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Systematics, biogeography, and evolution of *Hemidactylus* geckos (Reptilia: Gekkonidae) elucidated using mitochondrial DNA sequences

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Abstract

With more than 80 species inhabiting all warm continental land masses and hundreds of intervening continental and oceanic islands, *Hemidactylus* geckos are one of the most species-rich and widely distributed of all reptile genera. They consequently represent an excellent model for biogeographic, ecological, and evolutionary studies. A molecular phylogeny for *Hemidactylus* is presented here, based on 702 bp of mtDNA (303 bp cytochrome *b* and 399 bp 12S rRNA) from 166 individuals of 30 species of *Hemidactylus* plus *Briba brasiliana, Cosymbotus platyurus*, and several outgroups. The phylogeny indicates that *Hemidactylus* may have initially undergone rapid radiation, and long-distance dispersal is more extensive than in any other reptilian genus. In the last 15 My, African lineages have naturally crossed the Atlantic Ocean at least twice. They also colonized the Gulf of Guinea, Cape Verde and Socotra islands, again sometimes on more than one occasion. Many extensive range extensions have occurred much more recently, sometimes with devastating consequences for other geckos. These colonizations are likely to be largely anthropogenic, involving the 'weedy' commensal species, *H. brookii* s. lat, *H. mabouia*, *H. turcicus*, *H. garnotii*, and *H. frenatus*. These species collectively have colonized the Mediterranean region, tropical Africa, much of the Americas and hundreds of islands in the Pacific, Indian, and Atlantic oceans. Five well-supported clades are discernable in *Hemidactylus*, with the African *H. fasciatus* unallocated. 1. Tropical Asian clade: (*Cosymbotus platyurus* (*H. bowringii, H. karenorum, H. garnotii*)) (*H. flaviviridis* (Asian *H. brookii, H. frenatus*)). 2. African *H. angulatus* and Caribbean *H. haitianus*. 3. Arid clade, of NE Africa, SW Asia, etc.: (*H. modestus* (*H. citernii, H. foudai*)) (*H. pumilio* (*H. granti, H. dracaenacolus*) (*H. persicus*, *H. macropholis, H. robustus, H. turcicus* (*H. oxyrhinus* (*H. homoeolepis, H. forbesii*))). 4. *H. mabouia* clade (*H. yerburii, H. mabouia*). 5. African–Atlantic clade: *H. platycephalus* ((*H. agrius, H. palaichthus*) (*H. longicephalus, H. greeffi*, *H. bouvieri, Briba brasiliana*))). *Cosymbotus* and *Briba* are synonymized with *Hemidactylus*, and African populations of *H. brookii* separated as *H. angulatus*, with which *H. haitianus* may be conspecific. Some comparatively well-sampled widespread species show high genetic variability (10–15% divergence) and need revision, including *Cosymbotus platyurus, H. bowringii*, Asian *H. brookii*, *H. frenatus*, *H. angulatus*, and *H. macropholis*. In contrast, most populations of *H. mabouia* and *H. turcicus* are very uniform (1–2% divergence). Plasticity of some of the morphological features of *Hemidactylus* is confirmed, although retention of primitive morphologies also occurs.

Keywords: *Hemidactylus* gecko; *Briba*; *Cosymbotus*; Transmarine colonization; Anthropogenic colonization; Mitochondrial DNA

1. Introduction

Hemidactylus Gray, 1845 is one of the most species-rich genera of the family Gekkonidae and comprises about 80 recognized species. Most are listed, together

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with their synonymies, by Wermuth (1965), Kluge (1991), and Bauer and Henle (1994), but some have been described only recently (Baha el Din, 2003, 2005; Bauer and Pauwels, 2002; Henle and Böhme, 2003; Rösler and Wranik, 1999). *Hemidactylus* geckos are mainly nocturnal and often climb. They occur naturally through much of tropical Asia and Africa and in the intervening more arid areas of Northeast Africa and Southwest Asia, and also extend into the Mediterranean region, and have reached South America apparently by natural transmarine colonization (Kluge, 1969). More recent introductions of Old World species have also been made into other areas of the Americas and the West Indies, and into Australia and the islands of the Indian, Pacific, and Atlantic Oceans. *Hemidactylus* has more apparent cases of such large range extensions than any other reptilian group.

The great majority of *Hemidactylus* species have relatively small distributions confined to southern Asia and Africa, and just eight species are responsible for most of the huge geographical area covered by the genus, namely *H. mabouia*, *H. turcicus*, *H. brookii*, *H. frenatus*, *H. garnotii*, *H. persicus*, *H. flaviviridis*, and *H. bowringii*. The first five of these are especially widespread and are present in both the Old and New Worlds, with *H. mabouia* also occurring on islands in the Atlantic and *H. frenatus* and *H. garnotii* being widespread in the Pacific. These forms are sometimes called 'weedy' species (Kluge, 1969). They are very frequently commensal with people, often occurring in and around human habitations and in anthropogenically modified habitats and in ecotones. It is therefore possible that much of their range is the result of human introduction, but some very long transmarine journeys may have been natural (Kluge, 1969). Recent molecular studies have included some populations of some 'weedy' *Hemidactylus* species, in the Cape Verde (Jesus et al., 2001), Gulf of Guinea (Jesus et al., 2005), Comoro islands (Rocha et al., 2005) and in Madagascar (Vences et al., 2004), and results have been interpreted as indicating both natural and human-mediated colonizations. On occasion, the recent spread of *Hemidactylus* has had devastating consequences for endemic species. The arrival of *H. frenatus* in the Mascarene islands decimated a radiation of six species of *Nactus* geckos, three now being entirely extinct and the remainder limited to relict populations on the offshore islets of Mauritius (Arnold, 2000; Cole et al., 2005).

The species of *Hemidactylus* share a unique combination of derived features in toe morphology. These include the unusual form and interrelationships of the antepenultimate phalanx of digits III–V of the pes (Russell, 1977), the distal extent of the dorsal interossei muscles along the digit, and the means of tendinous insertion of these muscles onto the scansors (Bauer and Russell, 1995; Russell, 1976, 1977). These features also occur in the monotypic South American *Briba*, in southeast Asian *Cosymbotus*, and in the two Indian species of *Teratolepis* (Bauer and Russell, 1995). Toe structure strongly suggests that all these geckos form a clade (Bauer and Russell, 1995). The monotypic Indian *Dravidogecko*, which has similar digits has already been placed in the synonymy of *Hemidactylus* (Bauer and Russell, 1995), and it may be appropriate to treat the other three genera similarly.

Hemidactylus is morphologically conservative in many features, such as skull structure and number of presacral vertebrae (usually 26, a primitive trait in gekkonids). There is however considerable variation in a range of external features including the following: body size; proportions of the head, body and limbs, and of the unregenerated tail which may be laterally expanded or swollen; number of internasal granules; size of dorsal scales and their degree of posterior imbrication; presence or absence of enlarged dorsal tubercles and, when they are present, their number, size, detailed shape, and extent on body head and limbs; number and extent of femoral pores in males or their complete absence; size of adhesive pads on digits and the number of expanded subdigital lamellae that constitute them externally (especially on toes 1 and 4), and whether or not the lamellae extend proximally onto the sole of the foot; presence or absence of the distal section of digit I of manus and pes including the claw; presence or absence of webbing on the toes; presence or absence of enlarged tubercles on the tail and whether these are spinose; whether subcaudal scales are enlarged and laterally expanded or small; dorsal and ventral colouring and pattern. Conditions in the apparent close relatives of the *Hemidactylus* group and in other gekkonids suggest that the following features are derived: unregenerated tail laterally expanded or swollen; enlargement and posterior imbrication of dorsal scales; absence or reduction of dorsal tubercles; reduction or loss of femoral pores; loss of distal section of digit I; presence of webbing on toes; and enlarged tubercles on tail spinose or absent.

Hemidactylus is taxonomically difficult. Many of its external features appear quite plastic, often varying within species or between otherwise similar ones. Some species are quite variable geographically, and these and others may be easily confused. This variation makes it hard to construct unambiguous identification keys for them, especially as some are known from few specimens. The last extensive revision of *Hemidactylus* was of the African species nearly sixty years ago (Loveridge, 1947). It has not been possible to produce even a tentative phylogeny for the genus using morphology, and studies of DNA sequence to date have focused instead on relatively small assemblages of species, often on islands (Jesus et al., 2001, 2005; Rocha et al., 2005; Vences et al., 2004).

In lizard groups like *Hemidactylus* where there are many systematic problems, DNA sequences are often very illuminating, as they have been in the other gekkonid genera *Tarentola* (Carranza et al., 2000, 2002), *Phelsuma* (Austin et al., 2004), and *Pachydactylus* (Lamb and Bauer, 2001, 2002). In the present study, we use fragments of two mitochondrial genes, cytochrome *b* and 12S rRNA, from 30 species of *Hemidactylus* to explore the phylogeny, evolution, and biogeography of the genus. The phylogenetic positions of *Briba* and *Cosymbotus* are investigated and a systematic framework produced to facilitate further studies. The validity of several species is tested in terms of their genetic homogeneity and separation from other taxa. Finally, long-distance colonizations are identified, and ancient ones that are certainly natural differentiated from more recent ones that may be anthropogenic, with special attention being paid to some of the 'weedy' species.

2. Materials and methods

2.1. Samples, DNA extraction, and amplification

In total 183 specimens were used for this study, 166 *Hemidactylus*, 4 specimens of *Cosymbotus platyurus*, 4 *Briba brasilianus*, and 8 *Tarentola* and 1 *Pachydactylus* employed as outgroups. Specimens used in the present study, their localities, specimen codes, and GenBank accession numbers for the two genes analyzed are listed in Table 1. Partial sequences of the mitochondrial genes encoding cytochrome *b* (cytb) and the mitochondrial ribosomal 12S rRNA (12S) were amplified and sequenced following standard PCR conditions and methods described elsewhere (Carranza et al., 1999, 2000). Primers used in both amplification and sequencing were cytochrome *b*1 and cytochrome *b*2 for the cytb gene and 12Sa and 12Sb for the 12S gene (both sets of primers from Kocher et al., 1989).

2.2. Phylogenetic analyses

Cytb and 12S mitochondrial DNA sequences were aligned using ClustalX (Thompson et al., 1997) with default parameters. No gaps were necessary to align the cytb sequences. These were translated into amino acids prior to analysis and did not show any stop codons, suggesting that all are functional. Three different methods of phylogenetic analysis were employed and the results compared: maximum-likelihood (ML), Bayesian inference (BI), and maximum-parsimony (MP). MODELTEST (Posada and Crandall, 1998) was used to select the most appropriate model of sequence evolution for the ML and BI analyses using the Akaike Information Criterion. This was in all cases the general time reversible (GTR) model, taking into account the shape of the Gamma distribution (G) and the number of invariable sites (I). The ML analysis was performed using PHYML (Guindon and Gascuel, 2003) with model parameters fitted to the data by likelihood maximization. MP analyses were performed in PAUP* 4.0b10 (Swofford, 1998). Because of the large size of the data set, a search strategy was used that avoided unnecessary branch swapping involving replicates outside the "islands" containing optimal trees (Giribet et al., 1999). This strategy involved setting the maxtrees command in PAUP* to 10,000, followed by a heuristic search with TBR branch swapping, specifying that not more than 10 trees of length $\geqslant 1$ should be stored. This constraint was then inactivated and all stored trees swapped to completion. In all MP analyses, transitions (ts) were given the same weight as transversions (tv) and gaps were included as a fifth state. Nodal support for the ML and MP trees was assessed using bootstrap analysis (Felsenstein, 1985) involving 1000 bootstrap pseudoreplications.

