto 1% agarose gels, stained with ethidium bromide, and visualized with UV radiation. If results were satisfying, products were purified using QIA quick spin columns (Qiagen) prior to cycle sequencing. Sequences were resolved on ABI 3100 automated sequencers. New sequences have been submitted to GenBank (Accession Nos. EF210578–EF210711; see Appendix A).

2.4. Sequence partitioning and analysis

The length of the parts of the 16S sequences and corresponding start and end positions in the *Xenopus laevis* mitochondrial genome are given in Table 1. Sequences were manually aligned using the computer program Sequence Navigator (Applied Biosystems).

Separate evolution models for stem and loop regions of rRNA genes are preferable over a single evolution model for the entire sequence (Telford et al., 2005). We therefore divided sequences in stem and loop partitions based on published secondary structure models. For the two skinks we used a closely fitting model for the skink *Eumeces egregius* (Brown, 2005). The secondary structure of the sequences of the geckos and chameleons were estimated from a model designed for the frog *X. laevis* (Gutell and Fox, 1988).

For each of the six species, separate evolutionary models (Table 1) were selected for the stem and loop partitions, respectively, using PAUP* 4.0b10 (Swofford, 2000) software and the Akaike Information Criterion in MrModel-

test version 2.2 (Nylander, 2004). These models were used as priors in a partitioned Bayesian analysis in the program MrBayes, version 3.0.

We ran two independent analyses consisting of four Markov chains that ran for 40×10^6 generations, sampled every 1000 generations, with a maximum likelihood starting tree, default priors, and the option “prset ratepr” set as “variable”. Only in the case of the *Furcifer* data matrix, we lowered the temp variable to 0.10 in order to achieve a better mixing of the search chains. We used the online program AWTY (Wilgenbusch et al., 2004) to check for convergence and estimate the burnin parameter. After discarding the first 20 million generations, remaining trees from both analyses were combined and a 50% majority rule consensus tree was calculated.

We compared the partitioned analysis with a non-partitioned analysis, using the Bayes factor as described in the MrBayes 3.1 manual (Ronquist et al., 2005) and discussed in Brandley et al. (2005) and Nylander et al. (2004). According to this criterion, the analysis with separate models for stem and loop regions performed significantly better in all cases.

To visualize the absolute number of nucleotide transformations between clades we performed unweighted Maximum Parsimony (MP) analyses in Paup* 4.0b10. We carried out heuristic searches with tree bisection-reconnection branch swapping and 10 random addition sequence replicates. Strict consensus trees were constructed from the obtained most parsimonious trees. These MP trees were preferred over the construction of haplotype networks because the networks, computed with TCS (Clement et al., 2000), yielded many unconnected subnetworks due to the large genetic differentiation encountered among populations of the same species. In the case of *Trachylepis*, much resolution was lost in a strict consensus tree. For this reason we here show a 50% majority rule consensus tree of all *Trachylepis* specimens included, but emphasize that in this case the nodes without bootstrap or Bayesian support should not be seen as indicative of phylogenetic relationships. Bootstrapping (500 or 2000 replicates) under the MP criterion was performed to obtain support values for branches. These support values and support from Bayesian posterior probabilities are shown on the MP consensus trees in Figs. 2–6. Distance matrices for the major haplotype groups per species are provided in Tables 2–6.

Table 1

The lengths of the partial 16S sequences used for the six Malagasy species in this study, their corresponding start and end positions in the *Xenopus laevis* mitochondrial genome (GenBank Accession No. M10217, Roe et al., 1985) and substitution models selected for stem and loop regions

Taxon	Total length (bp)	Corresponding to <i>X. laevis</i>	Substitution model stems	Substitution model loops
<i>P. lineata</i>	496	4023–4550	K80+I	GTR+G
<i>H. mercatorius</i>	508	4009–4550	HKY	GTR+G
<i>F. lateralis</i>	419	4065–4550	K80+I	HKY+I
<i>C. brevicorne</i> complex	453	4025–4550	K80+I	HKY+I
<i>T. elegans</i> & <i>T. gravenhorsti</i>	495	4009–4550	K80+I	HKY+I

Length refers to the aligned sequences including gaps.

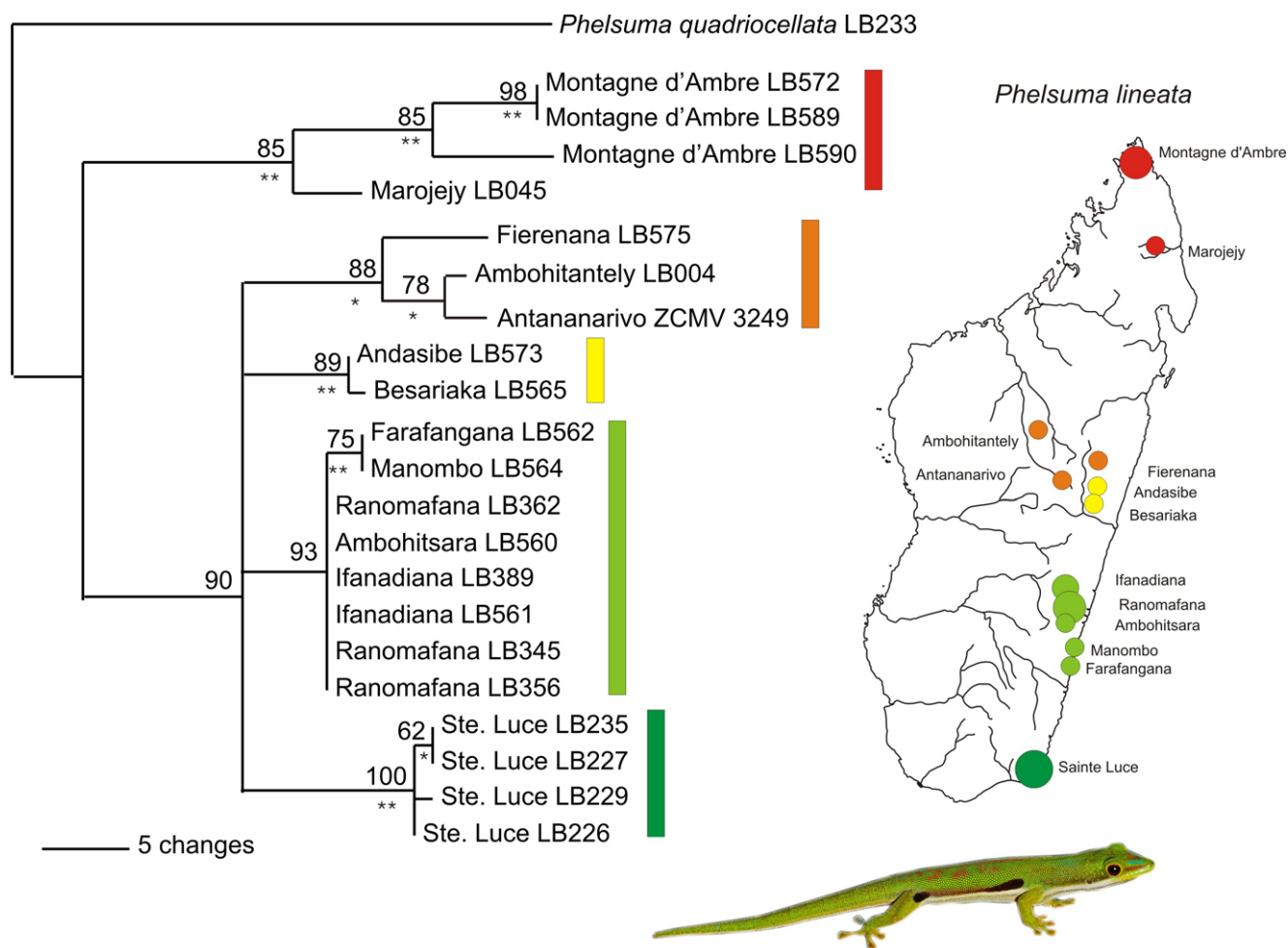


Fig. 2. Phylogenetic tree based on sequences of partial 16S rDNA from individuals of *Phelsuma lineata*. The tree is a strict consensus tree of 25 equally parsimonious trees (123 steps; 418 of 500 characters constant, and 51 parsimony-informative; CI 0.756, RI 0.836) selected under the MP optimality criterion. *Phelsuma quadriocellata* was used as the outgroup. Numbers on branches are values of MP bootstrap support in percent (2000 replicates; values under 50% not shown). Branches with a posterior probability >0.95 or >0.99 are indicated by * and **, respectively. The scale bar indicates the number of inferred substitutions. The map shows the distribution of the major clades marked by different colors; circle size corresponds to the number of specimens examined per locality. (For interpretation of the references in color in this figure legend, the reader is referred to the web version of this article.)

