Origin and in situ diversification in *Hemidactylus* geckos of the Socotra Archipelago

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Abstract

The Socotra Archipelago is an ancient continental fragment of Gondwanan origin and one of the most isolated landforms on Earth and a biodiversity hot spot. Yet, the biogeography and evolutionary history of its endemic fauna still remain largely overlooked. We investigate the origin, tempo and mode of diversification in the *Hemidactylus* geckos of the Socotra Archipelago. Concatenated and multilocus species coalescent analyses of *Hemidactylus* from Arabia and North Africa indicate that the *Hemidactylus* from Socotra do not form a monophyletic group and branch as three independent and well-supported clades instead. Both the chronogram inferred using the gene tree approach of BEAST and the age-calibrated multilocus species tree obtained using *BEAST suggest that the origin of *Hemidactylus* from Socotra may have involved a first vicariance event that occurred in the Early Miocene, followed by two independent transoceanic dispersal events that occurred more recently, during the Pliocene. Within Socotra, we analysed patterns of genetic diversity, the phylogeography and the demographic history in all seven nonintroduced species of *Hemidactylus*. Results based on two mitochondrial and two nuclear loci from 144 individuals revealed complex patterns of within-island diversification and high levels of intra-species genetic divergence. The interplay of both historical and ecological factors seems to have a role in the speciation process of this group of geckos. Interestingly, the case of *H. forbesii* and *H. oxyrhinus*, which inhabit the island of Abd al Kuri with an area of 133 km^2, may represent one of the most extreme cases of intra-island speciation in reptiles ever reported.

Keywords: continental fragment, Gondwana, historical demography, multilocus coalescence, oceanic dispersal, phylogeography, species delimitation

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Introduction

Continental islands are very important hot spots of biodiversity and provide premier settings for studying the evolutionary and ecological processes that have resulted in such unique biotas. As continental fragments (*sensu* Whittaker & Palacios 2007) were connected for a time to a continent, most of their biotas probably correspond to relict endemics of a vicariant origin. These continental islands are old enough so that

their fauna and flora have probably experienced dynamic evolutionary trajectories and species turnover, thus resulting in a unique assemblage of taxa (De Queiroz 2005). Although certain continental fragments have been studied extensively, for example, Madagascar or New Zealand (Yoder & Nowak 2006; Goldberg *et al.* 2008; Grandcolas *et al.* 2008), key topics about the origin (vicariance vs. dispersal) and the assemblage of these island communities over the evolutionary time (in situ diversification) remain unresolved.

The Socotra Archipelago, in the western Indian Ocean, is a case example of an ancient continental fragment, a

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block of Precambrian Gondwanaland with a long biogeographic history. The Archipelago comprises four islands: Socotra (3625 km^2), Abd al Kuri (133 km^2) and 'The Brothers', that is, Darsa (16 km^2) and Samha (40 km^2) and is located in the Arabian Sea, situated 380 km south-east from the coast of Yemen and about 100 km east from the Horn of Africa (Somalia) (Fig. 1). The archipelago rests on a shelf platform at the triple junction of the Gondwanan plates of India, Arabia and Africa. Tectonic activity in the Red Sea/Gulf of Aden region during the Oligocene marked the onset of the rifting between Arabia and Somalia continental blocks about 30–17.6 Ma (syn-rift) following by a continental break-up and oceanic spreading at 17.6 Ma (postrift) that increased the distance between the Socotra Archipelago and Arabian mainland (Laughton 1966; Bosworth *et al.* 2005; Autin *et al.* 2010). Remarkably, the archipelago is considered the '*jewel of the Arabian Sea*' because of its high level of diversity and endemism. For example, 37% of Socotra's 825 plant species, 90% of its 30 reptile species and 95% of its 100 land snail species are not found anywhere else in the world (Van Damme 2009; Razzetti *et al.* 2011). A few studies have examined the congruence between the geological history of Socotra and the cladogenesis in the molecular phylogenies of such a unique fauna and flora (Nagy *et al.* 2003; Thiv *et al.* 2006; Macey *et al.* 2008). While evidence for some taxa suggests an ancient vicariant origin that fits the first

phases of Gondwanan break-up (Nagy *et al.* 2003), several cases of transoceanic colonization have also been proposed (Thiv *et al.* 2006; Macey *et al.* 2008; Sindaco *et al.* in press). Yet, the nature and timing of the origin of the Socotra archipelago itself and its biota are complex matters that still remain under debate.

Both theoretical and empirical data show that intra-island speciation can be facilitated in large and remote areas as a consequence of long-term gene flow restriction or when ecological or topographical complexity is pronounced (Kisel & Barraclough 2010; Rosindell & Phillimore 2011). Socotra fits most of these predictions; that is, its long period of isolation from the Afro-Arabian mainland, its geological and orographic diversity and a unique climate probably played important roles in the assemblage of such a rich and diverse insular biota. Once it became isolated (about 17.6 Ma), Socotra was subjected to recurrent tectonic and volcanic events and several marine transgressions (Fleitmann *et al.* 2004). Likewise, paleoclimate reconstructions suggest that weather conditions have shifted abruptly as a result of the origin (8–10 Ma) and subsequent intensification cycles of the Indian monsoon during the Pliocene (5.33–2.58 Ma) (Gupta & Thomas 2003; Gupta *et al.* 2004; Chang *et al.* 2010), and linked to the events that followed last glaciations during the Quaternary (2.58 Ma to present) (Fleitmann *et al.* 2004, 2007; Shakun *et al.* 2007). In terms of ecological diversity, the Socotra
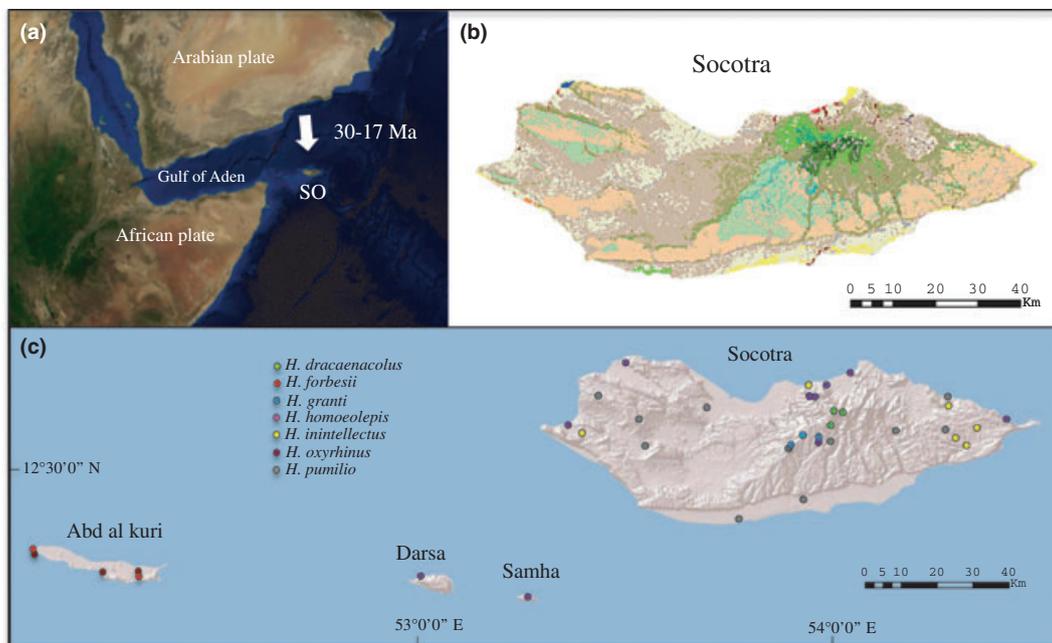

Fig. 1 (A) Map of the study area showing the Gulf of Aden and Dhorfar region in southern Oman as the possible geographic origin of Socotra. (B) Island biotopes within Socotra Island. C) Distribution of the *Hemidactylus* sampling sites and topography on the Socotra archipelago. Colours of locality dots correspond to different taxa. Detailed information on sampling localities and specimens is found in Table S1 (Supporting information).

Archipelago is clearly distinct from nearby continental areas in North Africa and Arabia and displays an outstanding diversity of habitat types and microclimates (see Van Damme 2009). Three clearly distinct geomorphological zones can be distinguished, more than eight vegetation types and 20 land cover classes have been identified (Král & Pavliš 2010; Banfield *et al.* 2011), and there is a marked temporal, spatial and altitudinal climatic variability (Scholte & De Geest 2010) (Fig. 1). Nevertheless, we know little about the real extent of Socotra's biodiversity or the role of historical and contemporary factors (i.e. island size, geographic isolation, biogeographic history and ecological disparity) in shaping these patterns.