Bayesian analyses were performed with MrBayes 3.0 (Huelsenbeck and Ronquist, 2001) with model parameters for each gene partition (cytb and 12S) being independently estimated as part of the analysis. All analyses were run with four incrementally heated Markov chains, using the default heating values. They were started with randomly generated trees and ran for 2.5×10^6 generations, with sampling at intervals of 100 generations that produced 25,000 sampled trees. To ensure that the analyses were not trapped on local optima, all data sets were run three times independently, each run beginning with a different starting tree. The log-likelihood values of the 25,000 trees in each analysis were plotted against the generation time. After verifying that stationarity had been reached, both in terms of likelihood scores and parameter estimation, the first 5000 trees were discarded in all three runs and a majority-rule consensus tree was generated from the remaining 15,000 (post-burnin) trees. The frequency of any particular clade among the individual trees contributing to the consensus tree represents the posterior probability of that clade (Huelsenbeck and Ronquist, 2001).

Clades are regarded as strongly supported if they have Bootstrap values approaching 100% in ML or MP analyses, or posterior probabilities of 95% or above in Bayesian analysis, or any combination of such values.

2.3. Recognizing and dating long-distance colonizations

The source area of geographically isolated species or populations of a group may be indicated by the presence of close relatives there. This is most convincing when the relatives include the sister group plus a series of increasingly more distant taxa, this assemblage forming a paraphyletic group with respect to the isolated species or populations (Carranza and Arnold, 2003). If the isolated populations form a clade relative to this group, there may have been just a single colonization event or sequence. When populations in a colonized area form

Table 1
Details of material and sequences used in the present study

Taxa	Specimen code (Fig. 1)	Locality	GenBank Accession Nos. cytb 12S	Specimen code
Pachydactylus turneri	1	Richtersveldt, NW Cape Province, South Africa	AF184990/AF186118	Pcla
Tarentola americana	2	Guantánamo, Cuba	AF184991/AF186119	Tamer
Tarentola boettgeri boettgeri	3	Arinaga, Gran Canaria, Canary islands, Spain	AF184997/AF186125	CA11GC
Tarentola boettgeri boettgeri	4	Tauro, Gran Canaria, Canary islands, Spain	AF184996/AF186124	CA10GC
Tarentola boettgeri boettgeri	5	Tauro, Gran Canaria, Canary islands, Spain	AF184995/AF186123	CA9GC
Tarentola boettgeri bischoffi	6	Selvagem Grande, Portugal (BEV.2239)	AF185000/AF186128	Tbobish
Tarentola boettgeri hierrensis	7	Tamaduste, El Hierro, Canary islands, Spain	AF184998/AF186126	CA16H
Tarentola boettgeri hierrensis	8	Los Llanillos, El Hierro, Canary islands, Spain	AF184999/AF186127	CA17H
Tarentola angustimentalis	9	Fuste, Fuerteventura, Canary islands, Spain	AF184993/AF186121	CA7VF
Cosymbotus platyurus	10	Kan-Pet-Let Township, Chin State, Myanmar (CAS222332)	DQ120297/DQ120468	E29104.3
Cosymbotus platyurus	11	Khim Aye Village, Sagaing Division, Myanmar (CAS215451)	DQ120296/DQ120467	E29104.4
Cosymbotus platyurus	12	Alaungdaw Kathapa NP, Sagaing Division, Myanmar (CAS204982)	DQ120295/DQ120466	E29104.5
Cosymbotus platyurus	13	Gon Nyin, Sagaing Division, Myanmar (CAS215734)	DQ120294/DQ120465	E29104.2
H. karenorum	14	Mandalay Division, Myanmar (CAS210670)	DQ120293/DQ120464	E509.19
H. garnotii	15	Yangon Division, Myanmar (CAS213517)	DQ120292/DQ120463	E509.8
H. garnotii	16	Palm Beach, Florida, USA (CASA184323)	DQ120291/DQ120462	E509.11
H. garnotii	17	Dade Co., Florida, USA (CAS184322)	DQ120290/DQ120461	E509.10
H. garnotii	18	Alaungdaw Kathapa, Sagaing Province, Myanmar (CAS210280)	DQ120289/DQ120460	E509.9
H. garnotii	19	Alaungdaw Kathapa, Sagaing Province, Myanmar (CAS210259)	DQ120288/DQ120459	E509.20
H. bowringii	20	Yangon Division: Mingalardon Township, Myanmar (CAS213333)	DQ120287/DQ120458	E1708.8
H. bowringii	21	Yunnan, Nujiang Prefacture, China (CAS207483)	DQ120286/DQ120457	E170810
H. bowringii	22	Shan State, Myanmar (CAS216345)	DQ120285/DQ120456	E1109.6
H. flaviviridis	23	Hadibu, Socotra island, Yemen	DQ120284/DQ120455	E912.2
H. flaviviridis	24	Fujairah, UAE	DQ120283/DQ120454	E1708.22
H. frenatus	25	Thiruvanan Thapuram, India	DQ120282/DQ120453	E509.5
H. frenatus	26	Mandalay Division, Myanmar (CAS214157)	DQ120281/DQ120452	E509.2
H. frenatus	27	Mwe Hauk, Ayeyarwade Division, Myanmar (CAS212900)	DQ120280/DQ120451	E509.1
H. frenatus	28	Puerto Carreño, Colombia	DQ120279/DQ120450	E509.3
H. frenatus	29	Kauai, Hawaii islands, USA (CAS200822)	DQ120278/ DQ120449	E509.7
H. frenatus	30	Kauai, Hawaii islands, USA (CAS200820)	DQ120277/DQ120448	E509.6
H. brookii brookii	31	Subrahmnya, Karnataka, India	DQ120276/DQ120447	E1109.10
H. brookii brookii	32	Kyauk Pan Tawn, Mandalay Division, Myanmar (CAS213939)	DQ120275/DQ120446	E1708.18
H. brookii brookii	33	Mingalardan, Yangon Division, Myanmar (CAS213515)	DQ120274/DQ120445	E1708.17
H. brookii brookii	34	Kollam, Kerala, India	DQ120273/DQ120444	E1109.11
H. brookii brookii	35	Mauritius	DQ120272/DQ120443	Hemb22b
H. brookii brookii	36	Mauritius	DQ120271/DQ120442	Hemb1b
H. platycephalus	37	Kijiado District, Rift Valley, Kenya (CAS198967)	DQ120270/DQ120441	E609.16
H. platycephalus	38	Kajiado District, Rift Valley, Kenya (CAS198966)	DQ120269/DQ120440	E609.15
H. platycephalus	39	Kajiado District, Rift Valley, Kenya (CAS198974)	DQ120268/DQ120439	E7014.9
H. platycephalus	40	Kajiado District, Rift Valley, Kenya (CAS198970)	DQ120267/DQ120438	E7014.8
H. platycephalus	41	Kajiado District, Rift Valley, Kenya (CAS198969)	DQ120266/DQ120437	E7014.7
H. fasciatus	42	Luba, Equatorial Guinea (CAS207778)	DQ120265/DQ120436	E1708.21
H. fasciatus	43	Luba, Equatorial Guinea (CAS207777)	DQ120264/DQ120435	E1708.20
H. palaichthus	44	Chacachaare, Trinidad	DQ120263/DQ120434	E1109.3
H. agrius	45	Touros, Genipabu, Brazil	DQ120262/DQ120433	E1708.1
H. agrius	46	Dom Expedito Lopes, Piaui, Brazil	DQ120261/DQ120432	E1708.2
H. agrius	47	Dom Expedito Lopes, Piaui, Brazil	DQ120260/DQ120431	E1708.7
H. agrius	48	Dom Expedito Lopes, Piaui, Brazil	DQ120259/DQ120430	E1708.6
H. agrius	49	Dom Expedito Lopes, Piaui, Brazil	DQ120258/DQ120429	E1708.5
Briba brasiliana	50	Dom Expedito Lopes, Piaui, Brazil	DQ120257/DQ120428	E1209.4
Briba brasiliana	51	Dom Expedito Lopes, Piaui, Brazil	DQ120256/DQ120427	E1209.2
Briba brasiliana	52	Dom Expedito Lopes, Piaui, Brazil	DQ120255/DQ120426	E1209.3
Briba brasiliana	53	Dom Expedito Lopes, Piaui, Brazil	DQ120254/DQ120425	E1209.1
H. bouvieri	54	São Vicente, Cape Verde islands, Cape Verde	DQ120253/DQ120424	HbouSvA
H. bouvieri	55	Boavista, Cape Verde islands, Cape Verde	DQ120252/DQ120423	11HbouBo
H. bouvieri	56	Boavista, Cape Verde islands, Cape Verde	DQ120251/DQ120422	2HbouBo

Table 1 (*continued*)