3. Results

The phylogenetic analyses (Figs. 2–6) revealed a large number of different haplotypes and deep haplotype clades in each of the species studied. The haplotype clades showed clear geographic correlation in all cases. Phylogenetic resolution was limited. Although in general the major clades were moderately to highly supported by Bayesian posterior probabilities and MP bootstrap values, the relationships among these clades were in many cases unresolved. However, in the two geckos and the chameleons of the *C. brevicorne* complex, the haplotypes distributed in northern Madagascar were the sister group of a well supported clade containing all other haplotypes. For detailed scores and indices of MP trees obtained, see captions of Figs. 2–6. Refer to Fig. 1 for the names and locations of the bio-geographic regions in the following descriptions.

In *Phelsuma lineata*, five clades were identified with high support (Fig. 2), distributed in (1) the North and North-East, (2) the Center and Northern Central East, (3) the

Northern Central East, (4) the Southern Central East and South East and (5) Ste. Luce in the South East (Fig. 2). All groups were supported by Bayesian posterior probabilities >0.99 and/or bootstrap support >80%, and the northern haplotype clades were sister to all others, which formed a monophyletic group supported by a bootstrap value of 90%. Differentiation among and within clades was high, for instance 13 substitutions (3.9% uncorrected pairwise divergence) between the two haplotypes from Montagne d'Ambre (an exceptionally high value for 16S divergence among Malagasy reptiles), and 22–37 substitutions (4.8–8.3%) between the northern haplotypes and those from other localities (Table 2).

In *Hemidactylus mercatorius*, each specimen included in this study turned out to have a unique 16S haplotype. Three clades supported by moderate to high posterior probabilities and partly by bootstrap values, were identified (Fig. 3): (1) the North and North East, (2) three sites in the Center, North West and Northern Central East, and (3) the most common haplotype clade, occurring both

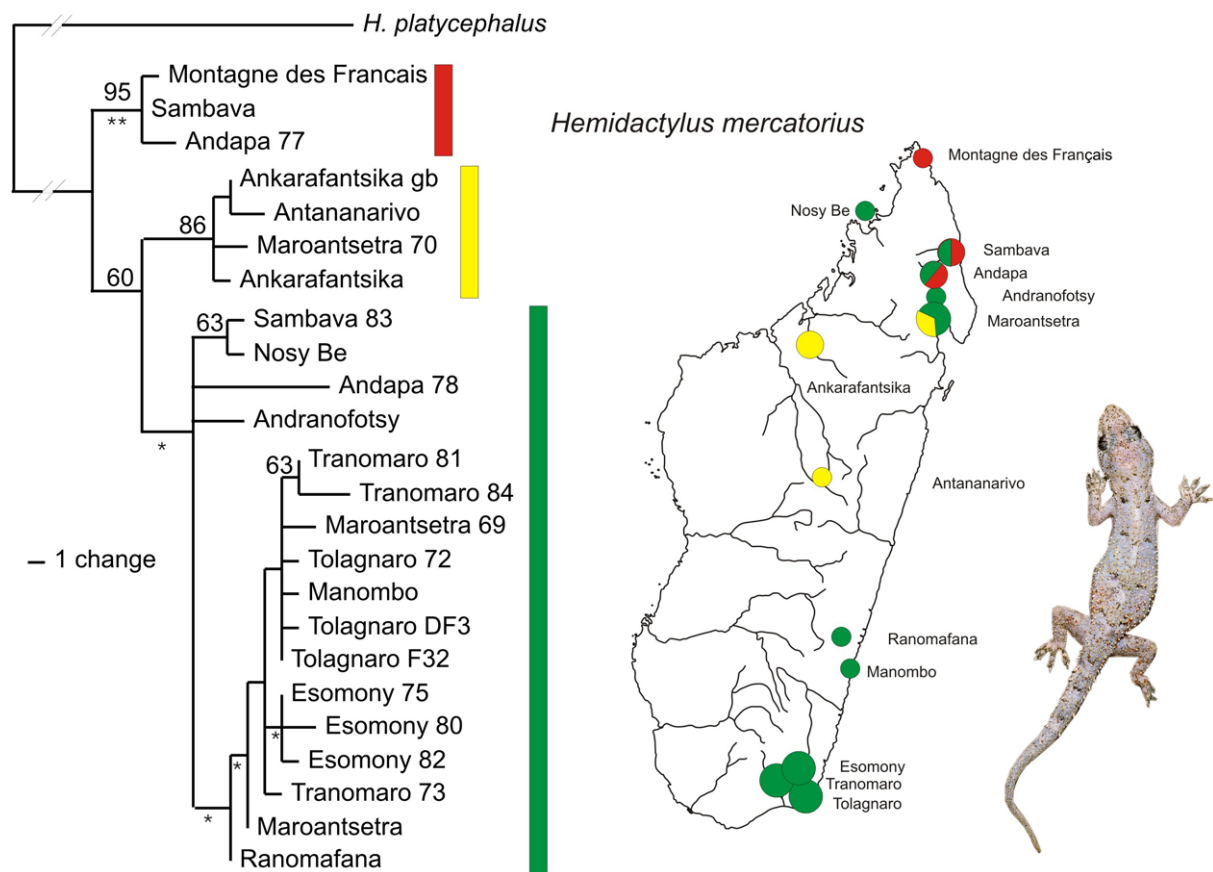


Fig. 3. Phylogenetic tree based on sequences of partial 16S rDNA from individuals of *Hemidactylus mercatorius*. The tree is a strict consensus tree of 72 equally parsimonious trees (112 steps; 426 of 528 characters constant, and 23 parsimony-informative; CI 0.848, RI 0.821) selected under the MP optimality criterion. *Hemidactylus platycephalus* was used as the outgroup. Numbers on branches are values of MP bootstrap support in percent (2000 replicates; values under 50% not shown). Branches with a posterior probability >0.95 or >0.99 are indicated by * and **, respectively. The scale bar indicates the number of inferred substitutions. The map shows the distribution of the major clades marked by different colors; circle size corresponds to the number of specimens examined per locality. (For interpretation of the references in color in this figure legend, the reader is referred to the web version of this article.)

in the Sambirano and North East and in the Southern Central East, South East and South, where it was the only haplotype clade detected. Clades 2 and 3 were sister groups, with weak MP bootstrap support. Unlike all other species studied, in *Hemidactylus*, haplotypes belonging to different clades were found in syntopy: clades 1 and 3 in Sambava and Andapa, clades 2 and 3 in Maroantsetra. Differentiation among the three major clades was rather high: 9–17 substitutions (1.8–3.9%) between the North/North West clade and other haplotypes, and 5–15 substitutions (1.3–3.6%) between the second and third clade (Table 3).