Lizards represent key models to unravel evolutionary patterns and processes of island colonization and diversification (Camargo *et al.* 2010). Indeed, some of the most outstanding cases of adaptive radiations have occurred in island lizards (i.e. *Anolis*, see Losos 2009). Reptiles constitute the most relevant vertebrate fauna of the Socotra Archipelago, with 30 species and a very high level of endemism at both the specific (90%) and generic (41%) levels (Rösler & Wranik 2004; Sindaco *et al.* 2009; Razzetti *et al.* 2011). These reptile assemblages are in most cases composed of species that show distinct patterns of spatial distribution and habitat use (Razzetti *et al.* 2011). One of these groups of lizards inhabiting Socotra that show high species diversity and distinct island ecotypes is the geckos of the genus *Hemidactylus* (Sindaco *et al.* 2009; Razzetti *et al.* 2011). This group represents an excellent model because it is distributed worldwide, with numerous island species, and has experienced rapid radiations and multiple cases of transmarine colonization (Rocha *et al.* 2005; Carranza & Arnold 2006; Arnold *et al.* 2008; Bansal & Karanth 2010; Bauer *et al.* 2010; Busais & Joger 2011). Although the genus is considered to be morphologically conservative in many features (i.e. skull structure), there is a considerable variation in a range of external features including body size and proportions as well as dorsal and ventral colouring and pattern (see Carranza & Arnold 2006). *Hemidactylus* inhabiting Socotra indeed display a wide range of specialized ecomorphs including ground-dwelling, rock-dwelling and arboreal species (Table 1). An extreme case example is the pair of sympatric species *H. forbesii* and *H. oxyrhinus*, which inhabit the island of Abd al Kuri and show distinct ecologies and disparate morphologies (Boulenger 1903; Rösler & Wranik 2004; Razzetti *et al.* 2011). However, we know little about their evolutionary trajectories and the adaptive significance of their trait divergences. At present, no genetic or ecological studies of endemic reptiles of Socotra have been performed so far, and thus, the occurrence of a

Table 1 Main morphological traits and habitat preferences of native *Hemidactylus* taxa from the Socotra Archipelago

	SVL	HL*	HW*	Weight	Habitat/ecology
H. dracaenacolus	63.6 ± 6.4 (75) N = 17	19.8 ± 2.2 (22.3) N = 5	14.2 ± 1.7 (16.4) N = 5	7.3 ± 1.9 (10.8) N = 6	Nocturnal; arboreal restricted to *Dracaena* trees, from 762 to 1004 m asl
H. granti	64.6 ± 4.4 (70) N = 7	18.0 ± 2.9 (21) N = 6	12.1 ± 1.8 (13.8) N = 6	6.8 ± 1.3 (8.7) N = 7	Nocturnal; rock-dwelling; from 970 to 1463 m asl
H. inintellectus†	53.0 ± 5.1 (60.5) N = 14	16.6 ± 1.3 (18.2) N = 14	11.5 ± 1.0 (12.8) N = 14	4.8 ± 1.0 (5.8) N = 6	Nocturnal; rock-dwelling; mainly in rock boulders and cliffs from sea level to 762 m asl
H. homoeolepis	37.6 ± 2.9 (43) N = 15	10.8 ± 1.6 (13.2) N = 18	7.0 ± 1.4 (9.1) N = 18	1.4 ± 0.4 (2.3) N = 15	Nocturnal; mainly ground-dwelling but also found in boulders and tree trunks; from sea level to 995 m asl
H. pumilio	29.1 ± 3.2 (39) N = 18	8.4 ± 0.7 (9.3) N = 8	5.2 ± 0.5 (6.0) N = 8	0.7 ± 0.2 (1.2) N = 18	Nocturnal; strictly ground-dwelling where it moves and hides among the little stones; from sea level to 995 m asl
H. forbesii	86.6 ± 5.9 (95.0) N = 14	23.6 ± 2.2 (22.3) N = 8	16.6 ± 1.0 (17.9) N = 8	16.4 ± 3.1 (21) N = 14	Nocturnal; rock-dwelling; mainly found on rocks, but also on piles of fossil corals and among debris close to the sea
H. oxyrhinus	42.3 ± 4.9 (50.0) N = 22	12.5 ± 1.5 (15.0) N = 14	8.3 ± 1.2 (10.1) N = 14	2.2 ± 0.8 (3.6) N = 22	Nocturnal; ground-dwelling; stony and sandy places

Measurements correspond to mean and standard deviation and are expressed in millimetres or grams. The maximum value for each measurement is indicated in brackets.
SVL, snout-vent length; HL, head length; HW, head width.
* indicates that measurements of the character have been taken on preserved specimens and the number of specimens measured for this character. SVL and weight refers to living specimens only.
†Data of *H. inintellectus* are according Sindaco *et al.* (2009), except weights (unpublished data).

possible pattern of adaptive diversification in *Hemidactylus* geckos remains largely unexplored.

In this study, we first applied concatenated and multilocus coalescent approaches to unravel the timing of colonization and diversification patterns of *Hemidactylus* geckos from the Socotra Archipelago. Then, to uncover the existence of new putative species within Socotra, we investigated genetic diversity and genetic divergence at multiple nuclear and mitochondrial loci using several species delimitation methods at hand. Finally, a comprehensive sampling of multiple individuals from multiple locations and a wide geographic coverage of the archipelago allowed us to investigate the phylogeographic structure and demographic history of these recently evolved lineages.

Material and methods

Taxon sampling

A total of 262 *Hemidactylus* specimens were used for this study. These included 144 Socotran specimens corresponding to all the seven nonintroduced species of *Hemidactylus* that occur in the archipelago (Table S1, Supporting information), plus 118 non-Socotran *Hemidactylus* that include 116 representatives of the 'Arid Clade' *sensu* Carranza & Arnold (2006, in press), which comprise all the Socotran *Hemidactylus* species analysed to date (Carranza & Arnold 2006, in press; Busais & Joger 2011), and two specimens of *H. flaviviridis* (Tropical Asian Clade, Carranza & Arnold 2006) that were used as outgroups (Table S2, Supporting information). Main morphological and habitat features for each *Hemidactylus* species endemic to the Socotra Archipelago are shown in Table 1.

DNA extraction and amplification

Tissue samples were collected from the specimen's tail, and total genomic DNA was extracted using the DNeasy Blood and Tissue kit (Qiagen, Valencia, CA, USA) following the manufacturer's protocol. Partial sequences of three mitochondrial genes: the cytochrome *b* (*cytb*), the ribosomal 12S rRNA (*12S*) and the NADH dehydrogenase 4 (*nd4*), and one nuclear protein-coding gene, the melanocortin 1 receptor (*mc1r*), were amplified and sequenced following laboratory protocols described elsewhere (Shimodaira & Hasegawa 1999; Carranza *et al.* 2000). In the case of *Hemidactylus* samples from Socotra, one intron, *prdx4* (Leaché & Fujita 2010), was also amplified. Some *12S* and *cytb* sequences were used in previous phylogenetic studies of *Hemidactylus* (Carranza & Arnold 2006, in press), but a total of 320 unique sequences from 144

Socotran *Hemidactylus* are new to this study (Table S1, Supporting information). Primers, PCR conditions and source references are detailed in Table S3 (Supporting information).

Sequence analysis

Chromatograms were checked manually, assembled and edited using Geneious v. 5.3.6 (Biomatters Ltd.). Sequences were aligned for each gene independently using the online version of MAFFT v.6 (Katoh *et al.* 2009, http://mafft.cbrc.jp/alignment/server/) with default parameters (gap opening penalty = 1.53, gap extension = 0.0).

For nuclear loci, *mc1r* and *prdx4*, we identified heterozygous individuals based on the presence of two peaks of approximately equal height at a single nucleotide site. We used SEQPHASE (Flot 2010, http://www.mnhn.fr/jfflot/seqphase/), to convert the input files, and the software PHASE v. 2.1.1, to resolve phased haplotypes (Stephens *et al.* 2001; Stephens & Scheet 2005). We used all default settings of PHASE except for phase probabilities that were set as ≥ 0.7 (see Harrigan *et al.* 2008). All polymorphic sites with a probability of <0.7 were coded in both alleles with the appropriate IUPAC ambiguity code.

Basic genetic statistics and standard diversity estimates were calculated for each gene and *Hemidactylus* taxa from Socotra using the software DNASP v.5 (Librado & Rozas 2009). We tested for the signature of recombination in nuclear data using the phi-test (Bruen *et al.* 2006) as implemented in Splitstree v. 4.10 (Huson & Bryant 2006). As no recombination was detected, we used the entire sequence of the two loci for all subsequent analyses.