Taxa	Specimen code (Fig. 1)	Locality	GenBank Accession Nos. cytb 12S	Specimen code
H. bouvieri	57	Boavista, Cape Verde islands, Cape Verde	DQ120250/DQ120421	12HbouBo
H. bouvieri	58	Sal, Cape Verde islands, Cape Verde	DQ120249/DQ120420	10HbouS
H. bouvieri	59	Sal, Cape Verde islands, Cape Verde	DQ120248/DQ120419	9HbouS
H. bouvieri	60	Sal, Cape Verde islands, Cape Verde	DQ120247/DQ120418	1HbouS
H. longicephalus	61	São Tomé, São Tomé and Príncipe (CAS219294)	DQ120246/DQ120417	E7014.6
H. longicephalus	62	São Tomé, São Tomé and Príncipe (CAS219278)	DQ120245/DQ120416	E7014.5
H. greeffi	63	Príncipe, São Tomé and Príncipe (CAS219212)	DQ120244/DQ120415	E7014.3
H. greeffi	64	Príncipe, São Tomé and Príncipe (CAS219198)	DQ120243/DQ120414	E7014.4
H. greeffi	65	Príncipe, São Tomé and Príncipe	DQ120242/DQ120413	E509.14
H. brookii angulatus	66	Kajiado District, Rift valley, Kenya (CAS198856)	DQ120241/DQ120412	E1708.15
H. brookii angulatus	67	Kajiado District, Rift valley, Kenya (CAS198855)	DQ120240/DQ120411	E1708.14
H. brookii angulatus	68	Nouadhibou, Dakhllet-Nouadhibou, Mauritania	DQ120239/DQ120410	E2503321
H. brookii angulatus	69	El Wad to Zoueina, Hodh el Gharbi, Mauritania	DQ120238/DQ120409	E25033.18
H. brookii angulatus	70	Sal, Cape Verde islands, Cape Verde	DQ120237/DQ120408	2B25HbrS
H. brookii angulatus	71	Sal, Cape Verde islands, Cape Verde	DQ120236/DQ120407	2B23HbrS
H. brookii angulatus	72	Sal, Cape Verde islands, Cape Verde	DQ120235/DQ120406	2B8HbrS
H. brookii angulatus	73	Nouadhibou, Dakhllet-Nouadhibou, Mauritania	DQ120234/DQ120405	E25033.20
H. brookii angulatus	74	Santo Antão, Cape Verde islands, Cape Verde	DQ120233/DQ120404	35HbrSA
H. brookii angulatus	75	Santo Antão, Cape Verde islands, Cape Verde	DQ120232/DQ120403	34HbrSA
H. brookii angulatus	76	Santo Antão, Cape Verde islands, Cape Verde	DQ120231/DQ120402	33HbrSA
H. brookii angulatus	77	Santiago, Cape Verde islands, Cape Verde	DQ120230/DQ120401	20HbrSt
H. brookii angulatus	78	Santiago, Cape Verde islands, Cape Verde	DQ120229/DQ120400	18HbrSt
H. brookii angulatus	79	Guinea-Bissau	AF324797/AF324798	Jesus et al., 2001
H. brookii angulatus	80	Santiago, Cape Verde islands, Cape Verde	DQ120228/DQ120399	6HbrSt
H. brookii angulatus	81	Cabo Blanco, Mauritania	DQ120227/DQ120398	26HbrAf
H. brookii angulatus	82	Santiago, Cape Verde islands, Cape Verde	DQ120226/DQ120397	19HbrSt
H. brookii angulatus	83	Boa Vista, Cape Verde islands, Cape Verde	DQ120225/DQ120396	163HbrBo
H. brookii angulatus	84	Boa Vista, Cape Verde islands, Cape Verde	DQ120224/DQ120395	161HbrBo
H. brookii angulatus	85	Boa Vista, Cape Verde islands, Cape Verde	DQ120223/DQ120394	160HbrBo
H. brookii angulatus	86	Boa Vista, Cape Verde islands, Cape Verde	DQ120222/DQ120393	159HbrBo
H. brookii angulatus	87	Boa Vista, Cape Verde islands, Cape Verde	DQ120221/DQ120392	7HbrBo
H. brookii angulatus	88	Lake Mahmude, Hodh Ech Chargui, Mauritania	DQ120220/DQ120391	E25033.19
H. brookii angulatus	89	Mali	DQ120219/DQ120390	E1708.24
H. brookii angulatus	90	Malabo, Bioko island, Equatorial Guinea (CAS207977)	DQ120218/DQ120389	E1708.12
H. haitianus	91	Matanzas, Matanzas province, Cuba	DQ120217/DQ120388	HhaitiS
H. haitianus	92	Matanzas, Matanzas province, Cuba	DQ120216/DQ120387	HhaitiL
H. modestus	93	Kijiado District, Rift Valley Province, Kenya (CAS198934)	DQ120215/DQ120386	E1109.7
H. foudaii	94	Gebel Elba, Egypt	DQ120214/DQ120385	E612.22
H. citernii	95	Somalia (CAS227535)	DQ120213/DQ120384	E7014.2
H. citernii	96	Somalia (CAS227534)	DQ120212/DQ120383	E7014.1
H. pumilio	97	Firmihin, Haghier, Socotra island, Yemen	DQ120211/DQ120382	E912.7
H. granti	98	Firmihin, Haghier, Socotra island, Yemen	DQ120210/DQ120381	E912.4
H. dracaenacolus	99	Diksam, Socotra island, Yemen	DQ120209/DQ120380	E912.1
H. macropholis	100	11 km SE of Bosasso, Bari Region, Somalia (CAS227511)	DQ120208/DQ120379	E7014.10
H. yerburii	101	Najran, Saudi Arabia	DQ120207/DQ120378	E1109.12
H. mabouia	102	Lake Nabugabo, Masaka District, Uganda (CAS202428)	DQ120206/DQ120377	E609.20
H. mabouia	103	Watamu, Kilifi District, Kenya (CAS186501)	DQ120205/DQ120376	E609.14
H. mabouia	104	Praia da Pipa, Rio Grande do Norte, Brazil	DQ120204/DQ120375	E609.9
H. mabouia	105	Península de Jobos, Puerto Rico (CAS200755)	DQ120203/DQ120374	E1109.1
H. mabouia	106	Península de Jobos, Puerto Rico (CAS200754)	DQ120202/DQ120373	E609.24
H. mabouia	107	Cocoa Beach, Trinidad	DQ120201/DQ120372	E609.19
H. mabouia	108	Cocoa Beach, Trinidad	DQ120200/DQ120371	E609.18
H. mabouia	109	Exu, Pernambuco, Brazil	DQ120199/DQ120370	E609.13
H. mabouia	110	Praia da Pipa, Rio Grande do Norte, Brazil	DQ120198/DQ120369	E609.8
H. mabouia	111	Genipabu, Rio Grande do Norte, Brazil	DQ120197/DQ120368	E609.6
H. mabouia	112	Pocone, Mato Grosso, Brazil	DQ120196/DQ120367	E609.4
H. mabouia	113	Pocone, Mato Grosso, Brazil	DQ120195/DQ120366	E609.3
H. mabouia	114	Pocone, Mato Grosso, Brazil	DQ120194/DQ120365	E609.2
H. mabouia	115	Chapada dos Guimarães, Mato Grosso, Brazil	DQ120193/DQ120364	E609.1
H. mabouia	116	Iguazu, Argentina	DQ120192/DQ120363	E509.22
H. mabouia	117	Pigeon Point, Tobago	DQ120191/DQ120362	E1109.9
H. mabouia	118	Pigeon Point, Tobago	DQ120190/DQ120361	E1109.8
H. mabouia	119	Coast Prov. Kilifi District, Kenya (CAS186500)	DQ120189/DQ120360	E509.21
H. mabouia	120	Vila dos Remedios, Fernando de Noronha, Brazil	DQ120181/DQ120352	E609.12
H. mabouia	121	São Tomé, São Tomé and Príncipe	DQ120187/DQ120358	37HmabSTo

(*continued on next page*)

Table 1 (*continued*)

Taxa	Specimen code (Fig. 1)	Locality	GenBank Accession Nos. cytb 12S	Specimen code
H. mabouia	122	São Vicente, Cape Verde islands, Cape Verde	DQ120186/DQ120357	32HbouSV
H. mabouia	123	São Vicente, Cape Verde islands, Cape Verde	DQ120185/DQ120356	31HbouSV
H. mabouia	124	Monroe Co. Florida, USA (CAS174850)	DQ120184/DQ120355	E609.23
H. mabouia	125	Monroe Co. Florida, USA (CAS174849)	DQ120183/DQ120354	E609.22
H. mabouia	126	Rukungiri District, Uganda (CAS201744)	DQ120182/DQ120353	E609.21
H. mabouia	127	Vila dos Remedios, Fernando de Noronha, Brazil	DQ120180/DQ120351	E609.11
H. mabouia	128	Genipabu, Brazil	DQ120179/DQ120350	E609.7
H. mabouia	129	Genipabu, Brazil	DQ120178/DQ120349	E609.5
H. mabouia	130	Malabo, Bioko island, Equatorial Guinea (CAS207978)	DQ120177/DQ120348	E1708.13
H. mabouia	131	Vila dos Remedios, Fernando de Noronha, Brazil	DQ120188/DQ120359	E609.10
H. robustus	132	Safaga, Egypt	DQ120176/DQ120347	E612.20
H. robustus	133	Abu Dhabi, United Arab Emirates	DQ120175/DQ120346	E1008.17
H. robustus	134	Jebel Dhanna, near Ruweis, Abu Dhabi, United Arab Emirates	AF184989/AF186117	Hturc2
H. robustus	135	Jebel Dhanna, near Ruweis, Abu Dhabi, United Arab Emirates	DQ120174/DQ120345	E1008.16
H. oxyrhinus	136	Abd al Kuri island, Socotra archipelago, Yemen	DQ120173/DQ120344	E912.6
H. macropholis	137	11 km NW of Bargal, Bari Region, Somalia (CAS227519)	DQ120172/DQ120343	E7014.11
H. homoeolepis	138	Firmihin, Haghier, Socotra island, Yemen	DQ120171/DQ120342	E912.5
H. homoeolepis	139	Socotra island, Yemen	DQ120170/DQ120341	E509.17
H. homoeolepis	140	Socotra island, Yemen	DQ120169/DQ120340	24Hhomo
H. forbesii	141	Abd al Kuri island, Socotra archipelago, Yemen	DQ120168/DQ120339	E912.3
H. persicus	142	4.5 km N. of Tanuf, Wilayat Nizwa, Oman (CAS227614)	DQ120167/DQ120338	E7014.13
H. persicus	143	4.5 km N. of Tanuf, Wilayat Nizwa, Oman (CAS227612)	DQ120166/DQ120337	E7014.12
H. turcicus lavadeserticus	144	Dair al Khaf, Jordan (vouhcer in National Museum, Prague)	DQ120165/DQ120336	E28104.10
H. turcicus turcicus	145	Wadi al Burbeyath, Jordan (vouhcer in National Museum, Prague)	DQ120164/DQ120335	E28104.8
H. turcicus turcicus	146	Erzin, Turkey	DQ120163/DQ120334	E2505.2
H. turcicus turcicus	147	Andalucía, Spain	DQ120162/DQ120333	E1008.13
H. turcicus turcicus	148	Islet of Marathi, near Patmos, North Dodekanese, Greece	DQ120161/DQ120332	E1008.9
H. turcicus turcicus	149	Iraklio, Crete, Greece	DQ120160/DQ120331	E1008.8
H. turcicus turcicus	150	Crete, Greece	DQ120159/DQ120330	E612.23
H. turcicus turcicus	151	Kos island, Greece	DQ120158/DQ120329	E1008.6
H. turcicus turcicus	152	Near Gafsa, Tunisia	DQ120157/DQ120328	E2505.18
H. turcicus turcicus	153	Menorca, Balearic islands, Spain	DQ120156/DQ120327	E1008.15
H. turcicus turcicus	154	Chergui island, Kerkenah, Tunisia	DQ120155/DQ120326	E2505.22
H. turcicus turcicus	155	Chergui island, Kerkenah, Tunisia	DQ120154/DQ120325	E2505.21
H. turcicus turcicus	156	Chergui island, Kerkenah, Tunisia	DQ120153/DQ120324	E2505.20
H. turcicus turcicus	157	Chergui island, Kerkenah, Tunisia	DQ120152/DQ120323	E2505.19
H. turcicus turcicus	158	5 km south of Le Kef, Tunisia	DQ120151/DQ120322	E2505.17
H. turcicus turcicus	159	Obejo, Cordoba, Spain	DQ120150/DQ120321	E2505.6
H. turcicus turcicus	160	El Alquian, Almeria, Spain	DQ120149/DQ120320	E2505.4
H. turcicus turcicus	161	Cuevas de Almanzora, Almeria, Spain	DQ120148/DQ120319	E612.29
H. turcicus turcicus	162	Castillejos, Morocco	DQ120147/DQ120318	E612.26
H. turcicus turcicus	163	Castillejos, Morocco	DQ120146/DQ120317	E612.25
H. turcicus turcicus	164	South of Jendouba, Tunisia	DQ120145/DQ120316	E2505.12
H. turcicus turcicus	165	Qariat Arkmane, Morocco	DQ120144/DQ120315	E2505.16
H. turcicus turcicus	166	Qariat Arkmane, Morocco	DQ120143/DQ120314	E2505.15
H. turcicus turcicus	167	Barcelona city, Spain	DQ120142/DQ120313	E612.27
H. turcicus turcicus	168	Qariat Arkmane, Morocco	DQ120141/DQ120312	E2505.14
H. turcicus turcicus	169	Torregorda, Cadiz (Spain)	DQ120140/DQ120311	E1008.14
H. turcicus turcicus	170	Kato Gatzea, near Volos, Greece	DQ120139/DQ120310	E1008.3
H. turcicus turcicus	171	Erzin, Turkey	DQ120138/DQ120309	E2505.1
H. turcicus turcicus	172	Carmona, Sevilla, Spain	DQ120137/DQ120308	E2505.5
H. turcicus turcicus	173	Valdeinfierno, Cordoba, Spain	DQ120136/DQ120307	E2505.8
H. turcicus turcicus	174	Junqueira, Portugal	DQ120135/DQ120306	E2505.9
H. turcicus turcicus	175	Zaframagon, Cadiz, Spain	DQ120134/DQ120305	E2505.11
H. turcicus turcicus	176	Gran Canaria, Canary islands, Spain	AF364319/AF363568	HturcGC
H. turcicus turcicus	177	Baton Rouge, Louisiana, USA (CAS175646)	DQ120133/DQ120304	E1008.20
H. turcicus turcicus	178	Dade Co., Florida, USA	DQ120132/DQ120303	E1008.19
H. turcicus turcicus	179	El Garrobo, Ayo de la Torre, Spain	DQ120131/DQ120302	E1008.12
H. turcicus turcicus	180	Kato Gatzea, near Volos, Greece	DQ120130/DQ120301	E1008.4
H. turcicus turcicus	181	Kato Gatzea, near Volos, Greece	DQ120129/DQ120300	E1008.2
H. turcicus turcicus	182	Las Palmas de Gran Canaria, Gran Canaria, Canary islands, Spain	DQ120128/DQ120299	E612.28
H. turcicus turcicus	183	Zaranikh reserve, North Sinai, Egypt	DQ120127/DQ120298	E612.21

Specimen codes identify individuals on the phylogeny shown in Fig. 1. BEV—Laboratoire de Biogeographie et Ecologie des Vértebrés, Universite de Montpellier II, France; CAS—California Academy of Sciences, San Francisco, USA.

one or more distinct species, an old natural colonization is likely, rather than a recent, perhaps anthropogenic one. Another possible indication of an older natural colonization is genetic differentiation between populations in a source area and one that was colonized (Carranza and Arnold, 2003; Maca-Meyer et al., 2003). This would apply whether the colonizing populations were specifically distinct from those in the source area or not. However, if the populations in the source area are actually themselves genetically diverse, poor sampling may give a false impression of differentiation between the source population and one resulting from colonization. This is because a genetically different population in the source region may have been inadvertently sampled, even though a much more similar one exists. Such a possibility always has to be borne in mind, especially when dealing with situations where source and colonizing populations are apparently conspecific.