In the *Calumma brevicorne* complex, a high genetic differentiation among populations was found. The two species *C. amber* and *C. crypticum* as described by Raxworthy and Nussbaum (2006) received support from our analysis, although partly at a shallow level, and important differentiation was also noted within *C. crypticum*. Most localities turned out to have an exclusive haplotype lineage (Fig. 4). In *C. crypticum*, clear associations were found in the Southern Central East, between the area of Ranomafana (Ranomafana and Vohiparara) and Andringitra (Imaitso). The association of Andohahela in the South East and Ambositra in the Center received high

statistical support. Haplotypes of *C. amber* from Montagne d’Ambre in the North were sister to all other haplotypes, which formed a highly supported clade with a posterior probability of >0.99 and 95% bootstrap support. Divergence of the northern haplotype to the others was of 12–21 substitutions (3.2–5.0%).

In *Furcifer lateralis* four main haplotype clades were identified (Fig. 5): (1) Antananarivo and Ambatolampy in the Center (a single, shared haplotype), (2) Southern Central East and adjacent areas of South East and Center, (3) Ambohitantely in the northern Center and (4) South with adjacent parts of Center and South East. Relationships between these clades were not satisfyingly resolved. Interestingly, the northernmost haplotype of Ambohitantely was placed sister to the South clade with high support, suggesting the possible existence of a western clade in *Furcifer lateralis*. The South clade, in turn, was strongly supported as monophyletic. Differences of clades 1 and 2 to the southern clade 4 were 8–15 substitutions (2.2–3.6%), while the difference between the Ambohitantely haplotype and the southern clade was 6–9 substitutions (1.5–2.2%; Table 5).

Explorative trees of haplotypes assigned to *T. gravenhorstii*, *T. elegans* and their close relative *T. madagascariensis*



Calumma brevicorne complex

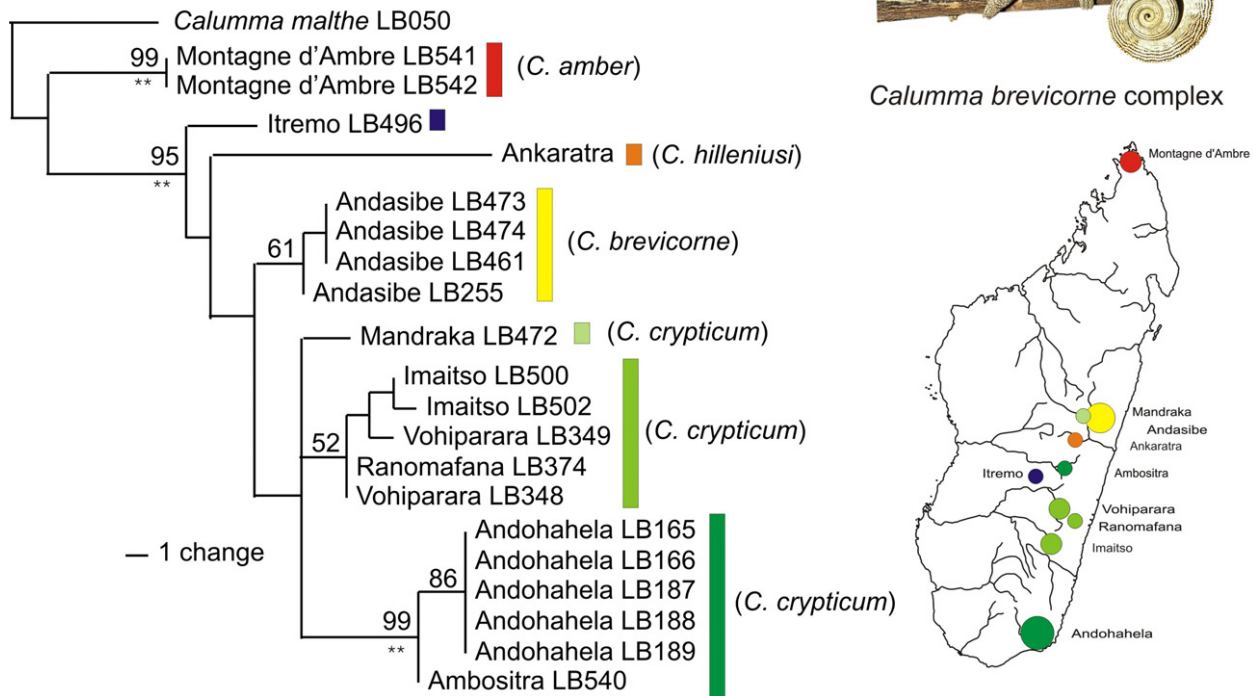


Fig. 4. Phylogenetic tree based on sequences of partial 16S rDNA from individuals of the *Calumma brevicorne* complex. The tree is a strict consensus tree of three equally parsimonious trees (57 steps; 414 of 457 characters constant, and 28 parsimony-informative; CI 0.807, RI 0.887) selected under the MP optimality criterion. *Calumma malthe* was used as the outgroup. Numbers on branches are values of MP bootstrap support in percent (2000 replicates; values under 50% not shown). Branches with a posterior probability >0.95 or >0.99 are indicated by * and **, respectively. The map shows the distribution of the major clades marked by different colors; circle size corresponds to the number of specimens examined per locality. (For interpretation of the references in color in this figure legend, the reader is referred to the web version of this article.)

sis revealed a complex pattern of relationships. We therefore decided to enter all haplotypes of these three species in a joint analysis (Fig. 6). *T. madagascariensis*, originally not a focal species of this study, turned out to be deeply nested within haplotypes of *T. gravenhorstii*. All haplotypes of this montane specialist were identical, although they came from two rather distant localities, the Ankaratra and Andringitra massifs. *T. elegans* specimens were equally nested within *T. gravenhorstii*, but did not form a well-supported monophyletic group. Two haplotypes (one from an uncertain locality and one from Ifaty in the South) had isolated positions; moreover, these correspond to juvenile specimens of questionable attribution. The other *T. elegans* haplotypes did not unambiguously form a clade and in a strict consensus tree as well as in a Bayesian analysis were unresolved (not shown), although they clustered together in a 50% majority rule consensus tree of the most parsimonious MP trees (Fig. 6). Divergence within *T. elegans* was relatively low and amounted to a maximum of nine substitutions (2.2%; Table 6). Divergence of the *T. elegans* haplotypes from those assigned to *T. gravenhorstii* was of 12–21 substitutions (2.8–5.0%). Some geographic structure was apparent among *T. elegans* haplotypes but the clades received little support. All northern localities (North,

North West and North East zones) had an identical haplotype differing by 5–9 substitutions (1.0–2.0%) from all other haplotypes of this species (Table 6).

In *T. gravenhorstii* four clades were identified which all received at least some bootstrap support but low Bayesian posterior probabilities (Fig. 6): (1) a northern clade distributed in the Sambirano, North-East and Northern Central East zones; (2) Southern Central East, plus Analalava in the Center; (3) South and South East; (4) North West, West and Center. The northern clade is basal in the tree with at least some bootstrap support (55%). It differs from all other haplotypes by 11–23 substitutions (2.5–5.4%). The distances among the other clades are similar; only the possible sister clades 3 and 4 are less strongly differentiated with 8–13 substitutions (1.7–3.0%; Table 6).