Phylogenetic analysis and divergence dating

To clarify the evolutionary history of *Hemidactylus* geckos from the Socotra Archipelago, we first inferred phylogenies using concatenated maximum likelihood (ML) and Bayesian analyses (BI) on the complete *Hemidactylus* data set (see above) comprising four genes with the nuclear *mc1r* gene unphased (heterozygous positions coded as ambiguities). A single-gene phylogeny on the *mc1r* locus only was also inferred to compare the phylogenetic signal of this nuclear locus with the mitochondrial loci. ML and BI data sets both included 260 ingroup taxa and two specimens of *H. flaviviridis* that were used as outgroups. jModelTest (Posada 2008) was used to select the most appropriate model of nucleotide substitution under the Akaike Information Criterion (Akaike 1973) for each gene partition (see Table S4, Supporting information). ML analyses were performed

with RAXML v.7.0.3 (Stamatakis 2006) using the GTR + G model with 100 random addition replicates and per-partition branch lengths (Townsend *et al.* 2011). Reliability of the ML tree was assessed by bootstrap analysis (Felsenstein 1985) including 1000 replications. Bayesian analyses were performed with MrBayes v.3.1.2 (Huelsenbeck & Ronquist 2001). Two independent runs of 5×10^6 generations were carried out, sampling at intervals of 1000 generations, producing 5000 trees. Convergence and appropriate sampling were confirmed by examining the standard deviation of the split frequencies between the two simultaneous runs and the potential scale reduction factor diagnostic. After discarding the first 500 trees of each run, a majority-rule consensus tree was generated from the remaining trees. Nodes were considered strongly supported if they received ML bootstrap proportions ≥70% and posterior probability support values ≥0.95 (Wilcox *et al.* 2002; Huelsenbeck & Rannala 2004).

Topological constraints to test two alternative topologies (single origin for clades I, II and III and single origin for clades II and III; see Fig. 2) were enforced using MacClade v. 4.0 (Maddison & Maddison 2000) and compared to the unconstrained ML tree using the approximately unbiased (AU) and Shimodaira-Hasegawa (SH) tests (Shimodaira & Hasegawa 1999; Shimodaira 2002). Per-site log likelihoods were estimated in RAXML 7.2.6 (Stamatakis 2006), and *P* values were calculated using CONSEL (Shimodaira & Hasegawa 2001).

The lack of internal calibration points in *Hemidactylus* precludes here any direct estimation of the time of the cladogenetic events in our phylogeny. Alternatively, the substitution rate of the same mitochondrial region calculated for other lizard groups can be used for this purpose. Mean substitution rates and their standard errors for the *12S* and *cytb* gene regions were extracted from fully calibrated phylogenies of various lizard groups from the Canary islands: *Tarentola* sp. (Gekkonidae) (Carranza *et al.* 2000, 2002), *Gallotia* sp. (Lacertidae) (Cox *et al.* 2010) and *Chalcides* sp. (Scincidae) (Brown & Pestano 1998; Carranza *et al.* 2008; Brown & Yang 2010). These values were used as informative priors in all divergence dating analyses. Specifically, we set a normal distribution prior for the ucld.mean parameter of the *12S* and *cytb* partitions based on the combined meanRate posteriors (mean and standard error) of all three independent calibration analyses of *Tarentola*, *Gallotia* and *Chalcides* (0.00755 ± 0.00247 for the *12S* and 0.0228 ± 0.00806 for the *cytb*) (see Carranza & Arnold in press).

We used BEAST v.1.6.2 (Drummond & Rambaut 2007) to estimate dates of the cladogenetic events in the *Hemidactylus* phylogeny. The data set comprised sequences from all four genes (*mc1r* unphased), but as is customary for such analyses, we used a phylogeny pruned arbitrarily to include one representative from each of the major lineages uncovered with the concatenated analysis (47 specimens in total; Fig 2, Tables S1 and S2, Supporting information). This method excludes closely related terminal taxa because the Yule tree prior (see below) does not include a model of coalescence, which can complicate rate estimation for closely related sequences (Ho *et al.* 2005). Models, priors and parameter specifications are available in Table S4 (Supporting information, otherwise by default).

The advantages of multilocus coalescent approaches compared to single-gene and concatenated tree methods have been reviewed extensively (Degnan & Rosenberg 2009; Knowles 2009; Heled & Drummond 2010). Here, we applied the coalescent-based species tree approach implemented in *BEAST to test the origin and diversification patterns in *Hemidactylus* and to compare these results to those obtained from the ML, BI and BEAST analyses. Importantly, multilocus approaches allow for joint estimation of the species tree and divergence times, while taking into account uncertainties associated with gene tree inference such as incomplete lineage sorting (ILS) (Heled & Drummond 2010). Apart from ILS, incongruence may arise because gene tree analyses tend to overestimate divergence times (Knowles & Carstens 2007; McCormack *et al.* 2011). Besides, multilocus coalescent methods have been proved useful for delimiting species (Knowles & Carstens 2007; Carstens & Dewey 2010). In our study, species traits for the *BEAST analysis were defined based on previous taxonomic designations for *Hemidactylus* geckos (Carranza & Arnold 2006, in press). In the case of the Socotra Archipelago for which little phylogenetic and taxonomic information is available, we delineated independent evolutionary lineages corresponding to the monophyletic groups inferred by the species delimitation methods applied in this study and that resulted in 14 'putative species' (see Results). Such approach allowed us to simultaneously estimate divergence times and test the monophyly, given by posterior support probabilities, of distinct evolutionary lineages within the archipelago. All *BEAST analyses were performed on the complete data set that consisted in four genes (*12S*, *cytb*, *nd4* and *mc1r*) (see Tables S1 and S2, Supporting information). Models, priors and parameter specifications are detailed in Table S4 (Supporting information).

Intra-specific diversity and species delimitation within Socotra

To examine patterns of intra-specific diversity in *Hemidactylus* geckos from the Socotra Archipelago, we built
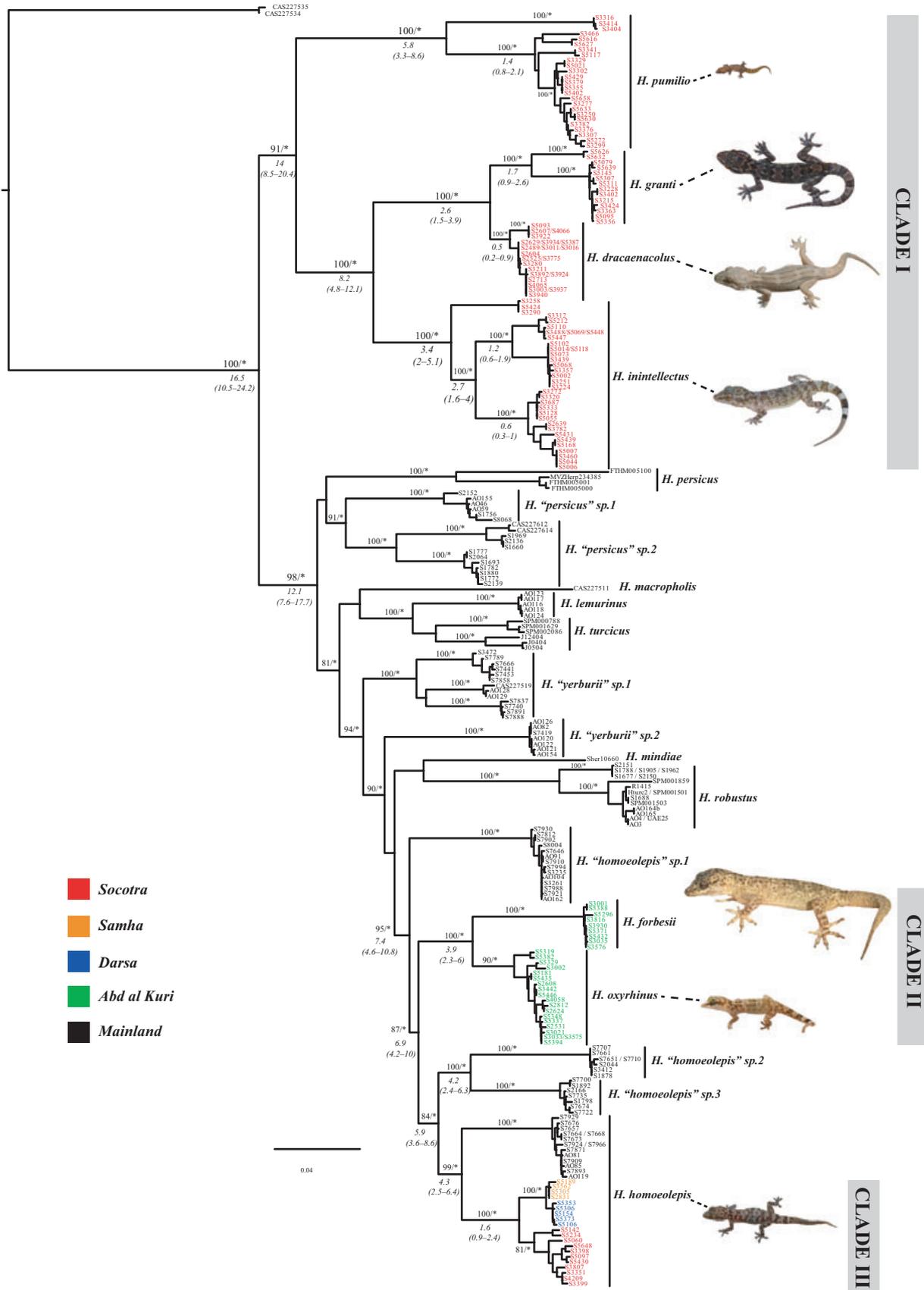
statistical parsimony networks on the concatenated mitochondrial dataset and the two phased individual nuclear loci by using TCS v1.21 (Clement *et al.* 2000), using default settings. For comparative purposes, only the 116 Socotran *Hemidactylus* with complete sequence information for all these four genes were included (see Table S1, Supporting information). Statistical parsimony analysis partitions the data into independent networks of haplotypes connected by changes that are nonhomoplastic with a 95% probability (Templeton 2001). Although this threshold does not necessarily correspond to species boundaries, this algorithm often does separate groups that are roughly coincident with named species or species groups (e.g. Hart & Sunday 2007).