A rough molecular clock may give some idea of the date of a colonization event, although such estimated dates must be treated with appropriate caution (Heads, 2005). The estimated age of the node where the colonizing clade separates from its nearest relative in the source area gives a maximum date, while the basal node of any divergence in the colonizing clade provides a minimum. Again, poor sampling in the source area may produce a false estimate of the maximum, as may extinction of some lineages in this region. Failure to use the source population most closely related to the colonizing clade will artificially exaggerate apparent age.

Lack of differentiation between a population resulting from colonization and the most closely related population in the source area indicates that the colonization was relatively recent and could have possibly arisen from accidental or deliberate human transport. However, it is very difficult to be sure about this because the gene fragments employed here change relatively slowly, so there might be no differentiation over a period much longer than that in which people have regularly travelled, especially across the sea. Other evidence for anthropogenic introduction includes actual records of the appearance of a species in an area, and its absence from archaeological or very recent fossil sites there.

Rough molecular clocks may give some idea of the absolute date of colonization and this can be used to distinguish different kinds of natural colonization. For example, an early date may show that colonization was across land before two terrestrial areas separated, while a later one may indicate that movement was across the sea after such separation occurred (Carranza and Arnold, 2003). At present, it is not possible to calibrate a molecular clock within *Hemidactylus*, but a divergence rate for the gene fragments used here has been calculated for *Tarentola*, another gekkonid genus. This calibration was based on the assumption that El Hierro island in the Canary archipelago, which has a well-established age of 1 My, was colonized soon after its appearance from the Selvages (Carranza et al., 2000, 2002; Nogales et al., 1998). The rate, 2.4% of uncorrected genetic divergence per My, lies between that calculated for exactly the same genetic region of other scleroglossan lizards from the Canary Islands, including *Chalcides* skinks (3.2% per My, Carranza and Arnold, unpublished) and lacertid lizards (1.35–1.6% per My, Carranza et al., 2004; Maca-Meyer et al., 2003).

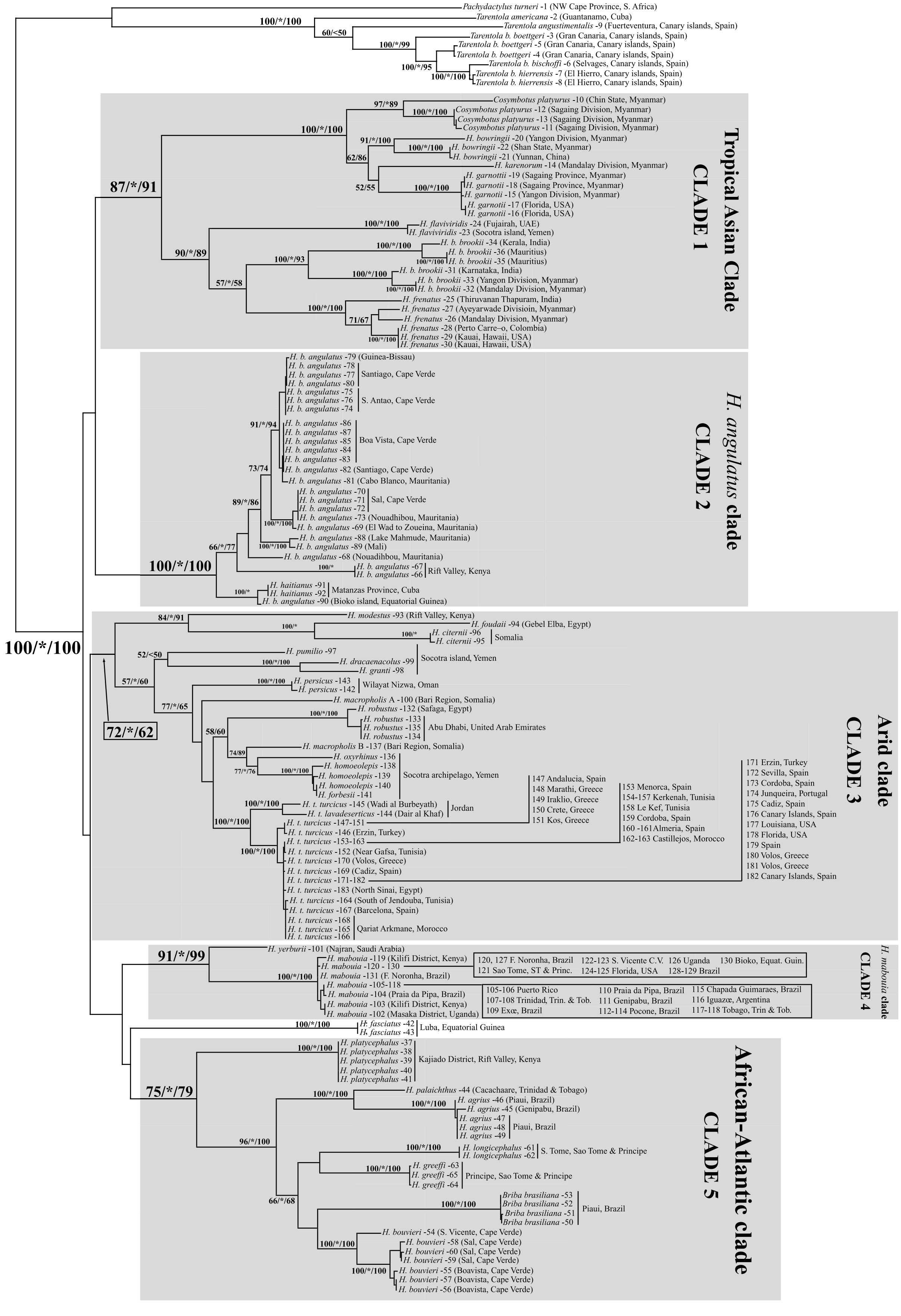
3. Results

A total of 702 characters (303 bp of the cytb and 399 of the 12S) were used in the phylogenetic analyses. Of these, 457 were variable and 423 parsimony-informative. Results are presented in Fig. 1. All three methods of analysis (ML, MP, and BI) gave very similar results and showed only minor differences, mainly at the base of the tree where relationships have little support. The phylogeny comprised five well-supported clades consisting of 2–13 species, with *H. fasciatus* occupying an isolated position. These clades are discussed below.

3.1. Clade 1, the Tropical Asian clade

This unit consists of two monophyletic groups. In one, *Cosymbotus platyurus* forms a clade with *H. bowringi*, *H. karenorum*, and *H. garnotii*. *C. platyurus* shows considerable internal variability within Myanmar, with a specimen from Chin State exhibiting a 12.2% uncorrected genetic distance from three individuals collected in the neighbouring Sagaing Division. Similarly, *H. bowringii* from Sagaing shows an 11% divergence from animals collected in Shan State and from Yunnan in neighbouring southwest China. In contrast, *H. garnotii*, which is a parthenogentic species, shows only 0.8% differentiation among specimens from the Sagaing and Yangon divisions of Myanmar and ones introduced into Florida.

In the second group, *H. flaviviridis* is the sister taxon to a unit consisting of *H. frenatus* and Asian *H. brookii*. Populations of *H. flaviviridis* from the United Arab Emirates and Socotra differ by only 1.3% uncorrected genetic distance. In contrast, *H. frenatus* has a maximum divergence of 6% in two samples from the Mandalay and Ayeyarwade Divisions of Myanmar, and an Indian specimen shows a divergence of 10% from these and presumed introductions in Hawaii and Colombia. Asian *H. brookii* are also diverse, with an animal from Karnataka, India and two from Myanmar showing a divergence of around 15% from one collected in Kerala, India, and apparent introductions in Mauritius.