4. Discussion

4.1. Comparative phylogeography

Comparing the phylogeography of a number of taxa is one out of several solutions to the problem that gene trees are not necessarily concordant with population trees (Avice, 2004). The observed genetic patterns of species

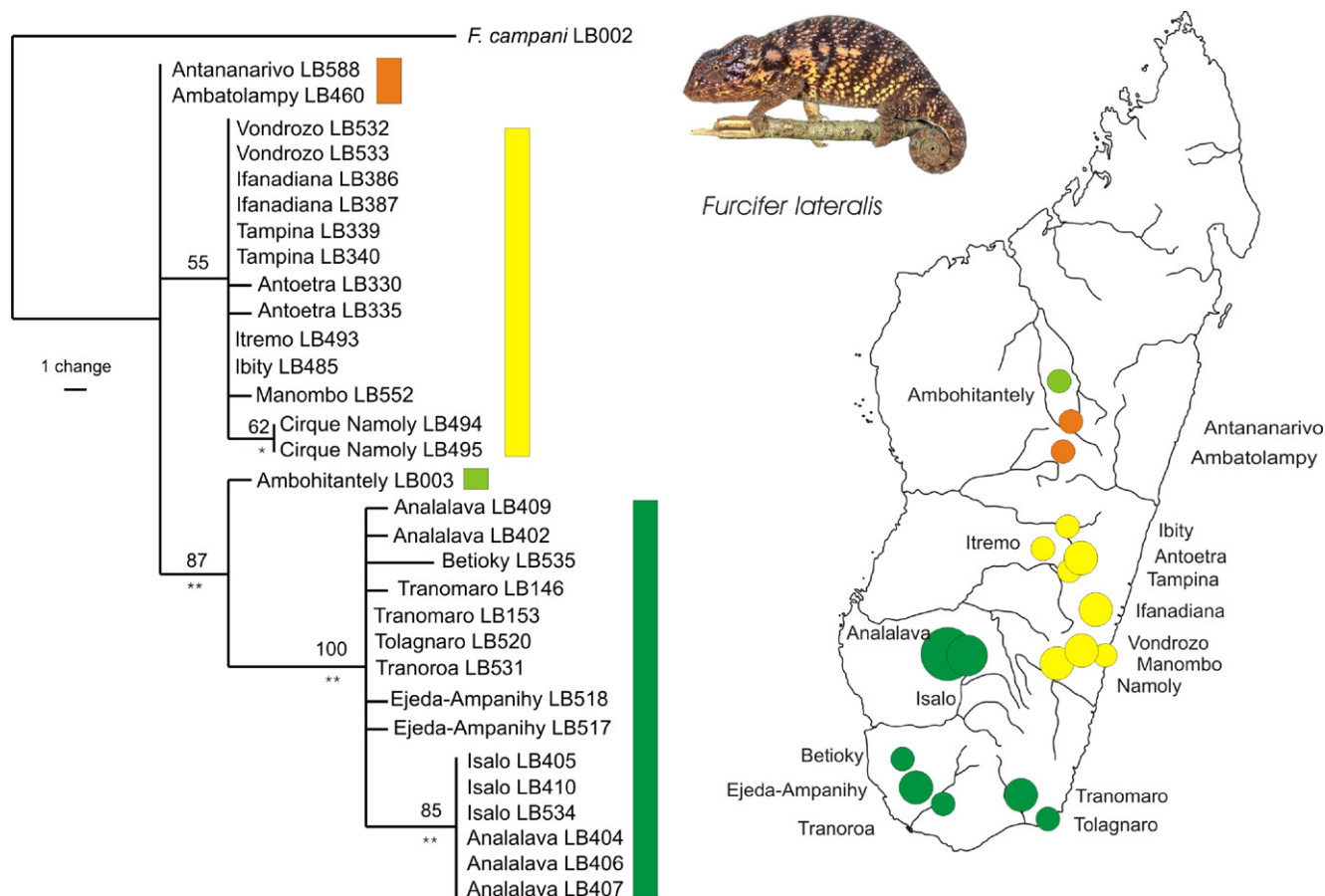


Fig. 5. Phylogenetic tree based on sequences of partial 16S rDNA from individuals of *Furcifer lateralis*. The tree is a strict consensus of 300,000 equally parsimonious trees (48 steps; 378 of 419 characters constant, and 22 parsimony-informative; CI 0.917, RI 0.976) selected under the MP optimality criterion. *Furcifer campani* was used as the outgroup. Numbers on branches are values of MP bootstrap support in percent (2000 replicates; values under 50% not shown). Branches with a posterior probability >0.95 or >0.99 are indicated by * and **, respectively. The scale bar indicates the number of inferred substitutions. The map shows the distribution of the major clades marked by different colors; circle size corresponds to the number of specimens examined per locality. (For interpretation of the references in color in this figure legend, the reader is referred to the web version of this article.)

may reveal historical processes at the landscape scale, but they may also be the result of the current balance between gene flow and genetic drift. The comparison of phylogeographic patterns of co-distributed taxa is able to reveal more general biogeographic patterns (Arbogast and Kenagy, 2001). In the present study, all species display a clear geographic clustering of haplotype clades, and several recurrent patterns are apparent:

(1) In several of the taxa studied, a distinct northern subclade was found. In *H. mercatorius*, the northern haplotypes occur in the North and North East, but populations also share other haplotypes, as can be expected in a commensal species that is commonly translocated by humans. In *P. lineata*, the two populations from Montagne d'Ambre and Marojejy form the northern clade and may also be taxonomically distinct (see below). In the *C. brevicorne* complex, the northern species *C. amber* turned out to be most basal. Geographical as well as taxonomical sampling gaps may partially affect these results: in the *C. brevicorne* complex, we miss the population from Marojejy that was described by Raxworthy and Nussbaum (2006) as *C. jejy*, and which may constitute a basal lineage in the complex

as well. In addition, we miss samples from the northern regions assigned to *C. brevicorne* and *C. crypticum*. In *P. lineata*, we miss samples from the subspecies *punctulata* from Tsaratanana and from the North West (subspecies *bombetokensis*). In addition, in both *Calumma* and *Phelsuma* there is a relatively large unsampled area separating the northern clade from the central and southern clades. This gap may be artificial since the concerned areas are among the less surveyed parts in Madagascar's eastern rainforest, but the fact that for both taxa there are no distribution records in this area (Glaw and Vences, 1994; Raxworthy and Nussbaum, 2006) may also indicate a real rareness of these reptiles in the region.

In *T. elegans*, the northern lineage is not the most basal one, but relationships among clades are poorly resolved. In *T. gravenhorstii*, northern haplotypes range much further south and reach into the Northern Central East around Andasibe.

Although a strong caveat is in place, and we cannot exclude that future studies reveal additional and more basal lineages in the areas we have not sampled, the basal position of the northern lineage is concurrent among various species