Two methods of species delimitation on mitochondrial and nuclear data, respectively, were conducted. First, we conducted the general mixed Yule-coalescent (GMYC) approach (Pons *et al.* 2006). The GMYC method identifies species boundaries as a shift in branching rates on a phylogenetic tree that contains multiple species and populations (see Pons *et al.* 2006; Monaghan *et al.* 2009). As this method relies on single-locus phylogenies, and given the low sequence variability of the nuclear data, we conducted the GMYC approach onto the mtDNA only after the removal of identical haplotypes. GMYC analyses were conducted using 'SPLITS' (Species Limits by Threshold Statistics) (http://r-forge.r-project.org/projects/splits) in R Version 2.14.1. The single threshold option was applied onto the tree to find the ML solution of the GMYC model. The ultrametric mitochondrial tree was generated using BEAST, and we considered different parameter combinations: Yule vs. coalescent prior and strict clock vs. relaxed lognormal clock (Monaghan *et al.* 2009). Bayes factors indicated that a coalescent prior with a relaxed lognormal clock gives a slightly better fit than a Yule prior (coalescent: −15002.88, Yule: −14997.35, log10 BF: 2.40). In this line, according to GMYC model fit estimates, the relaxed lognormal clock model with the coalescent prior performed better than all other possible combinations, but the number of entities was highly concordant between methods (coalescent relaxed lognormal: $N_{GMYC} = 45$ (CI 38–60), $L_{GMYC} = 1484.09$; Yule relaxed lognormal: $N_{GMYC} = 45$

(CI 38-59), $L_{GMYC} = 1471.53$). Second, a multilocus coalescent species delimitation analysis was conducted using the Bayesian Phylogenetics and Phylogeography program (BPP v.2.1, Yang & Rannala 2010). The method adopts the biological species concept and uses a species phylogeny represented by a user-specified guide tree. It then generates the posterior probabilities of species assignments by accommodating ILS and uncertainties because of unknown gene trees (see Yang & Rannala 2010). We applied the rjMCMC method of BPP to examine whether the mtDNA lineages from Socotra inferred by the GMYC analysis were supported by the nuclear data. Owing to the paraphyletic nature of the guide tree for the *Hemidactylus* from Socotra (see Fig. 2), BPP analyses were run separately on clades I (*H. pumilio*, *H. inintellectus*, *H. dracaenacolus* and *H. granti*), and II-III (*H. homoeolepis*, *H. oxyrhinus* and *H. forbesii*). We tested both algorithm 0 and 1 for species delimitation implemented in the program with the fine-tuning parameter ε = 5.0. Each species delimitation model was assigned equal prior probability. The prior distributions on the ancestral population size (θ) and root age (τ) can affect the posterior probabilities for models (Yang & Rannala 2010). As no empirical data were available for the studied species, we ran the analyses by considering three different combinations of priors (see Table S4, Supporting information, Leaché & Fujita 2010).

Phylogeographic patterns and historical demography

To test the existence of spatial patterns of genetic structuring within Socotra, we mapped the frequency and spatial distribution of mitochondrial haplotypes for each *Hemidactylus* species into a GIS framework using ArcGis Desktop v10.0 (ESRI, Spain). In species where significant intra-island diversity was detected (*H. inintellectus*, *H. pumilio* and *H. homoeolepis*, see Results), we conducted AMOVA analyses as implemented in Arlequin v3.5 (Excoffier & Lischer 2010), by grouping mitochondrial haplotypes in relation to distinct island biotopes as described by Král & Pavliš (2010). To examine the pattern of isolation by distance, we tested the correlation between a matrix of pairwise genetic distances between mitochondrial haplotypes, calculated as the Slatkin's lin-

Fig. 2 Maximum likelihood (ML) phylogenetic tree of 262 *Hemidactylus* specimens based on the concatenated sequences of three mitochondrial (*12S*, *nd4* and *cytb*) and one nuclear (*mc1r*) loci. Two specimens of *H. flaviviridis* were used to root the tree and have not been included in the figure. Tree topology and branch lengths are for the sampled tree with the highest likelihood by RAxML (100 searches, log likelihood = −18318.522630). Each sequence is labelled with the specimen code and taxa name (see Tables S1 and S2, Supporting information). Maximum likelihood bootstrap support values above 70% are indicated above branches, and asterisks indicate a posterior probability value of $P \geq 0.95$ in the Bayesian analysis. Relevant nodes for which calibrations have been inferred with BEAST are marked with a filled black dot. Age estimates are in italics below these nodes and include the mean and the HPD 95% confidence interval in brackets. Note that silhouettes of *Hemidactylus* taxa from the Socotra Archipelago are size-scaled (see Table 1 for more information).

earized Φ_{ST} ($\Phi_{ST}/1 - \Phi_{ST}$), and a matrix of the log of Euclidean geographic distances between localities using a Mantel test with 10000 permutations as implemented in Arlequin (Mantel 1967; Smouse *et al.* 1986; Slatkin 1993). Φ_{ST} and *P* values from pairwise differences between main GMYC mitochondrial lineages were also calculated.

To investigate the demographic history of *Hemidactylus* geckos from the Socotra archipelago, we estimated the shape of the population growth function through time by constructing extended Bayesian skyline plots (EBSP) as implemented in BEAST v1.6.2 (Heled & Drummond 2008). This approach explicitly incorporates multiple independent loci and estimates the number of coalescent intervals of population size changes (Heled & Drummond 2008). Compared to other methods, EBSP significantly improves the reliability of demographic inferences; increases power in detecting past population bottlenecks; and substantially reduces the estimation error (Ho & Shapiro 2011). Best-fit models of nucleotide substitution were inferred in each lineage and gene using jModelTest v0.1. Parameter and prior specifications are summarized in Table S4 (Supporting information).

For all analyses implemented in BEAST, convergence for all model parameters was assessed using Tracer v1.5 (Rambaut & Drummond 2007) after obtaining an effective sample size (ESS) > 200. Runs were combined using LogCombiner, and maximum credibility trees with divergence time means and 95% highest probability densities (HPDs) were produced using Tree Annotator (both part of the BEAST package). Trees were visualized using the FigTree v1.3.1 (http://tree.bio.ed. ac.uk/software/figtree).

Results

Phylogenetic analyses

The final alignment used to infer the ML and BI phylogenetic trees of *Hemidactylus* included a total of 1838 bp for 262 taxa (Tables S1, S2 and S4, Supporting information). Of the 1838 positions, 674 were variable and 627 parsimony-informative (145 and 135 for the *12S*, 158 and 148 for the *cytb*, 289 and 276 for the *nd4* and 82 and 68 for the *mc1r*, respectively). Both ML and BI analyses on the concatenated data set and the single *mc1r* locus (Figs 2 and S1) gave almost identical results and agreed in all the well-supported nodes with the results of the BEAST analysis on the pruned data set (data not shown) and with the multilocus species tree obtained using *BEAST (Fig. 3). Divergence date estimates for both gene tree (BEAST) and species tree (*BEAST) approaches were also similar, and the confidence inter-

vals (95% HPD) were largely overlapping (Table S5, Supporting information). Differences between the two methods were more pronounced at the base of the tree, but were almost nonexistent in the most recent nodes. In all cases, the gene tree estimations gave older values than the species tree estimations (see Table S5, Supporting information). In all four independent phylogenetic analyses, the *Hemidactylus* geckos from the Socotra Archipelago do not form a monophyletic group, and they branch as three independent and well-supported clades instead. Clade I, which includes the Socotra Island endemics *H. inintellectus*, *H. dracaenacolus*, *H. granti* and *H. pumilio*, branches off after *H. citernii* and is sister to the remaining *Hemidactylus* taxa from the Arid Clade [16.5 Ma (BEAST), 14.4 Ma (*BEAST)]. Clade II is the second Socotran clade to branch off [6.9 Ma (BEAST), 5.7 Ma (*BEAST)] and includes the two Abd al Kuri endemics (*H. forbesii* and *H. oxyrhinus*). Clade III, the most recent Socotran clade [4.3 Ma (BEAST), 3.9 Ma (*BEAST)], includes the nonendemic *H. homoeolepis* from Socotra, Samha and Darsa islands. Results of the two topology tests performed, the approximately unbiased (AU) and Shimodaira–Hasegawa tests (SH), further support such a biogeographic scenario and reject the null hypothesis of a monophyletic origin for Socotran *Hemidactylus*. In both tests, the constrained tree in which we enforced monophyly for clades I-II and III is significantly different from the best ML tree presented in Fig. 2 (AU test: $P < 0.001$, SH test: $P < 0.001$). Similar results are obtained when enforcing monophyly of the more closely related clades II and III only (AU test: $P < 0.001$, SH test: $P < 0.001$).