Pachydactylus turneri -1 (NW Cape Province, S. Africa)
Tarentola americana -2 (Guantanamo, Cuba)
Tarentola angustimentalis -9 (Fuerteventura, Canary islands, Spain)
Tarentola b. boettgeri -3 (Gran Canaria, Canary islands, Spain)
Tarentola b. boettgeri -5 (Gran Canaria, Canary islands, Spain)
Tarentola b. boettgeri -4 (Gran Canaria, Canary islands, Spain)
Tarentola b. bischoffi -6 (Selvages, Canary islands, Spain)
Tarentola b. hierrensis -7 (El Hierro, Canary islands, Spain)
Tarentola b. hierrensis -8 (El Hierro, Canary islands, Spain)
100/*/100
60/<50
100/*/99
100/*/95
100/*/100
Tropical Asian Clade
CLADE 1
Cosymbotus platyurus -10 (Chin State, Myanmar)
Cosymbotus platyurus -12 (Sagaing Division, Myanmar)
Cosymbotus platyurus -13 (Sagaing Division, Myanmar)
Cosymbotus platyurus -11 (Sagaing Division, Myanmar)
H. bowringii -20 (Yangon Division, Myanmar)
H. bowringii -22 (Shan State, Myanmar)
H. bowringii -21 (Yunnan, China)
H. karenorum -14 (Mandalay Division, Myanmar)
H. garnottii -19 (Sagaing Province, Myanmar)
H. garnotii -18 (Sagaing Province, Myanmar)
H. garnotii -15 (Yangon Division, Myanmar)
H. garnotii -17 (Florida, USA)
H. garnotii -16 (Florida, USA)
H. flaviviridis -24 (Fujairah, UAE)
H. flaviviridis -23 (Socotra island, Yemen)
H. b. brookii -34 (Kerala, India)
H. b. brookii -36 (Mauritius)
H. b. brookii -35 (Mauritius)
H. b. brookii -31 (Karnataka, India)
H. b. brookii -33 (Yangon Division, Myanmar)
H. b. brookii -32 (Mandalay Division, Myanmar)
H. frenatus -25 (Thiruvanan Thapuram, India)
H. frenatus -27 (Ayeyarwade Divisioin, Myanmar)
H. frenatus -26 (Mandalay Division, Myanmar)
H. frenatus -28 (Perto Carre–o, Colombia)
H. frenatus -29 (Kauai, Hawaii, USA)
H. frenatus -30 (Kauai, Hawaii, USA)
97/*89
100/*/100
100/*/100
91/*/100
100/*/100
62/86
52/55
100/*/100
87/*/91
100/*/100
100/*/100
100/*/100
90/*/89
100/*/93
100/*/100
100/*/100
57/*/58
100/*/100
71/67
100/*/100
H. angulatus clade
CLADE 2
H. b. angulatus -79 (Guinea-Bissau)
H. b. angulatus -78
H. b. angulatus -77
H. b. angulatus -80
Santiago, Cape Verde
H. b. angulatus -75
H. b. angulatus -76
H. b. angulatus -74
S. Antao, Cape Verde
H. b. angulatus -86
H. b. angulatus -87
H. b. angulatus -85
H. b. angulatus -84
H. b. angulatus -83
Boa Vista, Cape Verde
H. b. angulatus -82 (Santiago, Cape Verde)
H. b. angulatus -81 (Cabo Blanco, Mauritania)
H. b. angulatus -70
H. b. angulatus -71
H. b. angulatus -72
Sal, Cape Verde
H. b. angulatus -73 (Nouadhibou, Mauritania)
H. b. angulatus -69 (El Wad to Zoueina, Mauritania)
H. b. angulatus -88 (Lake Mahmude, Mauritania)
H. b. angulatus -89 (Mali)
H. b. angulatus -68 (Nouadihbou, Mauritania)
H. b. angulatus -67
H. b. angulatus -66
Rift Valley, Kenya
H. haitianus -91
H. haitianus -92
H. b. angulatus -90 (Bioko island, Equatorial Guinea)
Matanzas Province, Cuba
91/*/94
73/74
89/*/86
100/*/100
100/*/100
66/*/77
100/*
100/*/100
100/*
Arid clade
CLADE 3
H. modestus -93 (Rift Valley, Kenya)
H. foudaii -94 (Gebel Elba, Egypt)
H. citernii -96
H. citernii -95
Somalia
H. pumilio -97
H. dracaenacolus -99
H. granti -98
Socotra island, Yemen
H. persicus -143
H. persicus -142
Wilayat Nizwa, Oman
H. macropholis A -100 (Bari Region, Somalia)
H. robustus -132 (Safaga, Egypt)
H. robustus -133
H. robustus -135
H. robustus -134
Abu Dhabi, United Arab Emirates
H. macropholis B -137 (Bari Region, Somalia)
H. oxyrhinus -136
H. homoeolepis -138
H. homoeolepis -139
H. homoeolepis -140
H. forbesii -141
Socotra archipelago, Yemen
H. t. turcicus -145 (Wadi al Burbeyath)
H. t. lavadeserticus -144 (Dair al Khaf)
Jordan
H. t. turcicus -147-151
H. t. turcicus -146 (Erzin, Turkey)
H. t. turcicus -153-163
H. t. turcicus -152 (Near Gafsa, Tunisia)
H. t. turcicus -170 (Volos, Greece)
H. t. turcicus -169 (Cadiz, Spain)
H. t. turcicus -171-182
H. t. turcicus -183 (North Sinai, Egypt)
H. t. turcicus -164 (South of Jendouba, Tunisia)
H. t. turcicus -167 (Barcelona, Spain)
H. t. turcicus -168
H. t. turcicus -165
H. t. turcicus -166
Qariat Arkmane, Morocco
147 Andalucia, Spain
148 Marathi, Greece
149 Iraklio, Greece
150 Crete, Greece
151 Kos, Greece
153 Menorca, Spain
154-157 Kerkenah, Tunisia
158 Le Kef, Tunisia
159 Cordoba, Spain
160 -161Almeria, Spain
162-163 Castillejos, Morocco
171 Erzin, Turkey
172 Sevilla, Spain
173 Cordoba, Spain
174 Junqueira, Portugal
175 Cadiz, Spain
176 Canary Islands, Spain
177 Louisiana, USA
178 Florida, USA
179 Spain
180 Volos, Greece
181 Volos, Greece
182 Canary Islands, Spain
84/*/91
100/*
100/*
52/<50
100/*/100
57/*/60
100/*/100
77/*/65
100/*/100
58/60
74/89
77/*/76
100/*/100
100/*/100
100/*/100
100/*/100
72/*/62
100/*/100
H. mabouia clade
CLADE 4
H. yerburii -101 (Najran, Saudi Arabia)
H. mabouia -119 (Kilifi District, Kenya)
H. mabouia -120 - 130
H. mabouia -131 (F. Noronha, Brazil)
H. mabouia -105-118
H. mabouia -104 (Praia da Pipa, Brazil)
H. mabouia -103 (Kilifi District, Kenya)
H. mabouia -102 (Masaka District, Uganda)
120, 127 F. Noronha, Brazil
121 Sao Tome, ST & Princ.
122-123 S. Vicente C.V.
124-125 Florida, USA
126 Uganda
128-129 Brazil
130 Bioko, Equat. Guin.
105-106 Puerto Rico
107-108 Trinidad, Trin. & Tob.
109 Exœ, Brazil
110 Praia da Pipa, Brazil
111 Genipabu, Brazil
112-114 Pocone, Brazil
115 Chapada Guimaraes, Brazil
116 Iguazœ, Argentina
117-118 Tobago, Trin & Tob.
91/*/99
100/*/100
H. fasciatus -42
H. fasciatus -43
Luba, Equatorial Guinea
100/*/100
African-Atlantic clade
CLADE 5
H. platycephalus -37
H. platycephalus -38
H. platycephalus -39
H. platycephalus -40
H. platycephalus -41
Kajiado District, Rift Valley, Kenya
H. palaichthus -44 (Cacachaare, Trinidad & Tobago)
H. agrius -46 (Piaui, Brazil)
H. agrius -45 (Genipabu, Brazil)
H. agrius -47
H. agrius -48
H. agrius -49
Piaui, Brazil
H. longicephalus -61
H. longicephalus -62
S. Tome, Sao Tome & Principe
H. greeffi -63
H. greeffi -65
H. greeffi -64
Principe, Sao Tome & Principe
Briba brasiliana -53
Briba brasiliana -52
Briba brasiliana -51
Briba brasiliana -50
Piaui, Brazil
H. bouvieri -54 (S. Vicente, Cape Verde)
H. bouvieri -58 (Sal, Cape Verde)
H. bouvieri -60 (Sal, Cape Verde)
H. bouvieri -59 (Sal, Cape Verde)
H. bouvieri -55 (Boavista, Cape Verde)
H. bouvieri -57 (Boavista, Cape Verde)
H. bouvieri -56 (Boavista, Cape Verde)
100/*/100
75/*/79
100/*/100
100/*/100
96/*/100
100/*/100
100/*/100
66/*/68
100/*/100
100/*/100
100/*/100
100/*/100

3.2. Clade 2, the *H. angulatus* clade

Sampled African gecko populations customarily referred to *Hemidactylus brookii* do not form a monophyletic group with south Asian members of the species, which include its type material (see Fig. 1). Because of this and their isolated position within *Hemidactylus*, African *H. brookii* are best treated as a separate species, *H. angulatus*, as has sometimes been done in the past (for instance by Schmidt, 1919). This unit shows internal divergences of up to 13% in the gene fragments used in the present study. A basal dichotomy separates a clade, consisting of an individual *H. angulatus* from the Guinea coast of West Africa (Bioko island) and two *H. haitianus* from Cuba, from a clade comprising African samples of *H. angulatus* from drier areas farther north. The inclusion of the Cuban *H. haitianus* in the *H. angulatus* clade makes *H. angulatus* itself paraphyletic. The genetic divergence between the Bioko animal and the two Cuban *H. haitianus* is only 1.4%. The remaining African samples come from drier areas further north and the first dichotomy among these separates two Kenyan specimens from West African ones that include samples from Mali, Mauritania, Guinea, and the Cape Verde islands, although the bootstrap support for this group is very low. The West African clade has an internal divergence of around 9%, but there is no coherent geographical pattern. Three animals from Nouadhibou, northwest Mauritania, and its vicinity on the Atlantic coast (numbers 68, 73, and 81) show a divergence of around 7%, and two of them are very similar to individuals from southeast Mauritania (69 and 88) over 1200 km away. As already noted (Jesus et al., 2001), the haplotype of specimens from Sal in the Cape Verde archipelago shows a genetic divergence of about 5% from those of animals on other islands (São Nicolau, Boavista, Santiago, and Santo Antão), which exhibit little difference from each other. Both sets of Cape Verde haplotypes are similar or identical to ones found in coastal Mauritania and Guinea, about 460–600 km to the east.

3.3. Clade 3, the Arid clade

Twelve of the 13 species investigated occur in arid areas of northeast Africa (Kenya, Somalia, and Egypt), southwest Asia (Arabia, Iraq, Iran, and Pakistan) and the Socotra archipelago off the Horn of Africa, which includes Socotra itself and Abd al Kuri Island. The remaining species, *H. turcicus*, occurs mainly in the Mediterranean region and as an introduction in America. A basal dichotomy separates a clade, consisting of Kenyan *H. modestus*, north Somali *H. citernii*, and southeast Egyptian *H. foudai*, from a unit comprising all other members of the Arid clade. *H. citernii* and *H. foudai* are sister species, but with a large genetic divergence of 25%. Among the remaining species, the endemic Socotran *H. granti* and *H. dracaenocolus* are also sisters, but they are associated with *H. pumilio* from the same island only with very low bootstrap support. These three species are separated from a clade made up of Socotran *H. homoeolepis*, and *H. oxyrhinus* and *H. forbesii* from Abd al Kuri. The latter clade groups with relatively high bootstrap and high posterior probability values *H. persicus* from Oman, *H. robustus* from Egypt and the United Arab Emirates, *H. macropholis* of northern Somalia, and *H. turcicus*. The two Somali *H. macropholis* included in the study show considerable genetic divergence (14.8%) and do not form a monophyletic group. Thirty-eight samples of *H. turcicus* from the Mediterranean region and America are genetically uniform with a maximum uncorrected genetic divergence of less than 2%, despite the often very large geographical distances between them. Two *H. turcicus* from Jordan, including an example assigned to *H. t. lavadeserticus*, form a clade, which is sister taxon to the remaining samples of this species, diverging from them by 4.4%.

3.4. Clade 4, the *H. mabouia* clade

Among the species included in the present study, *H. mabouia* forms a well-supported clade with *H. yerburii* of southwest Arabia. The molecular evidence confirms *H. mabouia* is not close to *H. platycephalus*, which was once confused with it and clearly distinguished only by Broadley (1977). Samples of *H. mabouia* show a maximum genetic divergence of less than 1%, and most of the 30 individuals investigated are genetically identical (see Fig. 1), even though they come from 17 localities distributed over much of the huge range of the species. Regions covered include Kenya, Uganda, Equatorial Guinea, São Tomé, the Cape Verde archipelago, northeast Argentina, southwest, southeast and northeast Brazil, the island of Fernando de Noronha off this last area, Trinidad, Tobago, Puerto Rico and Florida.