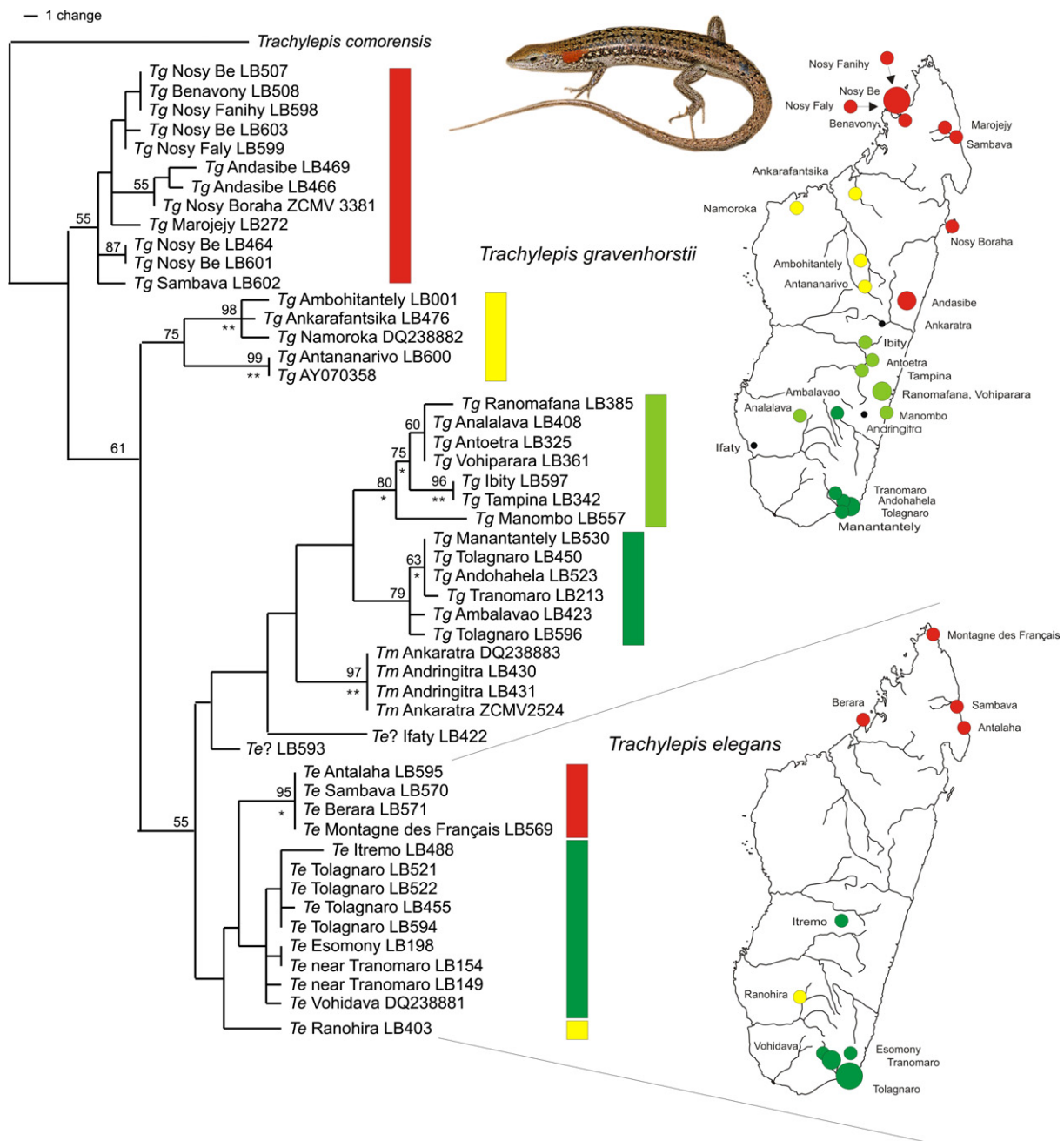


Fig. 6. Phylogenetic tree based on sequences of partial 16S rDNA from individuals assigned to *Trachylepis gravenhorsti* (Tg), *T. elegans* (Te) (inset photo) and *T. madagascariensis* (Tm). The tree is a 50%-majority rule consensus of 764 equally parsimonious trees (135 steps; 422 of 496 characters constant, and 44 parsimony-informative; CI 0.644, RI 0.888) selected under the MP optimality criterion. *Trachylepis comorensis* was used as the outgroup. Note that numerous equally parsimonious trees exist that have a conflicting topology to this tree, and only the nodes also supported by bootstrap values >50% were also supported by a strict consensus tree (not shown). The tree should therefore not be interpreted phylogenetically except where supported by bootstrapping or Bayesian analysis. Numbers on branches are values of MP bootstrap support (not majority rule consensus values) in percent (500 replicates; values under 50% not shown). Branches with a posterior probability >0.95 or >0.99 are indicated by * and **, respectively. The scale bar indicates the number of inferred substitutions. The map shows the distribution of the major clades marked by different colors; circle size corresponds to the number of specimens examined per locality. (For interpretation of the references in color in this figure legend, the reader is referred to the web version of this article.)

and species complexes based on the present data. It is well known that northern Madagascar is characterized by a rich species diversity of reptiles and other vertebrates, including many regional endemics. Several mountain massifs in this area (e.g., Montagne d’Ambre, Anjanaharibe and Marojejy) may act as biogeographic refugia and centers of endemism

(Andreone et al., 2000, and references therein; Raxworthy and Nussbaum, 1997). Also in one other lizard (*Hemidactylus frenatus*) and one frog (*Ptychadena mascareniensis*), haplotypes from the northern and north-western part of Madagascar differ remarkably from those found in the remainder of the island (Vences et al., 2004a,b). Moreover,

Table 2
Distance matrix for the five major haplotype groups of *Phelsuma lineata*

#	Subclade	1	2	3	4	5
1	North and North East	0–4.2% 0–19	5.6–7.6%	5.1–7.1%	4.8–7.6%	6.1–8.3%
2	Center and Northern Central East	28–34	0.6–2.2% 3–10	2.8–4.5%	3.0–3.9%	3.2–4.1%
3	Northern Central East	22–32	13–19	0.2% 1	1.7–2.2%	3.2–3.9%
4	Southern Central East and South East	22–35	15–18	7–10	0–0.4% 0–2	2.6–3.2%
5	South	30–37	16–19	15–16	13–15	0–0.4% 0–2

The lower left values are absolute distances (number of substitutions). Upper right values are uncorrected pairwise divergences in percent. Values shaded by gray are values of within-clade differentiation.

Table 3
Distance matrix for the three major haplotype groups of *Hemidactylus mercatorius*

#	Subclade	1	2	3
1	North and North West	0.2–0.7% 1–3	2.2–3.3%	1.8–3.9%
2	Center, North West and Northern Central East	10–15	0.4–1.1% 2–5	1.3–3.6%
3	Sambirano, North East, Southern Central East, South East and South	9–17	5–16	0.2–3.6% 1–16

The lower left values are absolute distances (number of substitutions). Upper right values are uncorrected pairwise divergences in percent. Values shaded by gray are values of within-clade differentiation.

Table 4
Distance matrix for the seven major haplotype groups of the *Calumma brevicorne* complex

#	Subclade	1	2	3	4	5	6	7
1	North (<i>C. amber</i>)	0.0% 0	5.0%	3.6%	3.5–4.3%	3.9%	3.2–3.5%	4.2–5.0%
2	Ankaratra (<i>C. hilleniusi</i>)	21	n.a.	3.9%	3.2–3.5%	3.9%	3.8–4.5%	3.5–4.2%
3	Center (Itremo)	14	15	n.a.	1.8–2.1%	2.4%	1.8–2.3%	3.1–3.6%
4	Northern Central East (Andasibe) (<i>C. brevicorne</i>)	15–16	13–16	7–8	0.0–0.3% 0–1	1.0–1.3%	1.3–2.4%	1.6–2.7%
5	Northern Central East (Mandraka) (<i>C. crypticum</i>)	15	15	9	4–5	n.a.	1.0–1.8%	1.9–2.4%
6	Southern Central East (<i>C. crypticum</i>)	12–15	16–19	7–9	6–9	4–7	0.0–0.8% 0–3	1.6–3.2%
7	South and Center (Andohahela, Ambositra) (<i>C. crypticum</i>)	18–20	15–19	12–14	7–10	7–9	7–12	0.0–0.5% 0–2

The lower left values are absolute distances (number of substitutions). Upper right values are uncorrected pairwise divergences in percent. Values shaded by gray are values of within-clade differentiation. n.a. = not applicable (only one sequence).

northern Madagascar is known to harbor a number of deep endemic lineages of frogs present nowhere else on Madagascar, i.e., the genera *Tsingymantis* and *Wakea* (Glaw et al., 2006; Glaw and Vences, 2006).

