

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

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serve as a model for
biogeo studies

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 brasiliiana*, *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. dracaenaculus*)) (*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. pallichthus*) (*H. longicephalus*, *H. greeffi*, *H. bowieri*, *Briba brasiliiana*)). *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.

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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.

truly
are
world
travelers

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).

Probably
all are
extremely
generalists

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 scapula (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 brasiliensis*, 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 *b1* and cytochrome *b2* 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 ≥ 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.		Specimen code
			cytb	12S	
<i>Pachydactylus turneri</i>	1	Richtersveldt, NW Cape Province, South Africa	AF184990/AF186118		Pcla
<i>Tarentola americana</i>	2	Guantánamo, Cuba	AF184991/AF186119		Tamer
<i>Tarentola boettgeri</i>	3	Arinaga, Gran Canaria, Canary islands, Spain	AF184997/AF186125		CA11GC
<i>Tarentola boettgeri boettgeri</i>	4	Tauro, Gran Canaria, Canary islands, Spain	AF184996/AF186124		CA10GC
<i>Tarentola boettgeri boettgeri</i>	5	Tauro, Gran Canaria, Canary islands, Spain	AF184995/AF186123		CA9GC
<i>Tarentola boettgeri bischoffi</i>	6	Selvagem Grande, Portugal (BEV.2239)	AF185000/AF186128		Tbobish
<i>Tarentola boettgeri hierrensis</i>	7	Tamaduste, El Hierro, Canary islands, Spain	AF184998/AF186126		CA16H
<i>Tarentola boettgeri hierrensis</i>	8	Los Llanillos, El Hierro, Canary islands, Spain	AF184999/AF186127		CA17H
<i>Tarentola angustimentalis</i>	9	Fuste, Fuerteventura, Canary islands, Spain	AF184993/AF186121		CA7VF
<i>Cosymbotus platyurus</i>	10	Kan-Pet-Let Township, Chin State, Myanmar (CAS222332)	DQ120297/DQ120468		E29104.3
<i>Cosymbotus platyurus</i>	11	Khim Aye Village, Sagaing Division, Myanmar (CAS215451)	DQ120296/DQ120467		E29104.4
<i>Cosymbotus platyurus</i>	12	Alaungdaw Kathapa NP, Sagaing Division, Myanmar (CAS204982)	DQ120295/DQ120466		E29104.5
<i>Cosymbotus platyurus</i>	13	Gon Nyin, Sagaing Division, Myanmar (CAS215734)	DQ120294/DQ120465		E29104.2
<i>H. karenorum</i>	14	Mandalay Division, Myanmar (CAS210670)	DQ120293/DQ120464		E509.19
<i>H. garnotii</i>	15	Yangon Division, Myanmar (CAS213517)	DQ120292/DQ120463		E509.8
<i>H. garnotii</i>	16	Palm Beach, Florida, USA (CASA184323)	DQ120291/DQ120462		E509.11
<i>H. garnotii</i>	17	Dade Co., Florida, USA (CAS184322)	DQ120290/DQ120461		E509.10
<i>H. garnotii</i>	18	Alaungdaw Kathapa, Sagaing Province, Myanmar (CAS210280)	DQ120289/DQ120460		E509.9
<i>H. garnotii</i>	19	Alaungdaw Kathapa, Sagaing Province, Myanmar (CAS210259)	DQ120288/DQ120459		E509.20
<i>H. bowringii</i>	20	Yangon Division: Mingalardon Township, Myanmar (CAS213333)	DQ120287/DQ120458		E1708.8