Species delimitation within Socotra

Diversity estimates and TCS statistical parsimony networks both revealed high levels of mitochondrial within-species diversity for six of the seven endemic Socotran *Hemidactylus* (Table 2, Figs 4 and 5). That is, except for *H. forbesii*, the majority of species consist of several lineages: *H. homoeolepis* (5), *H. inintellectus* (6) and *H. pumilio* (4) (Fig. 5). Such a high level of intraspecific genetic diversity (Figs 2 and 5) contrasts, however, with the relatively low levels of genetic variability found in the nuclear data (Table 2, Figs S1 and S2, Supporting information). We found no general agreement in the divergence patterns between mitochondrial and nuclear markers, except for *H. inintellectus* and *H. pumilio* at the *mc1r* locus. The species pairs *H. dracaenacolus—H. granti* and *H. oxyrhinus—H. forbesii* share nuclear alleles in the *mc1r* gene. No interspecific allele sharing in Socotran *Hemidactylus* was detected for the nuclear intron *prdx4* (Fig. S2, Supporting information).
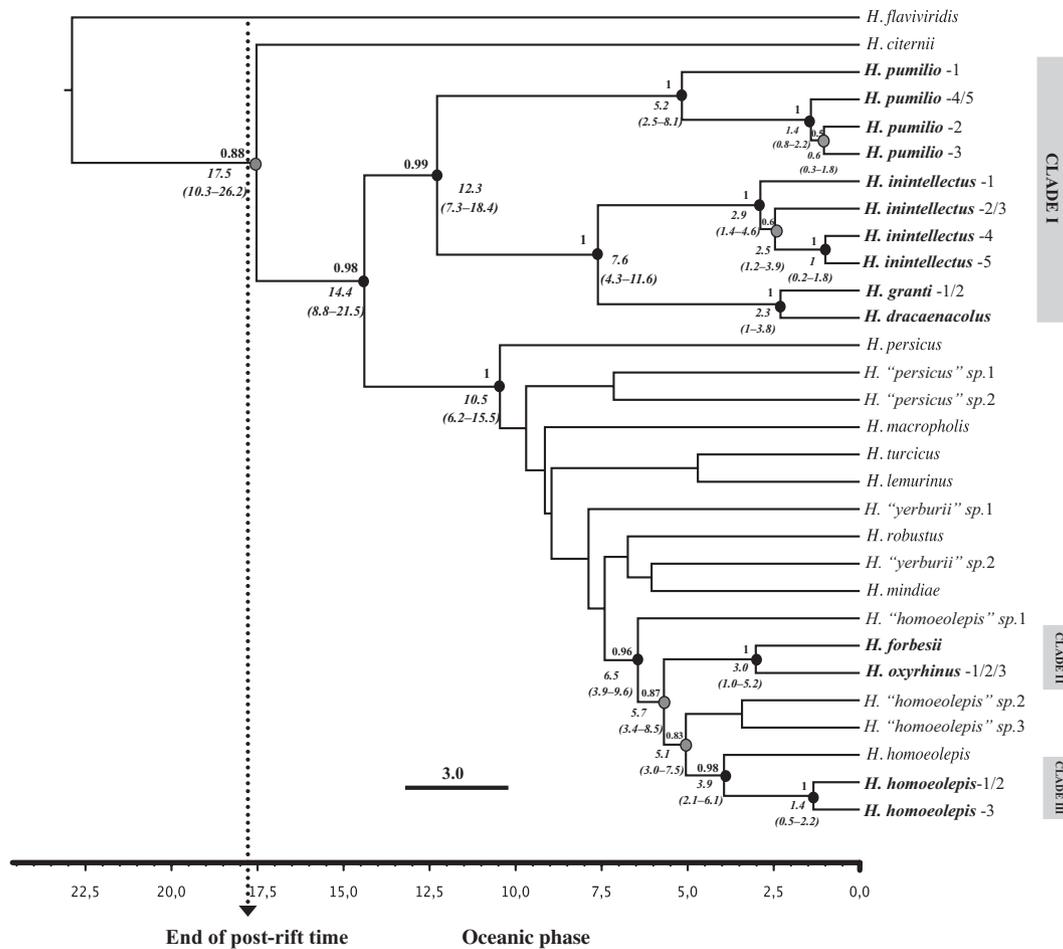
Fig. 3 Multilocus species tree chronogram inferred using *BEAST. Age estimates corresponding to mean, 95% highest probability density intervals (HPD) confidence intervals and posterior probability support values obtained from *BEAST are included for some relevant nodes [highlighted with a black ($P \geq 0.95$) or a grey dot ($P < 0.95$)]. The time axis is indicated at the bottom. The doted black line demarks the boundary of the Gulf of Aden postrift time (about 17.6 Ma).

The single threshold model of the GMYC analysis resulted in 19 putative species within Socotra (see Fig. S3 and Table S1, Supporting information). Concordant with these results, the Bayesian species delimitation approach of the BPP analysis on the nuclear data supported most of the lineages inferred by the GMYC analysis, with some exceptions (Fig. S4 and Table S1, Supporting information). In these analyses, the map tree with the highest posterior probability consisted of 10 species for clade I (map tree *111011011101*, Bayesian Posterior (BP) = 0.62) and 4 species for clades II and III (map tree *11010*, BP = 0.60) (Fig. S4, Supporting information), considering a speciation probability threshold for nodes of 0.90. The three combinations of priors applied to the *Hemidactylus* data gave identical results for the map tree, with slight differences in the posterior support values of the nodes. However, in all cases, these were >0.90. These results were also consistent across runs, and in all cases, ESS values exceed 200, assuring the convergence of MCMC chains (results not shown).

Phylogeography and demographic analyses

Mapping the frequency and geographic distribution of haplotypes on Socotra can provide important insights into patterns of historical divergence among populations. *Hemidactylus granti* and *H. dracaenacolus* display very restricted distributions within Socotra but no clear or shallow phylogeographic structure: haplotypes do not group by geography, divergent mitochondrial lineages co-occur in a single location, and there is haplotype sharing at some localities (Fig. 4). A similar pattern is found in *H. forbesii* and *H. oxyrhinus*, which are restricted to the island of Abd al Kuri (Fig. 4). In contrast, *H. inintellectus*, *H. pumilio* and *H. homoeolepis*

Table 2 Basic genetic statistics of *Hemidactylus* taxa from Socotra analysed in this study based on two mitochondrial (*cytb* and *nd4*) and two nuclear loci (*prdx4* and *mc1r*)

Species	*cytb*						*nd4*						*mc1r*						*prdx4*					
	N	P_S	N_A	π	R^2	D	N	P_S	N_A	π	R^2	D	N	P_S	N_A	π	R^2	D	N	P_S	N_A	π	R^2	D
H. dracaenacolus	22	12	4	0.0135	0.16	3.98	20	9	4	0.0056	0.16	2.88	42	2	3	0.0004	0.09	0.26	42	1	2	0.0001	0.15	0.05
H. forbesii	8	2	3	0.0023	0.20*	0.68	9	7	5	0.0040	0.19	2.06	18	4	4	0.0019	0.16	1.27	18	0	1	0.0000	ne	0.00
H. granti	14	29	8	0.0299	0.13	7.96	14	43	9	0.0229	0.13	11.77	28	4	3	0.0016	0.13	1.05	28	11	6	0.0031	0.09	2.05
H. homoeolepis	21	76	18	0.0571	0.13	16.77	18	47	14	0.0354	0.17	17.07	40	6	7	0.0005	0.06*	0.35	40	3	4	0.0008	0.08	0.36
H. inintellectus	30	51	13	0.0680	0.16	16.66	34	97	14	0.0635	0.17	32.45	68	7	9	0.0021	0.10	1.41	60	26	12	0.0152	0.19	9.77
H. oxyrhinus	19	14	10	0.0096	0.09	2.82	18	42	13	0.0193	0.11	9.91	38	4	4	0.0004	0.09	0.26	38	2	3	0.0010	0.13	0.48
H. pumilio	25	88	20	0.0736	0.12	21.57	23	112	16	0.0568	0.12	27.95	54	25	18	0.0030	0.04*	1.99	54	21	11	0.0046	0.05*	2.07

N, number of individuals sequenced, P_S, number of polymorphic sites; N_A, number of haplotypes/alleles; π, nucleotide diversity; R^2, Ramos-Onsins and Rozas statistic (population size deviations were tested by coalescent simulations); D, average number of nucleotide differences between sequences. The asterisk (*) indicates significance at $P < 0.05$. In the case of nuclear loci, estimates correspond to phased haplotypes.

all show substantial phylogeographic structure as spatially discrete monophyletic clusters (Figs 2, 5 and S3). In these four species, haplotype networks revealed some common patterns: (i) Φ_{ST} between lineages are high and mostly significant (not significant values likely result from low sample sizes, see Table S6, Supporting information), (ii) the distinct lineages are spatially segregated and there is no allele sharing across all remaining populations except for haplotype h2 of *H. inintellectus,* and iii) an east-west pattern of haplotype divergence within Socotra Island is apparent (Fig. 5). More in particular, in *H. homoeolepis*, the only species that occurs on multiple islands, there is a significant divergence of haplotypes between Socotra and 'The Brothers'—Samha and Darsa (Table S6, Supporting information). However, we detected no pattern of isolation by distance ($r = -0.53$, $P = 0.99$). Population structure by habitat type could not be tested in this species because of low sample sizes at the locality level and low biotope representativeness in the sampling. In *H. pumilio*, despite a marked within-population diversity ($\Phi_{SC} = 0.98$, $P < 0.001$) and high population differentiation ($\Phi_{ST} = 0.98$, $P < 0.001$), neither habitat types nor geographic distances between populations explain the patterns of genetic structure on this species ($\Phi_{CT} = -0.21$, $P = 0.62$; $r = 0.09$, $P = 0.49$). On the contrary, *H. inintellectus* displays a strong significant population structure by habitat type that explains 45.74% of the total variation ($\Phi_{SC} = 0.77$, $\Phi_{ST} = 0.87$, $\Phi_{CT} = 0.46$, all $P < 0.001$). Although haplotypes are clearly structured in east, central and west lineages, we did not find any significant correlation between genetic and geographic distances among populations ($r = 0.18$, $P = 0.13$).