At present, no obvious pattern is apparent that would allow to predict whether a given taxon displays a primary phylogeographic split between northern and southern, or

between eastern and western populations. Considering the examples listed in the Introduction and those analyzed herein, wide-ranging taxa that also occur in one or several of the northern regions can display either a north-south split (*C. brevicorne* complex, *P. lineata*, *H. mercatorius*, and others) or an east-west split (*B. doulioti/tephraeomystax*, *Sanzinia m. madagascariensis/S. m. volontany*). Species that do not

Table 5
Distance matrix for the four major haplotype groups of *Furcifer lateralis*

#	Subclade	1	2	3	4
1	Center (Antanarivo and Ambatolampy)	0.0% 0	0.3–0.6%	1.1%	2.2–3.0%
2	Southern Central East, South East and Center	1–2	0.0–0.7% 0–3	1.3–1.9%	2.4–3.6%
3	Center (Ambohitantely)	4	5–8	n.a.	1.5–2.2%
4	South, Center and South East	8–11	9–15	6–9	0.0–1.3 0–4

The lower left values are absolute distances (number of substitutions). Upper right values are uncorrected pairwise divergences in percent. Values shaded by gray are values of within-clade differentiation. n.a. = not applicable (only one sequence).

Table 6
Distance matrix for the major haplotype groups of *Trachylepis gravenhorstii* (G), *T. madagascariensis* (M) and *T. elegans* (E)

#	Subclade	G1	G2	G3	G4	M1	?1	E1	E2	E3
G1	Sambirano, North East and Northern Central East	0.0–1.8% 0–7	2.5–4.4%	3.5–5.4%	3.3–5.1%	3.1–4.1%	3.8–4.8%	2.9–4.1%	2.9–4.9%	3.5–4.9%
G2	North West, Center and West	11–18	0.0–2.5% 0–12	3.7–5.4%	3.9–5.4%	3.5–4.4%	4.8–5.4%	2.9–3.7%	2.3–4.3%	3.3–3.7%
G3	Southern Central East and Center	17–23	18–23	0.0–2.0% 0–9	1.7–3.0%	2.5–3.4%	3.7–4.2%	3.3–4.2%	3.1–5.0%	4.1–4.6%
G4	South and South East	15–20	18–23	8–13	0.0–0.6% 0–3	2.6–3.4%	3.0–4.1%	3.3–4.2%	2.8–5.0%	3.9–4.9%
M1	Andringitra, Ankaratra	13–17	17–20	12–16	12–15	0.0% 0	2.7%	2.3%	1.8–3.0%	2.9%
?1	Ifaty	18–19	23–24	17–20	14–18	13	n.a.	3.3%	2.7–3.6%	3.6%
E1	North, North East and North West	13–16	14–17	16–20	15–18	11	16	0.0% 0	1.0–2.0%	1.8%
E3	South (Ranohira)	17–19	16–17	19–22	18–21	14	17	9	n.a.	1.2–2.2%
E4	South and Center	14–19	12–17	12–20	14–20	7–12	13–15	5–8	6–9	0.0–1.3% 0–5

The haplotype from Ifaty is of unknown species identity. The lower left values are absolute distances (number of substitutions). Upper right values are uncorrected pairwise divergences in percent. Values shaded by gray are values of within-clade differentiation. n.a. = not applicable (only one sequence).

reach the northern regions may preferably show an east-west split (e.g., *Ebenavia*, *Matoatoa*, possibly *Furcifer lateralis*).

(2) At least in one species where sufficient sampling from eastern and western Madagascar was available, *F. lateralis*, the haplotype prevalent in the arid parts of the West and South also reached the humid areas around Tolagnaro.

(3) Distinct haplotype lineages occur in the northern part of the Center (Ambohitantely and Antananarivo) and some areas of the North West, in particular Ankarafantsika, insofar as the respective species occur here. This pattern is observed in *P. lineata* (not studied from Ankarafantsika) and *H. mercatorius*, and in *T. gravenhorstii*. A particular modification of the pattern is seen in *F. lateralis* where Ambohitantely harbors a special haplotype related to the southern haplotype lineage and not to the neighboring ones.

(4) Rivers can be important factors in shaping phylogeographic patterns of vertebrates (Capparella, 1991; Eriksson et al., 2004; Pellegrino et al., 2005; Peres et al., 1996), although some studies have failed to find support for this hypothesis (Gascon et al., 2000; Loughheed et al., 1999; Lugon-Moulin et al., 1999). In Madagascan reptiles, the plated lizards of the genus *Zonosaurus* are an example. *Zonosaurus quadrilineatus* and *Z. trilineatus* are closely related and possibly conspecific, and have their respective distributions separated by the Onilahy river in south-western Madagascar (Yoder et al., 2005). For many lemur taxa, the Mangoro river in the Northern Central East is a major dispersal barrier (Goodman and Ganzhorn, 2004). For four of the six taxa studied here we have sequence data that is informative regarding a possible subdivision of the east coast

in congruence with lemur biogeography (Martin, 1972; Pastorini et al., 2003). Three of these, *P. lineata*, *C. crypticum* and *T. gravenhorstii* show different subclades north and south of the Mangoro, which lends tentative support to the hypothesis that the river acts as a barrier.

The Mananara river, in the south east coast of Madagascar, is another potential barrier for some of the species studied, as it has been shown for several species of lemurs (Goodman and Ganzhorn, 2004). Although some species like *Hemidactylus* do not show distinctive clades in the South East, in others, like *P. lineata*, *C. crypticum*, and possibly *F. lateralis*, there is a clear differentiation between samples north and south of the Mananara river. The data shown here, together with studies available for several groups of vertebrates that inhabit this region in Madagascar (Goodman and Ganzhorn, 2004; Louis et al., 2005; Sterling and Ramarason, 1996; Vieites et al., 2006) make it plausible that these two east coast rivers act as barriers. More samples, particularly from localities close to the north and south banks of the Mangoro and Mananara rivers, are needed to test this hypothesis.

4.2. Levels of phylogeographic differentiation

Our study included a commensal species most common in anthropogenic habitat (*H. mercatorius*), three species common in disturbed, open landscape (*T. gravenhorstii*, *T. elegans*, *F. lateralis*), one species occurring in rainforest and in disturbed habitats (*P. lineata*) and one lineage of strict rainforest inhabitants (the *C. brevicorne* complex). Rainforest species may be hypothesized to be less vagile and more dependent on refugia during past climatic and habitat shifts, and thus could be expected to show more genetic structure among populations. It is remarkable that the general degrees of differentiation are at approximately the same scale in all taxa, although some trends in accordance with the above hypothesis can be identified (Tables 2–6). The highest values of divergence (up to 8.3%) are found among populations of *P. lineata* which at least in northern Madagascar are obligatory rainforest inhabitants.

The highest degree of subdivision, with almost each population representing a separate haplotype lineage, is that of the *C. brevicorne* complex which in fact has recently been divided into various species (Raxworthy and Nussbaum, 2006), although the maximum divergence only amounts to 5.0%. In contrast, the lowest degrees of differentiation (maxima of 2.2%, 3.6% and 3.9%) are found in *T. elegans*, *F. lateralis*, and *H. mercatorius*, hence in species mainly occurring in open landscape. In addition, as expected in a commensal species, different haplotype clades were found in three populations of *H. mercatorius*, all in large villages or small towns where intensive traffic by airplanes, ships and trucks may be responsible for translocation of specimens.

Without further data we are unable to distinguish whether the different phylogeographic divergences among species are caused by differences in rates of molecular evolution, induced by ecological differences, or simply reflect a

different depth of time in which the differentiation occurred. However, it is striking that in the reptile species studied, in various cases deep phylogeographic splits are found which cannot readily be explained by current potential barriers to gene flow such as major rivers, mountain ranges, or borders between bioclimatic regions.