3.5. Clade 5, the African–Atlantic clade

The seven forms studied here constitute a well-substantiated clade that includes species found on the Afri-

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Fig. 1. ML tree for a combination of the cytb and 12S rRNA mtDNA sequences obtained with PHYML and the GTR + I + G model of sequence evolution. Numbers and symbols by the nodes indicate (in this order): ML bootstrap value above 50%; when present, an asterisk indicates a posterior probability of ⩾0.95 in Bayesian analysis; MP bootstrap value above 50%. Specimen codes after species names permit reference to full data in Table 1. To speed tree inference, where there were several examples of *H. turcicus* and *H. mabouia* with identical haplotypes, only one of them was included in analyses and the remainder added to the figure afterwards. This involved samples 105–118, 120–130, 147–151, 153–162, and 171–182.

can mainland (*H. longicephalus*, *H. platycephalus*), on the Gulf of Guinea islands (*H. longicephalus*, *H. greeffi*), on the Cape Verde islands (*H. bouvieri*) and in tropical South America (*Briba brasiliana*, *H. agrius*, and *H. palaichthus*). The earliest split in this clade separates *H. platycephalus* from all the other species sampled. *H. agrius* of northeast Brazil and the more northern *H. palaichthus* of eastern Venezuela, Guyana, northwest Brazil, Trinidad and St. Lucia (distribution data from Vanzolini, 1978) are sister species and may form the sister group of the remaining forms.

4. Discussion

4.1. Relationships and systematics

4.1.1. Status of Briba and Cosymbotus

The molecular data clearly place members of the small genera, *Briba* and *Cosymbotus*, within specific groups of *Hemidactylus*, respectively, the Asian and African–Atlantic clades. It is therefore appropriate to transfer them to *Hemidactylus*. *Briba brasiliana* becomes *Hemidactylus brasilianus* **comb. nov.**, while *Cosymbotus playturus* becomes *Hemidactylus platyurus* **comb. nov**. (which is not the same as *H. platurus* Bleeker, 1858 = *Gehyra mutilata*, fide M.A. Smith, 1935). A second species assigned to *Cosymbotus*, *C. craspedotus*, may also need to be transferred to *Hemidactylus*, but was not included in the present study.

4.1.2. African H. angulatus and H. haitianus

As stated, sampled African populations assigned to *Hemidactylus brookii* are not closely related to that Asian species and should, at least for the present, all be called *H. angulatus*, although the high level of genetic diversity within *H. angulatus* indicates that it may be a species complex in need of revision. The genetic similarity between the two examples of *H. h. haitianus* from Cuba investigated here and a specimen of *H. angulatus* from the Gulf of Guinea, together with the morphological similarity between animals from the two areas (E.N. Arnold unpublished data), suggest that *H. haitianus* may not deserve separate species status. However, other New World populations need to be included in future molecular studies, among them *H. h. haitianus* from Hispaniola and Puerto Rico and *H. b. leightoni* from Colombia (for taxonomy see Kluge, 1969; Powell et al., 1996; Vanzolini, 1978).

4.1.3. Other genetically diverse species

Like *Hemidactylus angulatus*, several other widespread nominal species of *Hemidactylus* also show high levels of genetic diversity, including Asian *H. brookii* in its restricted sense, *H. bowringii* and *H.* (formerly *Cosymbotus*) *platyurus*. These too may represent species complexes, but much more extensive sampling is necessary before this can be established. The genetic diversity and disparate phylogenetic positions of the two animals assigned to *H. macropholis* indicates that this taxon needs revision. In addition, *H. bouvieri* also shows considerable variation among the Cape Verde islands.

4.1.4. The Arid clade

Hemidactylus robustus, of coastal Northeast Africa and Arabia, and probably Iran and Pakistan, has often been regarded as conspecific with *H. turcicus*, and its complex nomenclatorial history is most recently reviewed by Moravec and Böhme (1997). The present molecular study confirms their separate status. *H. robustus* populations from Egypt and the United Arab Emirates show approximately 14% genetic divergence from *H. turcicus*, and the two taxa have recently been found in sympatry on the Red Sea coast of Egypt (Baha el Din, 2005).

Other nominal species that may be part of the Arid clade but could not be sampled include: *H. albopunctatus*, *H. arnoldi*, *H. bavazzonoi*, *H. barbouri*, *H. barodanus*, *H. curlei*, *H. funaeolii*, *H. isolepis*, *H. jubensis*, *H. klauberi*, *H. laevis*, *H. laticaudatus*, *H. lemurinus*, *H. matschiei*, *H. megalops*, *H. mindiae*, *H. ophiolepis*, *H. ophiolepoides*, *H. puccionii*, *H. ruspolii*, *H. sinaitus*, *H. smithi*, *H. somalicus*, *H. squamulatus*, *H. tanganicus*, *H. taylori*, and *H. tropidolepis.* These forms cover a larger geographical area that the ones investigated in the present study, extending south into Tanzania and westwards at least to northern Nigeria.

4.1.5. Hemidactylus mabouia

The type locality of *H. mabouia* (Moreau de Jonnés, 1818) has been restricted to St Vincent in the Lesser Antilles (Stejneger, 1904), but the type specimen does not belong to the taxon to which this name is usually applied. Instead it is a *H. angulatus*, being especially similar to those from the Greater Antilles and Colombia, particularly the latter (Kluge, 1969). Nevertheless, the name *H. mabouia* should continue to be employed as it is at present, with special reference to the Lesser Antilles and South American populations (Broadley, 1977; Kluge, 1969). Mitochondrial DNA sequences confirm that populations on other Atlantic islands and across tropical Africa to Uganda and Kenya are conspecific with New World populations.

Animals in Madagascar and neighbouring regions have sometimes been assigned on morphological grounds to a separate species, *H. mercatorius* Gray, 1842. Studies of the 16S mitochondrial gene (Rocha et al., 2005; Vences et al., 2004) show that these populations exhibit significant genetic diversity. Most animals from Mayotte in the Comoro islands are similar to two samples from northeast Madagascar and also resemble *H. mabouia* from the Gulf of Guinea islands

(Rocha et al., 2005). This result may mean that northeast Madagascar and Mayotte animals are conspecific with *H. mabouia.* However, animals from the single small island of Mayotte show more variation (six haplotypes and over 2% genetic divergence) than the *H. mabouia* from three Gulf of Guinea islands, which have identical 16S sequence. These last animals are also identical in their cytochrome *b* and 12S mitochondrial–DNA sequences (Jesus et al., 2005), having the haplotypes that are found across most of the range of the *H. mabouia* sequenced in the present study. An animal from Mozambique assigned to *H. mercatorius* by Vences et al. (2004) is genetically distant from other specimens allocated to this form and from *H. mabouia* and may represent a separate species.

4.1.6. African–Atlantic group

Hemidactylus greeffi and *H.* (formerly *Briba*) *brasilianus* both lack the raised distal part of the first digit on both manus and pes, including its claw. This derived feature, which is found in no other *Hemidactylus*, may indicate relationship. Sequence from mitochondrial DNA (12S and 16S rRNA) and a nuclear gene (c-*mos*) suggest that *Hemidactylus newtoni* of Annobon island in the Gulf of Guinea is closely related to *H. greeffi* and *H. bouvieri* (Jesus et al., 2005) and is thus also likely to be a member of the African–Atlantic clade. Other African *Hemidactylus* that morphology indicates may belong to this assemblage include *H. ansorgii*, *H. aporus*, *H. bayonii*, *H. echinus*, *H. intestinalis*, *H. kamdemtohami*, *H. muriceus*, *H. pseudomuriceus*, and *H. richardsonii.* The status of some of these forms is discussed by Henle and Böhme (2003).

4.1.7. Retention of the genus Hemidactylus

The fact that several clades are discernable in the present study of *Hemidactylus* should not be used as grounds for partitioning it into several separate genera. Morphologically, the group is a very well defined, if *Teratolepis* is included. Species are easily recognized as belonging to the assemblage as a whole, but this is not true of its subunits, which are difficult to define anatomically. Retaining *Hemidactylus* in its present broad form also avoids the extensive changes in species names that would result from its division. Furthermore, less than 40% of currently recognized species are included in the present study, and the inclusion of the remainder may possibly blur the distinctness of the component clades.

4.2. Evolution

The lack of resolution at the base of the *Hemidactylus* clade is a pattern observable in several large lizard groups including the Lacertidae (Carranza et al., 2004; Fu, 2000; Harris et al., 1998) and the iguanid genus *Anolis* (Jackman et al., 1999). It may indicate that *Hemidactylus* underwent rapid cladogenesis and geographical spread early in its history, as has been suggested for these other two clades. Alternatively, the mitochondrial gene fragments used here may not be capable of resolving such deep relationships. Other more slowly evolving genes, including nuclear ones, may be more useful in this respect, as they have been elsewhere in lizard phylogeny (Townsend et al., 2004; Whiting et al., 2003). However, preliminary studies of *Hemidactylus* using the c-*mos* and α-Enolase nuclear genes suggests that these particular nuclear components may be evolving too slowly to be useful at this level (Jesus et al., 2005).

The partial phylogeny of *Hemidactylus* confirms the plasticity of some of the morphological features commonly used in the systematics of the genus. These vary within more than one of the clades discovered here, an indication that homoplasy exists and multiple changes must have occurred. For instance, enlarged dorsal tubercles are both present and absent, or at least strongly reduced, in the two subclades of the Asian clade (Clade 1), the Arid clade (Clade 3), and the African–Atlantic clade (Clade 5). Number and extent of femoral pores are reduced in some members of both the last two units. In some cases, mtDNA sequences shows that morphological stasis has occurred and relatively primitive morphologies have been retained for long periods. Distantly related forms may be very similar in their anatomical features, even though they show great divergence in their mtDNA. This is true of *Hemidactylus brookii* and *H. angulatus*, and is the cause of these being previously regarded as conspecific. In contrast, some taxa are very uniform in their mtDNA, even when they have very large and well-sampled ranges. This is especially marked in *H. turcicus* and *H. mabouia.*

Many species and assemblages of *Hemidactylus* retain what seems to be the primitive life mode of the genus, being habitual climbers on trees and rocks in often relatively mesic situations. In contrast, others have shifted to a more ground-dwelling existence in drier areas, something that is often accompanied by considerable morphological change. The biggest radiation of this sort is in the Arid clade (Clade 3) in northeast Africa. Many of the forms concerned have evolved small body-size, relatively large and sometimes imbricate dorsal scales, reduction or loss of enlarged dorsal tubercles, and reduction in number of femoral pores. The phylogeny presented in Fig. 1 indicates that these trends have developed independently in the Cape Verde Islands in *H. bouvieri* (a member of the African–Atlantic clade), and probably again in the two species of *Teratolepis* in the northern Indian subcontinent.

4.3. Long-distance colonization

Morphology suggests that the closest relatives of *Hemidactylus* are *Cyrtodactylus* of southern Asia and the largely Asian *Cyrtopodion* and associated genera. This suggests that the ancestral lineage of the genus may have originated in Asia, with later spread to the Arabian-African region. Such spread is likely to have occurred at an early stage, as five of the six main groupings of *Hemidactylus* are rooted there. Long-distance colonizations have occurred both from this region and from Asia and differ considerably in their timing.

4.3.1. Ancient transmarine colonizations of the Atlantic islands and America

Topology of the African–Atlantic clade and the distribution of other groups of *Hemidactylus* (Fig. 1) indicate that it originated in continental Africa. From here, it has reached the oceanic islands of the Gulf of Guinea 250–350 km away, producing *H. greeffi* on São Tomé and Príncipe, and *H. newtoni* and probably *H. aporus* on Annobon; *H. longicephalus* has also reached São Tomé and Príncipe. Additionally, the clade has colonized the Cape Verde islands 460 km offshore, producing *H. bouvieri*, and made the much longer journey to South America, where it is represented by the sister species *H. agrius* and *H. palaichthus*, and by *H. brasilianus.* The pattern of water circulation in the Atlantic suggests that the ancestor of *H. bouvieri* reached the Cape Verdes from extreme west Africa on the southwest-running Canary current, while ancestors of the South American forms travelled over 3000 km with the west-running Equatorial current, which arises further south and east in the Gulf of Guinea.