Regarding population demographic analyses, we estimated the changes in effective population size of the lineages through time, using extended Bayesian skyline plots (EBSP) as implemented in BEAST. Most species/lineages plots showed no significant departures from a constant population model because the majority of credible sets contain zero population size changes (results not shown). On the contrary, *H. oxyrhinus* underwent a recent population expansion according to the population demographic function generated in BEAST. We also detect significant population size changes in the two lineages of *H. homoeolepis* from Socotra and Darsa–Samha, respectively. The use of EBSPs also allowed us to estimate the approximate time of the demographic change. That is, population expansion in *H. oxyrhinus* from Abd al Kuri dates back about 100 Ka. In the Darsa—Samha lineage of *H. homoeolepis*, population expansion occurred more recently about 50 Ka, whereas in *H. homoeolepis* from Socotra, this event dates back 1 Ma (Fig. 6).
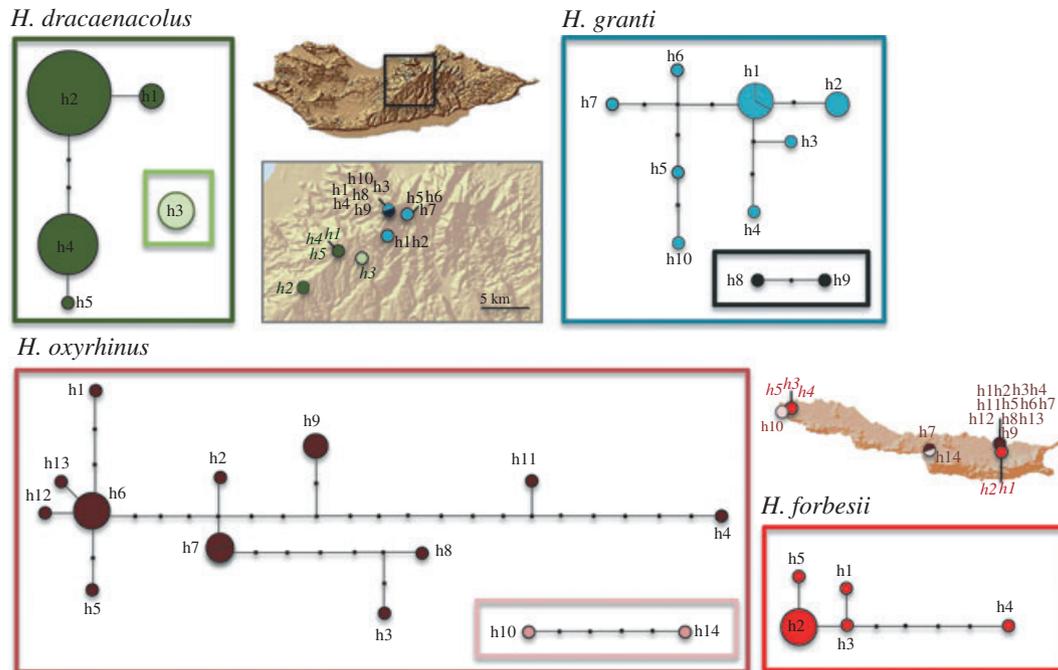
Fig. 4 Statistical parsimony mitochondrial haplotype networks for *Hemidactylus* species with no significant phylogeographic structure (see text). In all species, genetically related haplotypes from distinct localities are coded with similar colours that define lineages. The sizes of the circles are proportional to the number of individuals with each haplotype. Black dots represent mutational steps.

Discussion

Origin and timing of diversification of Hemidactylus geckos from Socotra

This study shows that *Hemidactylus* geckos of the Socotra Archipelago have three independent origins (Figs 2 and 3). The inferred dates and associated confidence intervals for the split of clade I roughly coincide with the continental break-up and posterior oceanic spreading that occurred at 17.6 Ma in the eastern part of the Gulf of Aden (see Fig. 3). This event separated Socotra from the Arabian mainland, triggering the oceanic phase of the Socotra Archipelago (Laughton 1966; Bosworth *et al.* 2005; Autin *et al.* 2010), and which suggests that the origin of clade I may have been the result of vicariance. We are aware that the present phylogeny of *Hemidactylus* does not include all possible representatives of the Arid clade from the Horn of Africa (Eritrea, Djibouti, Ethiopia and Somalia) and Arabia (Loveridge 1936, 1947; Parker 1942; Arnold 1980, 1986; Lanza 1983, 1990; Spawls *et al.* 2002; Largen & Spawls 2006, 2010; Sindaco *et al.* 2007). However, in this study, none of the African or Arabian species appear as sister to the Socotran clade I or within that clade. Further, although recent studies obtained contrasting topologies with regards to clade I (Busais & Joger 2011), our results also

agree with previous analysis by Carranza & Arnold (2006), which using similar gene regions recovered these taxa as monophyletic and in a very similar phylogenetic position to that shown in this study (Figs 2 and 3).

Our calibrated phylogenetic analyses indicate that the ancestor of *H. forbesii* and *H. oxyrhinus* (clade II) colonized Abd al Kuri Island between 5.7 and 3 Ma, while clade III of *H. homoeolepis* colonized Socotra, Samha or Darsa Islands between 3.9 and 1.4 Ma (Figs 2 and 3). According to several authors, the timing of these maximum-inferred colonization events of the Socotra Archipelago by clades II and III corresponds to its oceanic phase, when the islands had already drifted close to their actual position in the Arabian Sea (Laughton 1966; Fleitmann *et al.* 2004; Bosworth *et al.* 2005; Autin *et al.* 2010, among others). Even the oldest dates for the associated confidence intervals for the origin of each one of the two clades (clade II: 8.5 Ma, clade III: 6.1 Ma) clearly fall into this oceanic phase, thus meaning that the two colonization events were probably the result of over-water dispersal.