<i>H. bowringii</i>	21	Yunnan, Nujiang Prefecture, China (CAS207483)	DQ120286/DQ120457		E170810
<i>H. bowringii</i>	22	Shan State, Myanmar (CAS216345)	DQ120285/DQ120456		E1109.6
<i>H. flaviviridis</i>	23	Hadibu, Socotra island, Yemen	DQ120284/DQ120455		E912.2
<i>H. flaviviridis</i>	24	Fujairah, UAE	DQ120283/DQ120454		E1708.22
<i>H. frenatus</i>	25	Thiruvananthapuram, India	DQ120282/DQ120453		E509.5
<i>H. frenatus</i>	26	Mandalay Division, Myanmar (CAS214157)	DQ120281/DQ120452		E509.2
<i>H. frenatus</i>	27	Mwe Hauk, Ayeyarwade Division, Myanmar (CAS212900)	DQ120280/DQ120451		E509.1
<i>H. frenatus</i>	28	Puerto Carreño, Colombia	DQ120279/DQ120450		E509.3
<i>H. frenatus</i>	29	Kauai, Hawaii islands, USA (CAS200822)	DQ120278/DQ120449		E509.7
<i>H. frenatus</i>	30	Kauai, Hawaii islands, USA (CAS200820)	DQ120277/DQ120448		E509.6
<i>H. brookii brookii</i>	31	Subrahmnaya, Karnataka, India	DQ120276/DQ120447		E1109.10
<i>H. brookii brookii</i>	32	Kyauk Pan Tawn, Mandalay Division, Myanmar (CAS213939)	DQ120275/DQ120446		E1708.18
<i>H. brookii brookii</i>	33	Mingalardon, Yangon Division, Myanmar (CAS213515)	DQ120274/DQ120445		E1708.17
<i>H. brookii brookii</i>	34	Kollam, Kerala, India	DQ120273/DQ120444		E1109.11
<i>H. brookii brookii</i>	35	Mauritius	DQ120272/DQ120443		Hemb22b
<i>H. brookii brookii</i>	36	Mauritius	DQ120271/DQ120442		Hemb1b
<i>H. platycephalus</i>	37	Kajiado District, Rift Valley, Kenya (CAS198967)	DQ120270/DQ120441		E609.16
<i>H. platycephalus</i>	38	Kajiado District, Rift Valley, Kenya (CAS198966)	DQ120269/DQ120440		E609.15
<i>H. platycephalus</i>	39	Kajiado District, Rift Valley, Kenya (CAS198974)	DQ120268/DQ120439		E7014.9
<i>H. platycephalus</i>	40	Kajiado District, Rift Valley, Kenya (CAS198970)	DQ120267/DQ120438		E7014.8
<i>H. platycephalus</i>	41	Kajiado District, Rift Valley, Kenya (CAS198969)	DQ120266/DQ120437		E7014.7
<i>H. fasciatus</i>	42	Luba, Equatorial Guinea (CAS207778)	DQ120265/DQ120436		E1708.21
<i>H. fasciatus</i>	43	Luba, Equatorial Guinea (CAS207777)	DQ120264/DQ120435		E1708.20
<i>H. palaichthus</i>	44	Chacachaare, Trinidad	DQ120263/DQ120434		E1109.3
<i>H. agrius</i>	45	Touros, Genipabu, Brazil	DQ120262/DQ120433		E1708.1
<i>H. agrius</i>	46	Dom Expedito Lopes, Piauí, Brazil	DQ120261/DQ120432		E1708.2
<i>H. agrius</i>	47	Dom Expedito Lopes, Piauí, Brazil	DQ120260/DQ120431		E1708.7
<i>H. agrius</i>	48	Dom Expedito Lopes, Piauí, Brazil	DQ120259/DQ120430		E1708.6
<i>H. agrius</i>	49	Dom Expedito Lopes, Piauí, Brazil	DQ120258/DQ120429		E1708.5
<i>Briba brasiliiana</i>	50	Dom Expedito Lopes, Piauí, Brazil	DQ120257/DQ120428		E1209.4
<i>Briba brasiliiana</i>	51	Dom Expedito Lopes, Piauí, Brazil	DQ120256/DQ120427		E1209.2
<i>Briba brasiliiana</i>	52	Dom Expedito Lopes, Piauí, Brazil	DQ120255/DQ120426		E1209.3
<i>Briba brasiliiana</i>	53	Dom Expedito Lopes, Piauí, Brazil	DQ120254/DQ120425		E1209.1
<i>H. bouvieri</i>	54	São Vicente, Cape Verde islands, Cape Verde	DQ120253/DQ120424		HbouSvA
<i>H. bouvieri</i>	55	Boavista, Cape Verde islands, Cape Verde	DQ120252/DQ120423		11HbouBo
<i>H. bouvieri</i>	56	Boavista, Cape Verde islands, Cape Verde	DQ120251/DQ120422		2HbouBo