If *H. brasilianus* does not form a clade with *H. agrius* and *H. palaichthus*, it may have colonized South America independently from the ancestor of these. Possible relationship of *H. brasilianus* to *H. greeffi* indicates such colonization may have been via the Gulf of Guinea islands. South American *Hemidactylus* parallel *Mabuya* skinks, where there was also a the double invasion of the New World from Africa (Carranza and Arnold, 2003), with one colonizer, *Mabuya atlantica* of Fernando de Noronha off northeast Brazil, being morphologically most closely related to another Gulf of Guinea endemic, *Mabuya ozorii* of Annobon island (E.N. Arnold, unpublished data). On the basis of a rate of genetic divergence of 1.35–3.2% per My calculated for the same gene fragments studied here of several scleroglossans including *Tarentola* (see Section 2), these long-distance movements by lineages of the African–Atlantic clade of *Hemidactylus* are likely to have occurred between 6 and 16 My ago, long after the geological separation of Africa and South America occurred 105–119 My ago (McLaughlin, 2001), so migration must have been transmarine. Many members of the African–Atlantic clade of *Hemidactylus* are often arboreal (*H. platycephalus*—Broadley, 1977; *H. longicephalus*, *H. greeffi*—personal observations by J. Vindum, R. Drewes and J. Baillie on São Tomé and Príncipe; *Briba brasiliana* and *H. agrius*) and, like other gekkonid lizards, lay calcareous eggs that can often resist exposure to salt water. These features would have enhanced the chances of geckos being transported down rivers and across the sea on fallen trees.

4.3.2. Ancient transmarine colonizations of the Socotran archipelago

The Socotran arhipelago lies off the Horn of Africa, Abd al Kuri being about 100 km from this, while Socotra itself is 100 km further east and some 300 km from southwest Arabia. As noted, six endemic species investigated here all belong to the Arid clade, forming at least two separate clades within it, each with a different set of close mainland relatives. As parsimony indicates that the Arid clade is rooted on the African–Arabian mainland, it is likely that there were at least two separate colonizations of the archipelago followed by speciation. On the basis of an estimated genetic divergence rate of 1.35–3.2% per My, arrival of the ancestors of the *H. pumilio*–*H. granti*–*H. dracaenocolus* clade would have been about 6–13 My ago, and of the *H. oxyrhinus*–*H. forbesii*–*H. homoelepis* clade about 3.5–8 My ago. The islands are probably continental in origin but have a long history of isolation variously estimated as 17 My ago (Beydun and Bichan, 1970), and as long as 90 My ago (Kopp, 1999). Consequently, colonization is likely to have been transmarine.

In fact, colonization may have occurred later than the estimated time, as the molecular phylogeny excludes many mainland species for which DNA was not available. Some of these are morphologically similar to Socotran species. For instance, *H. pumilio* is very like the Somali *H. puccionii*, and there are populations in southern Arabia thought to be conspecific with *H. homoeolepis* (Arnold, 1980). If included in a molecular phylogeny, such species may well shorten the basal branches of the clades of Socotran endemics, reducing their estimated dates of separation. Transmarine colonization is made more likely by the monsoon currents and winds that run from the southwest in summer and from the northeast in winter. At these seasons they could have brought propagules to the Socotran archipelago from northeast Africa and Arabia, respectively.

4.3.3. Recent colonization by the Hemidactylus angulatus clade

Populations assigned to *H. haitianus* are believed to have reached the New World naturally (Kluge, 1969), but the genetic and morphological similarity of Cuban examples to *H. angulatus* from the Gulf of Guinea indicates they travelled quite recently and may consequently result from human activity. Only a single Gulf of Guinea specimen was investigated so, given the high variability in the *H. angulatus* clade, even more similar ones may exist. The similarity of *H. angulatus* over 1200 km inland in Mauritania to individuals on its coast may possibly result from overland transport westwards along the extensive trade routes that exist in this region. Finally, the near identity of the two very distinct kinds of haplotypes in the Cape Verde islands to ones on the adjoining African coast indicates that there was a double colonization of the archipelago, which again may be anthropogenic. A case, that the population on Sal island arrived naturally some millions of years ago rested on the apparent distinctiveness of its haplotype (Jesus et al., 2001), but the more extensive mainland material reported here gives no support for this hypothesis.

4.3.4. Recent colonization by H. mabouia

As with *H. angulatus*, natural colonization of the Americas by *H. mabouia* has been suggested, albeit with less confidence (Kluge, 1969), but the uniformity of *H. mabouia*, showing virtually no genetic variation over its huge range, indicates it too has spread comparatively rapidly and recently. Greater diversity on Mayotte island in the Comoros and northeast Madagascar, and relationship to Madagascan populations assigned to *H. mercatorius* and to Arabian *H. yerburyii*, indicates that the widespread haplotypes originated in East Africa and then spread westwards, across tropical Africa *H. mabouia* went on to reach various islands in the Atlantic and to colonise large parts of tropical America, where its range is still expanding (recently reported first records: Florida—Lawson et al., 1991; Exuma islands, Bahamas—Franz et al., 1993; Jamaica—Flaschendrager, 1999). Spread by human activity is consequently likely and the species has recently reached temperate areas of South Africa apparently by this means (Branch, 1998). In tropical Africa, *H. mabouia* is associated with human habitation in forested areas (Loveridge, 1947) and dispersal here may have been with trade along the Congo River, particularly as penetration into South America has also been along river systems, especially the Amazon (Kluge, 1969, map p. 30). If spread was anthropogenic, trans-Atlantic colonization must have happened very recently, in the 500 years or so that people have been crossing this ocean.

The ultimate source of *H. mabouia* is uncertain. Presence of similar populations but with much greater genetic diversity on the small island of Mayotte in the Comoro archipelago raises the possibility that the species originated here, from colonists related to *H. mercatorius* of Madagascar, and invaded the African mainland. Such colonizations of continental areas from islands are rare among reptiles but are known, for instance in *Anolis* iguanids in the Caribbean (Nicholson et al., 2005). In the present case, such a hypothesis needs testing by examining more extensive samples from southeast Africa and Madagascar.

4.3.5. Recent colonization by H. turcicus

As with *H. mabouia*, uniformity of most samples of *H. turcicus* indicates recent and rapid spread. The presence of divergent populations in Jordan, and of related species further east, suggests that movement was from this area westwards across the whole Mediterranean region and then across the Atlantic Ocean. Here *H. turcicus* has reached the Canary Islands, where it has only appeared very recently (Geniez, 2002), and America, where the species is found in Mexico (recorded from Yucatan as long ago as 1906 as *H. exsul*), Cuba and Florida (Smith, 1946). *H. turcicus* is now also known from other areas of the United States, including North and South Carolina, Louisiana, Arkansas, Texas, New Mexico, Arizona, Georgia, Virginia, and Maryland (Pianka and Vitt, 2003; White and Tumlison, 1999). It has also been recently recorded from Argentina. Indications that spread was anthropogenic include absence of fossils in the Mediterranean region, in contrast to *Tarentola* and *Euleptes* geckos (Estes, 1983), and the recency of recorded arrivals in many parts of the New World. *Tarentola mauritanica* shows evidence of a more limited recent rapid spread in parts of the North Mediterranean (Harris et al., 2004a,b), although some North African and Iberian populations appear to be natural (Harris et al., 2004a; Estes, 1983).

4.3.6. Recent colonizations by Asian species of Hemidactylus

Mitochondrial DNA sequences indicate that several Asian species of *Hemidactylus* have also expanded their ranges comparatively recently, often reaching very distant areas. As noted, material of *H. garnotii* from Florida is almost identical to that from Myanmar in the southeast Asian source area more than 15,000 km away. Similarly, *H. frenatus* from Colombia are identical with ones from Hawaii, which are separated by more than 8500 km. This probably results from both areas being directly or indirectly colonized from some as yet uninvestigated source region in Southeast Asia. There are many records of the recent arrival of this species on islands in the Pacific and on the mainland of America and Australia (see for instance Petren et al., 1993).

Hemidactylus brookii from Mauritius in the Mascarene Islands show a 4.5% genetic divergence in the gene fragments used here from the most similar sample in the large south Asian source region. But this apparent differentiation may result from inadequate sampling. When the 16S gene is considered, animals from all three Mascarene islands, and from the Comoros 1500 km away are very similar (0.0–0.8% difference) to ones from a presumably natural population on Sri Lanka 3300–4500 km distant (Rocha et al., 2005; Vences et al., 2004), so natural colonization is not necessarily indicated. Human introduction would fit with the lack of marine currents from the source area to the Mascarenes and

Comoros, and the virtual absence of *H. brookii* from very recent fossil deposits on the Mascarene island of Rodrigues. These are very rich and contain virtually all endemic vertebrates known from the island (E.N. Arnold, unpublished data).

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References

Arnold, E.N., 1980. Reptiles and amphibians of Dhofar, Southern Arabia. In: Shaw-Reade, S.N., Sale, J.B., Gallagher, M.D., Daly, R.H. (Eds.), The Scientific Results of the Oman Flora and Fauna Survey 1977 (Dhofar). J. Oman Stud., Special Report, pp. 273–332.

Arnold, E.N., 2000. Using fossils and phylogenies to understand evolution of reptile communities on islands. Bonn. Zool. Monogr. 46, 309–323.

Austin, J.J., Arnold, E.N., Jones, C.G., 2004. Reconstructing and island radiation using ancient and recent DNA: the extinct and living day geckos (*Phelsuma*) of the Mascarene Islands. Mol. Phylogenet. Evol. 31, 109–122.

Baha el Din, S.M., 2003. A new species of *Hemidactylus* (Squamata: Gekkonidae) from Egypt. Afr. J. Herp. 52, 39–47.

Baha el Din, S.M., 2005. An overview of Egyptian species of *Hemidactylus* (Gekkonidae) with the description of a new species from the high mountains of South Sinai. Zool. Mid. East 34, 11–26.

Bauer, A.M., Henle, K., 1994. Gekkonidae (Reptilia, Sauria). Part 1: Australia and Oceania. Das Tierreich 109, 1–306.

Bauer, A.M., Pauwels, O.S.G., 2002. A new forest-dweling *Hemidactylus* (Squamata: Gekkonidae) from Gabon, West Africa. Afr. J. Herp. 51, 1–8.

Bauer, A.M., Russell, A.P., 1995. The systematic relationships of *Dravidogecko anamallensis*. Asiatic Herp. Res. 6, 30–35.

Beydun, Z.R., Bichan, H.R., 1970. The Geology of Socotra Island, Gulf of Aden. Q. J. Geol. Soc. Lond. 125, 413–446.

Branch, W.R., 1998. A Field Guide to Sankes and Other Reptiles of Southern Africa. Struik Publishers, Cape Town.

Broadley, D.G., 1977. A review of the *Hemidactylus mabouia* complex in southeastern Africa (Sauria: Gekkonidae). Arnoldia 8, 1–15.

Carranza, S., Arnold, E.N., 2003. Investigating the origin of transoceanic distributions: mtDNA shows *Mabuya* lizards (Reptilia, Scincidae) crossed the Atlantic twice. Syst. Biodiv. 1, 275–282.

Carranza, S., Arnold, E.N., Amat, F., 2004. DNA phylogeny of *Lacerta* (*Iberolacerta*) and other lacertine lizards (Reptilia: Lacertidae): did competition cause long-term mountain restriction? Syst. Biodiv. 2, 57–77.

Carranza, S., Arnold, E.N., Mateo, J.A., Geniez, P., 2002. Relationships and evolution of the North African geckos, *Geckonia* and *Tarentola* (Reptilia: Gekkonidae), based on mitochondrial and nuclear DNA sequences. Mol. Phylogenet. Evol. 23, 244–256.