In relation to other groups of reptiles from Socotra, only the snakes of the genera *Hemerophis* and *Ditypophis* (Nagy *et al.* 2003) and the skinks of the genus *Trachylepis* (Sindaco *et al.* in press) have been investigated
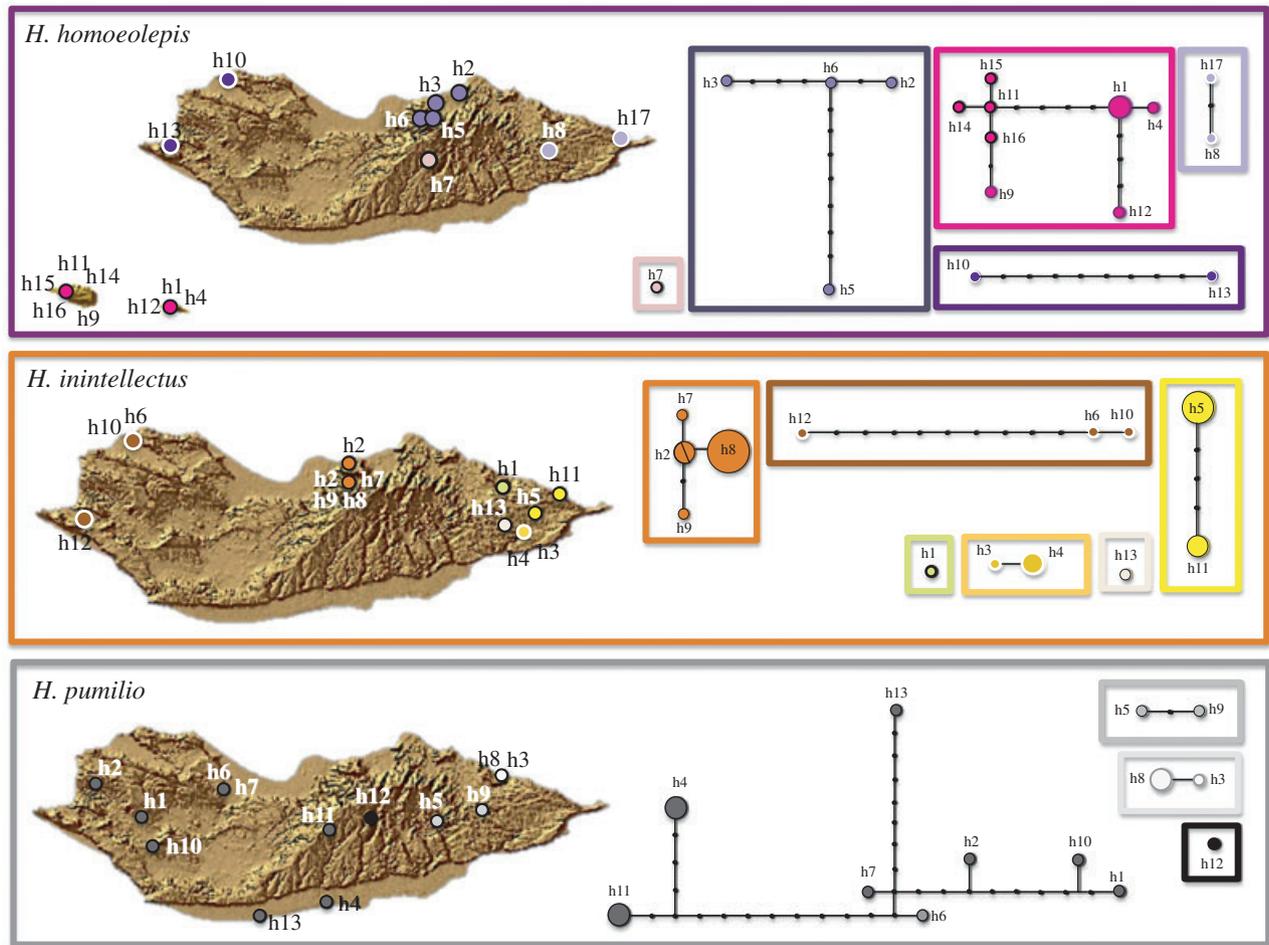
Fig. 5 Statistical parsimony mitochondrial haplotype networks for species with intra-specific genetic divergence and phylogeographic structure within Socotra (see text). Spatial distribution of haplotypes and lineages are mapped across Socotra. In all species, genetically related haplotypes from distinct localities are coded with similar colours that define lineages. The sizes of the circles are proportional to the number of individuals with each haplotype. Black dots represent mutational steps.

using similar dating techniques. Those studies suggest that the two snakes are relicts that were probably present on Socotra when it separated from mainland Arabia, thus making them examples of vicariance. Contrary, the *Trachylepis* skinks would have arrived at the Socotra Archipelago by transmarine colonization on two independent occasions: the first one to Socotra, Samha or Darsa Islands, and the second one to Abd al Kuri Island. Phylogenetic data for other groups such as *Pristurus* (Papenfuss *et al.* 2009), *Mesalina* (Joger & Mayer 2002; Kapli *et al.* 2008), *Hakaria simonyi* (Brandley *et al.* 2005; Austin *et al.* 2009) and *Chamaeleo monachus* (Macey *et al.* 2008) are much scarcer and in most cases do not allow us to draw any conclusions regarding the number, direction and time of the different colonization events. In the case of Abd al Kuri, although it lies just 66 km to the west of Samha and 105 km from Socotra (Fig. 1), our analyses clearly show that *H. forbesii* and

H. oxyrhinus are more closely related to *Hemidactylus* from south-eastern Arabia, located more than 350 km to the north, than to *Hemidactylus* from the neighbouring islands of the Socotra Archipelago. This biogeographic pattern is also found in other groups, especially in *Mesalina* (Joger & Mayer 2002) and *Trachylepis* (Sindaco *et al.* in press).

About the processes that may explain such patterns, long-distance transmarine colonization events are not rare in reptiles (see De Queiroz 2005 for a review), and geckos are among the best dispersers (Carranza *et al.* 2000, 2002; Jesus *et al.* 2001, 2005; Carranza & Arnold 2006; Weiss & Hedges 2007; Arnold *et al.* 2008; Gamble *et al.* 2011). The high level of geographic restriction of the mainland relatives of clades II and III indicates that both independent transmarine colonization events probably have their origin in southern Oman, 350 km to the north of the Socotra Archipelago. The transmarine colo-
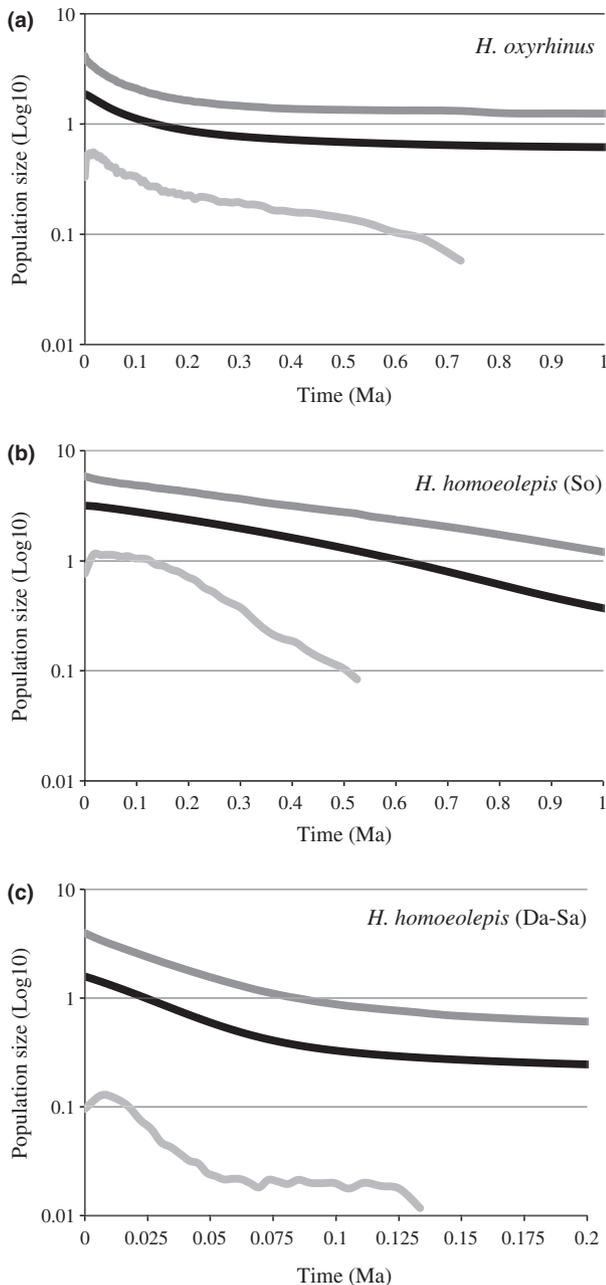
Fig. 6 Demographic history of *H. oxyrhinus* (A), and *H. homoeolepis* from Socotra (B), and Darsa and Samha (C). Extended Bayesian skyline plots showing changes in effective population size (Ne) through time estimated using uncorrelated lognormal relaxed molecular clock and a piecewise-linear model. The *y*-axis representing the effective population size is given on a logarithmic scale, and the *x*-axis represents time in millions of years ago (Ma). The thick solid black line is the median estimate, and area delimited by the upper and lower grey lines represents the HPD 95% confidence intervals for effective population size.

nization of the Socotra Archipelago by clades II and III occurred after the origin and intensification of the Indian monsoons as a result of the uplift of the Himala-

yas and the Tibetan Plateau, approximately 8–10 Ma (Gupta *et al.* 2004). At present, there are two annual monsoons that affect the Socotra Archipelago: the south-west monsoon, which blows from early June to early October, and the north-east monsoon, which blows from April to May, also affecting the direction of the oceanic currents. During winter, the flow of the upper ocean is directed westward from near the Indonesian Archipelago to the Arabian Sea. During summer, the direction reverses, with eastward flow extending from Somalia into the Bay of Bengal (Shankar *et al.* 2002). According to the results of this work and what has been inferred from other groups such as *Mesalina* and *Trachylepis* (Joger & Mayer 2002; Sindaco *et al.* in press), it is suggested that the westward winter monsoon current may have played a very important role in the transmarine colonization of the Socotra Archipelago by several groups.