Historical patterns of habitat stability are good predictors of species richness, especially in endemic low-dispersal taxa, and they better explain patterns of species turnover (Graham et al., 2006). This concept suggests that certain areas were stable during the Pleistocene glaciations and Holocene climatic events, functioning as refugia for many species. The contraction and retraction of these refugia in different recent climatic periods could have shaped much of the phylogeographic structure observed today in many Madagascan species. During the Pleistocene glaciations rainforest was present in the North and North East of Madagascar, while the eastern coast may have been covered by tropical woodland (Ray and Adams, 2001). If this was the case, northern Madagascar habitats have been stable through the Pleistocene glaciations until today. Such a major habitat break between the North and the rest of Madagascar, together with the stability in the north, would be congruent with the high degree of endemism in the north and the possible trend of basal phylogeographic lineages of various groups occurring in this region.

4.3. Taxonomic considerations

Our data indicate that in several cases the taxonomy of the included taxa is in need of revision. Vences and Glaw (1996) discussed the taxonomy of *C. brevicorne* and assumed that it is actually a complex of several species, and Raxworthy and Nussbaum (2006) described three of these as new species. Our study adds to these conclusions in three aspects. Firstly, we confirm the mitochondrial genetic distinctness between *C. brevicorne* and several of the new species (*C. amber*, *C. crypticum*) and one other species recently elevated to species status (*Calumma hilleni*) although the pairwise distances are partly remarkably low between two species (e.g. 1.0–1.3% between *brevicorne* from Andasibe and *crypticum* from Mandraka). Secondly, differences between haplotype lineages also within the newly defined species are large, at least in the case of *C. crypticum* where our sampling is geographically most comprehensive. And, thirdly, our sample from Itremo resulted to be genetically divergent from both *C. crypticum* and *C. brevicorne*. We have not studied the corresponding voucher specimen (ZSM 546/2001) in detail, but it is morphologically closest to *C. crypticum* and may represent yet another new taxon.

In *P. lineata*, some of the identified lineages correspond to morphologically defined subspecies, e.g., *P. l. dorsivittata* from Montagne d'Ambre, and *P. lineata elanthana* from the central highlands. However, populations attributed to the nominal subspecies *P. l. lineata* (Krüger, 1996) contain in fact several highly divergent haplotype clades (3, 4 and 5), possibly indicating the need for further subdivision if a subspecies con-

cept is to be applied. Morphologically, we have observed intergradation of individuals resembling either *P. l. lineata* or *P. l. elanthana* in the area of Fierenana. This may indicate the presence of a hybrid zone, and constitute an argument to continue considering these highly divergent lineages as conspecific. On the other hand, the large differentiation of *P. l. dorsivittata* may justify its recognition at the species level. Since we lack representatives of the North-Western and Sambirano subspecies *P. l. bombetokensis* and *P. l. punctulata*, we cannot make statements on their status.

In *F. lateralis*, populations from arid southern areas are sometimes referred to as subspecies *F. lateralis* 'major', characterized by larger size and slightly different coloration (Glaw and Vences, 1994: 254). Our present study confirms that specimens from the South constitute a monophyletic clade, which might thus correspond to this informal subspecies, although not all of these specimens share the mentioned morphological characteristics.

In *H. mercatorius*, its phylogeographic pattern concordant with other species and its high degree of haplotype diversity support the hypothesis that this species is native to Madagascar and has not been introduced by humans (Vences et al., 2004b).

Most complicated is the situation in the three species of *Trachylepis* studied here. Our data suggest an origin of *T. madagascariensis* and *T. elegans* out of a paraphyletic taxon *T. gravenhorstii*. These three taxa are best considered as distinct species because *T. gravenhorstii* and *T. elegans* occur syntopically over much of their distribution area, and sympatry of *T. madagascariensis* with *T. elegans* has also been recorded at least from the Andringitra area (Glaw and Vences, 1994: 309–312). A subspecies *T. elegans delphinensis* has been described from Tolagnaro in southeastern Madagascar (Brygoo, 1983), but a distinct subclade from this locality was not retrieved in our present genetic analysis. Andreone and Greer (2002) have suggested that *T. gravenhorstii* may be a composite species, but the possible morphological distinction of subclades and delimitation of species boundaries require intensive further work.

Acknowledgments

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Appendix A

Collection numbers of voucher specimens and GenBank accession numbers for the mitochondrial 16S rDNA fragment used in this study. The first column refers to the code number and the corresponding sequence is given in the trees (Figs. 2–6). Voucher numbers refer to the following collections: UADBA, Université d'Antananarivo, Département de Biologie Animale, Madagascar; USNM, United States National Museum, Washington, USA; ZFMK, Zoologisches Forschungsmuseum A. Koenig, Bonn, Germany; ZMA, Zoological Museum Amsterdam, Netherlands; ZSM, Zoologische Staatssammlung München, Germany. Furthermore, MV, FGMV, ZCMV and FGZC refer to fieldnumber series of Miguel Vences and Frank Glaw. Fieldnumber acronyms are partly given together with collection acronyms in which they are deposited but not yet catalogued.

Code in trees	Voucher	Locality	GenBank Accession Nos.
<i>Phelsuma lineata</i>			
LB004	ZSM 62/2005	Ambohitantely	EF210617
LB045	ZSM 63/2005	Marojejy	EF210611
LB226	ZSM 64/2005	Ste. Luce	EF210630
LB227	ZSM 65/2005	Ste. Luce	EF210631
LB229	UADBA/FGZC 2637	Ste. Luce	EF210628
LB235	UADBA/FGZC 2643	Ste. Luce	EF210629
LB345	UADBA/FGMV 2002.140	Ranomafana	EF210626
LB356	UADBA 20727	Ranomafana	EF210627
LB362	FGMV 2002.309	Ranomafana	EF210620
LB389	ZSM 787/2003	near Ifanadiana	EF210623
LB560	UADBA 24218	Ambohitsara	EF210621

Appendix A (continued)

Code in trees	Voucher	Locality	GenBank Accession Nos.
LB561	ZFMK 82143	Ifanadiana-Tolongoina	EF210624
LB562	ZFMK 82142	Farafangana	EF210622
LB564	ZFMK 82135	Manombo	EF210625
LB565	UADBA 24726	Besariaka	EF210619
LB572	UADBA 24777	Montagne d'Ambre	EF210613
LB573	MV 2001.1059	Andasibe	EF210618
LB575	ZMA 19302	Fierenana	EF210615
LB589	ZSM 249/2004	Montagne d'Ambre	EF210614
LB590	ZSM 250/2004	Montagne d'Ambre	EF210612
—	ZCMV 3249	Antananarivo	EF210616
<i>Phelsuma quadriocellata</i>			
LB233	ZSM 66/2005	Ste. Luce	EF210610
<i>Hemidactylus platycephalus</i>			
—	MVTIS 2000e64	Mtsamboro, Comoros	AY517573
<i>Hemidactylus mercatorius</i>			
—	MVTIS 2000.C33	Montagne des Français	AY517584
—	MVTIS 2000.D26	Sambava	AY517585
77	—	Andapa	EF210652
—	ZSM 488/2001	Ankarafantsika	AY517581
—	ZSM 209/2002	Antananarivo	AY517579
70	—	Maroantsetra	EF210653
gb	MV 2001.309	Ankarafantsika	AY517575
83	—	Sambava	EF210655
—	ZSM 207/2002	Nosy Be	AY517583
78	—	Andapa	EF210654
—	MVTIS 2002.A24	Andranofotsy	AY517582
81	—	Tranomaro	EF210664
84	—	Tranomaro	EF210665
69	—	Maroantsetra	EF210656
72	MVTIS 2002-B45	Tolagnaro	EF210657
—	—	Manombo	EF210662
DF3	UADBA-MV 1490	Tolagnaro	AY517577
F32	MVTIS 2002-B50	Tolagnaro	AY517576
75	—	Esomony	EF210659
80	—	Esomony	EF210660
82	—	Esomony	EF210661
73	—	Tranomaro	EF210658
—	ZSM 205/2002	Maroantsetra	AY517578
—	—	Ranomafana	EF210663
<i>Calumma amber</i>			
LB541	ZSM 260/2004	Montagne d'Ambre	EF210633
LB542	ZSM 261/2004	Montagne d'Ambre	EF210634
<i>Calumma brevicorne</i>			
LB255	ZSM 70/2005	Andasibe	EF210636
LB461	Specimen not collected	Andasibe	EF210639
LB473	ZSM 549/2001	Andasibe	EF210637
LB474	UADBA/MV 2001.241	Andasibe	EF210638
LB496 (uncertain species attribution)	ZSM 546/2001	Itremo	EF210635