Carranza, S., Arnold, E.N., Mateo, J.A., López-Jurado, L.F., 2000. Long-distance colonization and radiation in gekkonid lizards, *Tarentola* (Reptilia: Gekkonidae), revealed by mitochondrial DNA sequences. Proc. R. Soc. Lond. B 267, 637–649.

Carranza, S., Arnold, E.N., Thomas, R.H., Mateo, J.A., López-Jurado, L.F., 1999. Status of the extinct giant lacertid lizard *Gallotia simonyi simonyi* (Reptilia: Lacertidae) assessed using mtDNA sequences from museum specimens. Herp. J. 9, 83–86.

Cole, N.C., Jones, C.G., Harris, S., 2005. The need for enemy-free space: the impact of an invasive gecko on island endemics. Biol. Cons. 125, 467–474.

Estes, R., 1983. Handbuch der Palaeoherpetologie 10, Sauria terrestria, Amphisbaenia. Gustav Fischer Verlag, New York.

Felsenstein, J., 1985. Confidence-limits on phylogenies—an approach using the bootstrap. Evolution 39, 783–791.

Flaschendrager, A., 1999. Erstnachweis von *Hemidactylus mabouia* (Moreau de Jonnés, 1818) fur Jamaica. Herpetofauna (Weinsdadt) 21, 18.

Franz, R., Dodd, C.K., Burden, D.W., 1993. Distributional records of amphibians and reptiles from the Exuma islands, Bahamas, including the first reports of a freshwater turtle and an introduced gecko. Caribbean J. Sci. 29, 165–173.

Fu, J., 2000. Toward the phylogeny of the family Lacertidae—why 4708 base pairs of mtDNA sequences cannot draw the picture. Biol. J. Linn. Soc. 71, 203–2176.

Geniez, P., 2002. *Hemidactylus turcicus*. In: Pleguezuelos, J.M., Márquez, R., Lizana, M. (Eds.), Atlas y libro rojo de los anfibios y reptiles de España. Dirección General de Conservación de la Naturaleza-Asociación Herpetológica Española, Madrid, p. 584.

Giribet, G., Rambla, M., Carranza, S., Baguñà, J., Riutort, M., Ribera, C., 1999. Phylogeny of the arachnid order Opiliones (Arthropoda) inferred from a combined approach of complete 18S and partial 28S ribosomal DNA sequences and morphology. Mol. Phylogenet. Evol. 11, 296–307.

Guindon, S., Gascuel, O., 2003. A simple, fast, and accurate algorithm to estimate large phylogenies by maximum likelihood. Syst. Biol. 52, 696–704.

Harris, D.J., Arnold, E.N., Thomas, R.H., 1998. Relationships of lacertid lizards (Reptilia: Lacertidae) estimated from mitochondrial DNA sequences and morphology. Proc. R. Soc. Lond. B 265, 1939–1948.

Harris, D.J., Batista, V., Carretero, M.A., Ferrrand, N., 2004a. Genetic variation in *Tarentola mauritanica* (Reptilia: Gekkonidae) across the Strait of Gibraltar derived from mitochondrial and nuclear DNA sequences. Amphibia-Reptilia 25, 451–459.

Harris, D.J., Batista, V., Lymberakis, P., Carretero, M.A., 2004b. Complex estimates of evolutionary relationships in *Tarentola mauritanica* (Reptilia: Gekkonidae) derived from mitochondrial DNA sequences. Mol. Phylogenet. Evol. 30, 855–859.

Heads, M., 2005. Dating nodes on molecular phylogenies: a critique of molecular biogeography. Cladistics 21, 62–78.

Henle, K., Böhme, W., 2003. A new species of *Hemidactylus* (Squamata: Gekkonidae) from West Africa, and comments on species hitherto confused with *H. muriceus*. African J. Herp. 52, 23–38.

Huelsenbeck, J.P., Ronquist, F., 2001. MRBAYES: Bayesian inference of phylogeny. Bioinformatics 17, 754–755.

Jackman, T.R., Larson, A., de Queiroz, K., Losos, J.B., 1999. Phylogenetic relationships and tempo of early diversification in *Anolis* lizards. Syst. Biol. 48, 254–285.

Jesus, J., Brehm, A., Harris, D.J., 2005. Phylogenetic relationships of *Hemidactylus* geckos from the Gulf of Guinea islands: patterns of natural colonizations and anthropogenic introductions estimated from mitochondrial and nuclear DNA sequences. Mol. Phylogenet. Evol. 34, 480–485.

Jesus, J., Brehm, A., Pinheiro, M., Harris, D.J., 2001. Relationships of *Hemidactylus* (Reptilia: Gekkonidae) from the Cape Verde Islands: what mitochondrial DNA data indicate. J. Herp. 35, 672–675.

Kluge, A.G., 1969. The evolution and geographic origin of the New World *Hemidactylus mabouia-brookii* complex (Gekkonidae, Sauria). Misc. Publs. Mus. Zool. Univ. Michigan 138, 1–78.

Kluge, A.G., 1991. Checklist of gekkonid lizards. Smithsonian Herpetological Information Service 85, 1–35.

Kocher, T.D., Thomas, W.K., Meyer, A., Edwards, S.V., Pääbo, S., Villablanca, F.X., Wilson, A.C., 1989. Dynamics of mitochondrial DNA evolution in animals: amplification and sequencing with conserved primers. Proc. Natl. Acad. Sci. USA 86, 6196–6200.

Kopp, H. 1999. Abiotische Geofactoren. In: Wranik, W. (Ed.), Sokotra, Mensch und Natur. Jemen-Stud 14, pp. 3–22.

Lamb, T., Bauer, A.M., 2001. Relationships of the *Pachydactylus rugosus* group of geckos (Reptilia: Squamata: Gekkonidae). Afr. Zool. 35, 55–67.

Lamb, T., Bauer, A.M., 2002. Phylogenetic relationships of the large-bodied members of the African lizard genus *Pachydactylus* (Reptilia: Gekkonidae). Copeia 2002, 586–596.

Lawson, R., Frank, P.G., Martin, D.L., 1991. A gecko new to the United States herpetofauna, with notes on geckoes of the Florida Keys. Herp. Rev. 22, 11–12.

Loveridge, A., 1947. Revision of the African lizards of the family Gekkonidae. Bull. Mus. Comp. Zool. Harvard 98, 1–469.

Maca-Meyer, N., Carranza, S., Rando, J.C., Arnold, E.N., Cabrera, V.M., 2003. Status and relationships of the extinct giant Canary Island *Gallotia goliath* (Reptilia: Lacertidae), assessed using ancient mtDNA from its mummified remains. Biol. J. Linn. Soc. 80, 659–670.

McLaughlin, S., 2001. The breakup history of Gondwana and its impact on pre-Cenozoic floristic provincialism. Austral. J. Bot. 49, 271–3000.

Moravec, J., Böhme, W., 1997. A new subspecies of the Mediterranian gecko, *Hemidactylus turcicus* from the Syrian lava desert (Squamata, Sauria, Gekkonidae). Herpetozoa 10, 121–128.

Moreau de Jonnès., 1818. Monographie du *Mabouia* des murailles, ou Gecko *Mabouia* des Antilles. Bull. Scient. Soc. Philomathique Paris 3, 138–139.

Nicholson, E., Glor, R.E., Kolbe, J.J., Larson, A., Hedges, S.B., Losos, J.B., 2005. Mainland colonisation by island lizards. J. Biogeogr. 32, 1–10.

Nogales, M., López, M., Jiménez-Asensio, J., Larruga, J.M., Hernández, M., González, P., 1998. Evolution and Biogeography of the genus *Tarentola* (Sauria: Gekkonidae) in the Canary Islands, inferred from mitochondrial DNA sequences. J. Evol. Biol. 11, 481–494.

Petren, K., Bolger, D.T., Case, T.J., 1993. Mechanisms in the competitive success of an invading gecko over an asexual native. Science 259, 354–357.

Pianka, E.R., Vitt, L.J., 2003. Lizards, Windows to the Evolution of Diversity. University of California Press, Berkeley.

Posada, D., Crandall, K., 1998. MODELTEST: testing the model of DNA substitution. Bioinformatics 14, 817–818.

Powell, R., Henderson, R.W., Adler, K., Dundee, H.A., 1996. An annotated checklist of the West Indian amphibians and reptiles. In: Powell, R., Henderson, R.W. (Eds.), Contributions to West Indian Herpetology. Society for the Study of Amphibians and Reptiles, pp. 51–93.

Rocha, S., Carretero, M.A., Harris, D.J., 2005. Diversity and phylogenetic relationships of *Hemidactylus* geckos from the Comoro Islands. Mol. Phylogenet. Evol. 35, 292–299.

Rösler, H., Wranik, W., 1999. Beiträge zur Herpetologie der Republik Yemen 5. Drei neue Gecko-Arten vom Sokotra-Archipel (Reptilia: Sauria: Gekkonidae). Zool. Abh. Staatl. Mus. Tierkunde Dresden 50, 249–265.

Russell, A.P., 1976. Some comments concerning interrelationships amongst gekkonine geckos. In: Bellairs, A.d'A., Cox, C.B. (Eds.), Morphology and Biology of Reptiles. Linn. Soc. Symposium Ser. 3. Academic Press, London.

Russell, A.P., 1977. The phalangeal formula of *Hemidactylus* Oken, 1817 (Reptilia: Gekkonidae): a correction and a functional explanation. Zentralbl. Veterin. Med. C. Anat. Histol. Embryolog. 6, 332–338.

Schmidt, K.P. 1919. Contributions to the herpetology of the Belgian Congo based on the collection of the American Congo Expedition,1909–1915. Part I. Turtles, crocodiles, lizards and chameleons; with field notes by Herbert Lang and James P. Chapin. Bull. Amer. Mus. Nat. Hist. 39, 385–624.

Smith, H.M., 1946. Handbook of Lizards, Lizards of the United States and Canada. Comstock Publishing, Ithaca and New York.

Smith, M.A., 1935. Fauna of British India, including Ceylon and Burma. Reptilia and Amphibia, vol. 2. Taylor and Francis, London.

Stejneger, L., 1904. The herpetology of Puerto Rico. Rep. U.S. Nat. Mus. 1902, 549–724.

Swofford, D.L. 1998. PAUP*: Phylogenetic Analysis using Parsimony (and other methods), v 4.0. Sinauer Associates, Sunderland, MA.

Thompson, J.D., Gibson, T.J., Plewniak, F., Jeanmourgin, F., Higgins, D.G., 1997. The clustalX windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. Nucleic Acid Res. 24, 4876–4882.

Townsend, T., Larson, A., Louis, E., Macey, J.R., 2004. Molecular phylogenetics of Squamata: the position of snakes, amphisbaenians and dibamids, and the root of the squamate tree. Syst. Biol. 53, 735–757.

Vanzolini, P.E., 1978. On South American *Hemidactylus* (Sauria, Gekkonidae). Papéis Avulsos Zool. 31, 307–342.

Vences, M., Wanke, S., Vieites, D.R., Branch, B., Glaw, F., 2004. Natural colonisation or introduction? High genetic divergences and phylogeographic relationships of house geckos (*Hemidactylus*) from Madagascar. Biol. J. Linn. Soc. 83, 115–130.

Wermuth, H., 1965. Liste der rezenten Amphibien und Reptilien: Gekkonidae, Pygopodidae, Xantusiidae. Das Tierreich 80, 1–246.

White, G., Tumlison, R., 1999. *Hemidactylus turcicus* (Mediterranian gecko). Herpet. Rev. 30, 110.

Whiting, A.S., Bauer, A.M., Sites, J.W., 2003. Phylogenetic relationships and limb loss in sub-saharan African scincine lizards (Squamata: Scincidae). Mol. Phylogenet. Evol. 29, 582–598.