Within-island speciation and phylogeography

Our findings suggest that speciation in *Hemidactylus* from the Socotra Archipelago occurred in situ and that it has been a gradual process. That is, within the Socotra Archipelago, up to 14 monophyletic lineages corresponding to 7 distinct taxa can be identified. Several factors such as ecological diversity, island age and geographic isolation can explain within-island diversification in Socotra (Kisel & Barraclough 2010; Rosindell & Phillimore 2011). Available evidence, however, suggests that speciation in this group of geckos may be ecologically adaptive. Indeed, *Hemidactylus* taxa can be classified into three different ecotypes that are morphologically distinct: rock-dwelling (*H. inintellectus*, *H. granti* and *H. forbesii*), ground-dwelling (*H. pumilio*, *H. homoeolepis* and *H. oxyrhinus*) and arboreal (*H. dracaenacolus*) (Sindaco *et al.* 2009; Razzetti *et al.* 2011). Interestingly, the distribution of these ecomorphs is in most cases sympatric; thus, these species that co-occur occupy different ecological niches. There are, however, some cases of parapatry, like in the mountain endemic *H. granti*. In this case, no obvious geographic barriers exist, but species distribute into different geographic areas and show no overlapping ranges (see Table 1 and Fig. 1). *Hemidactylus* from the Arid clade are mainly rock-dwelling rather than arboreal geckos (Carranza & Arnold 2006); thus, the ancestor of Socotra species was probably rock-dwelling, like *H. inintellectus*. From that ancestor probably evolved the ground-dwelling morph, like *H. pumilio*. Finally, there is a transition in the split that separated *H. dracaenacolus* and *H. granti* about 2.3 Ma, which resulted in the only arboreal Socotran *Hemidactylus*, *H. dracaenacolus*, and a montane-endemic, *H. granti*. These two species are parapatric, and they

have very restricted distributions and represent the youngest and more specialized lineages of Socotran *Hemidactylus*. In this case, species divergences could match ecological changes in vegetation and climate that occurred during the Pliocene–Pleistocene as a consequence of the origin (8–10 Ma) and subsequent shifts (2.78–3.57 Ma) in the Indian monsoon cycles (Gupta & Thomas 2003; Gupta *et al.* 2004; Chang *et al.* 2010). Yet, with the evidence at hand, it remains difficult to decipher whether ecological opportunity or geographic isolation played a more important role in the diversification of Socotran *Hemidactylus*. Although this study sets the evolutionary basis for this type of questions, future studies on the ecomorphology of both mainland and island relatives are required to examine the direction and the magnitude of the phenotypic change as well as its ecological significance in terms of niche partitioning (see Harmon *et al.* 2008; Thomas *et al.* 2009).

A more deep understanding into the role of geographic and ecological factors on the speciation of Socotran *Hemidactylus* can be gained from patterns of intra-species phylogeography (Losos & Ricklefs 2009). Our multilocus species analyses recovered evidence for the persistence of multiple lineages within species that are restricted geographically. These lineages are highly divergent, and there is no allele sharing at the mtDNA level across populations. Despite the divergence pattern in each species was strongest at the mitochondrial locus and shallower or not evident in the nuclear loci, this is still consistent with the expected differences in coalescence times between nuclear and mitochondrial markers (Zink & Barrowclough 2008). But the processes that better explain these patterns differ across species. For instance, the imprint of geographic factors is marked in the case of *H. homoeolepis*, the only species present on multiple islands and which shows a phylogenetic break between the population of Socotra and those from Darsa and Samha. This divergence event dates to the Pleistocene probably matching the changes in the sea level that occurred during the Quaternary (Braithwaite 1987; Siddall *et al.* 2004). This is also concordant with our demographic analyses that show a significant population expansion event in Darsa and Samha about 50 Ka. In contrast, *H. inintellectus* is a case example of the impact of the ecological diversity of Socotra in patterns of intra-island divergence. Here, we found a significant correlation between genetic distances and habitat type and which is independent of the geographic distance. Whether the genetic and habitat structure observed in this species correlates with biometric differences among lineages, that is, if it is adaptive, still remains to be explored.

The case of *H. forbesii* and *H. oxyrhinus* from Abd al Kuri

Remarkably, the species pair *H. forbesii*–*H. oxyrhinus* represents one the most extreme examples of intra-island speciation ever reported. The monophyly of the clade is clear from both mitochondrial and nuclear data, while the presence of ILS at the *mc1r* nuclear loci (Figs S1 and S2, Supporting information) suggests that they correspond to a pair of sister species. Although evidence shows that in situ speciation is facilitated in ecologically rich and remote islands, it requires a minimum island size that has been reported for a range of plant and animal taxa (Coyne & Price 2000; Kisel & Barraclough 2010), including lizards (Losos & Schluter 2000; Losos & Parent 2009). Abd al Kuri, with an area of 133 km^2, represents one-thirtieth the size of Socotra Island, thus being the smallest island with a well-supported in situ speciation event ever reported. The case of *Phelsuma* day geckos in the island of Rodrigues (109 km^2) in the Indian Ocean possibly represents an in situ speciation event (*Phelsuma gigas*–*P. edwardnewtoni*); however, molecular analyses by Austin *et al.* (2004) and later on by Harmon *et al.* (2008) did not found support for this clade. Interestingly, in Abd al Kuri, *H. forbesii* and *H. oxyrhinus* are largely found in sympatry but differ markedly in habitat use and morphology: rock- and ground-dwelling, respectively, and *H. forbesii* being more than two times the size of *H. oxyrhinus* (Razzetti *et al.* 2011, Table 1). There are two compelling hypotheses that may explain such a contrasted pattern: sympatric ecological speciation or divergence in allopatry with subsequent secondary contact (Coyne & Orr 2004). Abd al Kuri is flat and elongated, particularly at the central isthmus (2.1 km of width and about 30 m of height). Island break-up and restored connectivity during flooding periods in the Pleistocene can explain species divergence by geographic isolation and the subsequent population expansion in *H. oxyrhinus* (Braithwaite 1987; Siddall *et al.* 2004). Age estimates for the split between these two taxa are also concordant with this hypothesis. Alternatively, species divergence could have resulted from ecological speciation in sympatry followed by a demographic expansion into the new niche. Similar phenomena have been reported in several *Anolis* island lizards (Losos 2009). Yet, these two views are often difficult to disentangle, and our data here remain limited to fully understand the evolutionary processes at work.

Concluding remarks

The Socotra Archipelago represents an area of conservation concern because of its high level of diversity and

endemism that still remains one of the most inaccessible and least explored regions of the world. Despite being recognized as a UNESCO's World Network of Biosphere Reserves and targeted by a UNDP major program (see http://www.biodiversityhotspots.org), it has received little international attention. From an evolutionary point of view, the archipelago is of particular significance because of its ecological diversity and long biogeographic history and thus represents a unique model to unravel the origin and speciation process in ancient continental fragments. The integration of phylogenetic and phylogeographic analyses at multiple loci and at various evolutionary time scales allowed us to reconstruct the evolutionary history of *Hemidactylus* from Socotra, giving an approximate time frame to the origin and in situ diversification in this group of geckos. More generally, this study opens new questions and new opportunities to study (i.e. *H. oxyrhinus–H. forbesii*), while it also serves as an a priori set of hypotheses to be tested in other co-distributed taxa. Finally, the high level of genetic divergence, long-term isolation and ecological specialization found in this study indicate the presence of several evolutionary independent lineages that can correspond to new species. Correctly delineating species in areas of conservation concern such as the Socotra Archipelago is crucial to designing management strategies, and this study represents a step forward to guarantee their preservation.

Acknowledgements

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EG-D is a junior scientist whose main research centers on the evolutionary ecology of host-parasite interactions. Other research interests include phylogeography and island evolution. RS research focuses on the reptiles of the Western Palearctic and the arid regions of East Africa, with particular interest in their taxonomy and distribution. FP is an herpetologist and museum curator, currently involved in the biology and conservation of the herpetofauna of Italy. MF research focuses on the ecology, ethology, zoogeography and ecotoxicology of vertebrates in Europe, Africa and Asia. SC is a tenured scientist interested in the diversity, biogeography and evolution of the herpetofauna of islands and dessert ecosystems.

Data accessibility

Supporting information

Additional supporting information may be found in the online version of this article.

Fig. S1 Maximum likelihood (ML) phylogenetic tree on 239 *Hemidactylus* specimens based on 667 bp of one nuclear (*mc1r*) loci.

Fig. S2 Statistical parsimony nuclear allele networks of *prdx4* and *mc1r* loci with colors corresponding to TCS mitochondrial lineages.

Fig. S3 Ultrametric gene tree based on the mitochondrial data from *Hemidactylus*.

Fig. S4 Bayesian species delimitation results for *Hemidactylus* from Socotra assuming 13 putative species for clade I, and 6 species for clades II and III.

Table S1. Details of the 144 *Hemidactylus* from the Socotra Archipelago included in the present study (25 *H. pumilio*, 35 *H. inintellectus*, 22 *H. dracaenacolus*, 14 *H. granti*, 9 *H. forbesii*, 19 *H. oxyrhinus* and 20 *H. homoeolepis*).

Table S2. *Hemidactylus* specimens from mainland Africa (Somalia and Egypt) and southwest Asia (Arabia and Iran) belonging to the Arid Clade plus two specimens of *H. flaviviridis* from the Asian Clade (Carranza & Arnold 2006).

Table S3. Amplification conditions and information on markers used in this study.

Table S4. Datasets, models and parameter setting for each particular analysis performed.

Table S5. Divergence time estimates (in Ma) for Socotran *Hemidactylus* derived from the BEAST and *BEAST analyses (see Figs 2 and 3).

Table S6. Pairwise Φ_{ST} mtDNA divergences among lineages within: *H. inintellectus*, *H. homoeolepis* and *H. pumilio*.

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