(continued on next page)

Appendix A (continued)

Code in trees	Voucher	Locality	GenBank Accession Nos.
<i>Calumma crypticum</i>			
LB165	ZSM 67/2005	Andohahela	EF210647
LB166	ZSM 68/2005	Andohahela	EF210648
LB187	ZSM 69/2005	Andohahela	EF210649
LB188	UADBA/FGZC 2504	Andohahela	EF210650
LB189	UADBA/FGZC 2505	Andohahela	EF210651
LB348	ZSM 684/2003	Vohiparara	EF210644
LB349	UADBA/FGMV 2002.290	Vohiparara	EF210645
LB374	ZSM 724/2003	Ranomafana NP	EF210643
LB502	UADBA/MV 2001.574	Imaitso	EF210642
LB472	ZSM 548/2001	Mandraka	EF210640
LB500	ZSM 547/2001	Imaitso	EF210641
LB540	Specimen not collected	Ambositra	EF210646
<i>Calumma malthe</i>			
LB050	ZSM 71/2005	Marojejy	EF210632
<i>Furcifer campani</i>			
LB002	ZSM 72/2005	Ankaratra	EF210578
<i>Furcifer lateralis</i>			
LB003	UADBA/ZCMV 751	Ambohitantely	EF210594
LB146	UADBA/FGZC 2346	Tranomaro	EF210600
LB153	ZSM 73/2005	Tranomaro	EF210599
LB330	UADBA/FGMV 2002.66	Antoetra	EF210586
LB335	Not preserved	Antoetra	EF210587
LB339	UADBA/FGMV 2002.117	Tampina forest	EF210592
LB340	ZSM 636/2003	Tampina forest	EF210593
LB386	ZSM 785/2003	near Ifanadiana	EF210590
LB387	ZSM 786/2003	near Ifanadiana	EF210591
LB402	UADBA 21083	Isalo/Analalava forest	EF210602
LB404	ZSM 936/2003	Isalo/Analalava forest	EF210607
LB405	ZSM 937/2003	Isalo	EF210604
LB406	ZSM 938/2003	Isalo/Analalava forest	EF210608
LB407	UADBA 21084	Isalo/Analalava forest	EF210609
LB409	UADBA 21082	Isalo/Analalava forest	EF210603
LB410	UADBA 21088	Isalo	EF210605
LB517	UADBA 24099	Between Ejeda-Ampanihy	EF210595
LB518	UADBA/FGZC 64	Between Ejeda-Ampanihy	EF210596
LB520	ZSM 41/2004	Tolagnaro	EF210598
LB531	ZSM 175/2004	Tranoroa	EF210597
LB532	UADBA/FGZC 348	Vondrozo	EF210588
LB533	ZSM 185/2004	Vondrozo	EF210589
LB534	ZSM 194/2004	Isalo	EF210606
LB535	ZSM 195/2004	Betioky	EF210601
LB552	UADBA 24496	Manombo	EF210581
LB588	ZSM 649/2000	Antananarivo	EF210579
LB485	ZSM 541/2001	Mont Ibity	EF210584
LB495	UADBA/MV 2001.567	Andringitra/Cirque Namoly	EF210583
LB494	ZSM 542/2001	Andringitra/Cirque Namoly	EF210582
LB493	UADBA/MV 2001.612	Itremo	EF210585
LB460	Not collected	Ambatolampy	EF210580
<i>Trachylepis comorensis</i>			
—	Unspecified	Unspecified	AF153565

Appendix A (continued)

Code in trees	Voucher	Locality	GenBank Accession Nos.
<i>Trachylepis elegans</i>			
LB149	UADBA/FGZC 2352	Near Tranomaro	EF210702
LB198	ZSM 74/2005	Esomony	EF210703
LB521	ZSM 44/2004	Tolagnaro	EF210706
LB522	UADBA/FGZC 74	Tolagnaro	EF210707
LB569	UADBA/MV 2000.283	Montagne des Français	EF210701
LB570	ZSM 544/2000	Sambava	EF210699
LB571	UADBA/MV 2000.171	Berara	EF210700
LB594	USNM 594222	Tolagnaro	EF210709
LB403	UADBA 21061	Ranohira	EF210710
LB488	UADBA 609	Itremo	EF210705
LB455	ZSM 196/2002	Tolagnaro	EF210708
LB154	UADBA/FGZC 2362	Near Tranomaro	EF210704
LB595	Not collected	Antalaha	EF210698
LB422	UADBA/FGMV 2002.2028	Ifaty	EF210697
LB593	ID uncertain Voucher and ID uncertain	Locality unknown	EF210711
—	—	Vohidava	DQ238881
<i>Trachylepis gravenhorstii</i>			
LB598	ZSM 439/2000	Nosy Fanihy	EF210675
LB599	ZSM 488/2000	Nosy Faly	EF210676
LB272	UADBA/FGZC 2740	Marojejy	EF210667
LB601	ZSM 437/2000	Nosy Be	EF210672
LB602	ZSM 557/2000	Sambava	EF210673
LB603	ZSM 438/2000	Nosy Be	EF210674
LB508	UADBA 16	Benavony	EF210671
LB469	ZSM 510/2001	Andasibe	EF210669
LB507	ZSM 509/2001	Nosy Be	EF210666
LB464	UADBA 2001.1234	Nosy Be	EF210668
LB001	UADBA/ZCMV 749	Ambohitantely	EF210678
LB600	ZSM 486/2000	Antananarivo-Mandraka	EF210680
LB476	ZSM 504/2001	Ankarafantsika	EF210679
LB557	ZMA 20139	Manombo	EF210681
LB385	ZMA 19394	Ranomafana	EF210684
LB523	ZSM 134/2004	Andohahela	EF210692
LB213	ZSM 75/2005	Tranomaro	EF210693
LB325	Probably ZMA 19584	Antoetra	EF210686
LB361	FGMV 2002.308	Vohiparara	EF210687
LB450	ZSM 197/2002	Tolagnaro	EF210691
LB342	FGMV 2002.120	Tampina forest	EF210683
LB530	ZSM 174/2004	Manantantely	EF210690
LB596	USNM 336441	Tolagnaro	EF210689
LB597	UADBA/MV 2001.438	Ibity	EF210682
LB408	UADBA 21070	Isalo/Analalava forest	EF210685
LB423	ZMA 19619	near Ambalavao	EF210688
LB466	UADBA/MV 2001.1003	Andasibe	EF210670
—	ZCMV 3381	Nosy Boraha	EF210677
—	—	—	AY070358
<i>Trachylepis madagascariensis</i>			
LB430	FGMV 2002.2105	Andringitra	EF210694
LB431	ZMA 19515	Andringitra	EF210695

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Appendix A (continued)

Code in trees	Voucher	Locality	GenBank Accession Nos.
—	—	Ankaratra	DQ238883
—	ZCMV 2524	Ankaratra	EF210696

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