Table 1 (continued)

Taxa	Specimen code (Fig. 1)	Locality	GenBank Accession Nos.		Specimen code
			cytb	12S	
<i>H. bowieri</i>	57	Boavista, Cape Verde islands, Cape Verde	DQ120250/DQ120421		12HbouBo
<i>H. bowieri</i>	58	Sal, Cape Verde islands, Cape Verde	DQ120249/DQ120420		10HbouS
<i>H. bowieri</i>	59	Sal, Cape Verde islands, Cape Verde	DQ120248/DQ120419		9HbouS
<i>H. bowieri</i>	60	Sal, Cape Verde islands, Cape Verde	DQ120247/DQ120418		1HbouS
<i>H. longicephalus</i>	61	São Tomé, São Tomé and Príncipe (CAS219294)	DQ120246/DQ120417		E7014.6
<i>H. longicephalus</i>	62	São Tomé, São Tomé and Príncipe (CAS219278)	DQ120245/DQ120416		E7014.5
<i>H. greeffi</i>	63	Príncipe, São Tomé and Príncipe (CAS219212)	DQ120244/DQ120415		E7014.3
<i>H. greeffi</i>	64	Príncipe, São Tomé and Príncipe (CAS219198)	DQ120243/DQ120414		E7014.4
<i>H. greeffi</i>	65	Príncipe, São Tomé and Príncipe	DQ120242/DQ120413		E509.14
<i>H. brookii angulatus</i>	66	Kajiado District, Rift valley, Kenya (CAS198856)	DQ120241/DQ120412		E1708.15
<i>H. brookii angulatus</i>	67	Kajiado District, Rift valley, Kenya (CAS198855)	DQ120240/DQ120411		E1708.14
<i>H. brookii angulatus</i>	68	Nouadhibou, Dakhlet-Nouadhibou, Mauritania	DQ120239/DQ120410		E2503321
<i>H. brookii angulatus</i>	69	El Wad to Zouaina, Hodh el Gharbi, Mauritania	DQ120238/DQ120409		E25033.18
<i>H. brookii angulatus</i>	70	Sal, Cape Verde islands, Cape Verde	DQ120237/DQ120408		2B25HbrS
<i>H. brookii angulatus</i>	71	Sal, Cape Verde islands, Cape Verde	DQ120236/DQ120407		2B23HbrS
<i>H. brookii angulatus</i>	72	Sal, Cape Verde islands, Cape Verde	DQ120235/DQ120406		2B8HbrS
<i>H. brookii angulatus</i>	73	Nouadhibou, Dakhlet-Nouadhibou, Mauritania	DQ120234/DQ120405		E25033.20
<i>H. brookii angulatus</i>	74	Santo Antão, Cape Verde islands, Cape Verde	DQ120233/DQ120404		35HbrSA
<i>H. brookii angulatus</i>	75	Santo Antão, Cape Verde islands, Cape Verde	DQ120232/DQ120403		34HbrSA
<i>H. brookii angulatus</i>	76	Santo Antão, Cape Verde islands, Cape Verde	DQ120231/DQ120402		33HbrSA
<i>H. brookii angulatus</i>	77	Santiago, Cape Verde islands, Cape Verde	DQ120230/DQ120401		20HbrSt
<i>H. brookii angulatus</i>	78	Santiago, Cape Verde islands, Cape Verde	DQ120229/DQ120400		18HbrSt
<i>H. brookii angulatus</i>	79	Guinea-Bissau	AF324797/AF324798		Jesus et al., 2001
<i>H. brookii angulatus</i>	80	Santiago, Cape Verde islands, Cape Verde	DQ120228/DQ120399		6HbrSt
<i>H. brookii angulatus</i>	81	Cabo Blanco, Mauritania	DQ120227/DQ120398		26HbrAf
<i>H. brookii angulatus</i>	82	Santiago, Cape Verde islands, Cape Verde	DQ120226/DQ120397		19HbrSt
<i>H. brookii angulatus</i>	83	Boa Vista, Cape Verde islands, Cape Verde	DQ120225/DQ120396		163HbrBo
<i>H. brookii angulatus</i>	84	Boa Vista, Cape Verde islands, Cape Verde	DQ120224/DQ120395		161HbrBo
<i>H. brookii angulatus</i>	85	Boa Vista, Cape Verde islands, Cape Verde	DQ120223/DQ120394		160HbrBo
<i>H. brookii angulatus</i>	86	Boa Vista, Cape Verde islands, Cape Verde	DQ120222/DQ120393		159HbrBo
<i>H. brookii angulatus</i>	87	Boa Vista, Cape Verde islands, Cape Verde	DQ120221/DQ120392		7HbrBo
<i>H. brookii angulatus</i>	88	Lake Mahmude, Hodh Ech Chargui, Mauritania	DQ120220/DQ120391		E25033.19
<i>H. brookii angulatus</i>	89	Mali	DQ120219/DQ120390		E1708.24
<i>H. brookii angulatus</i>	90	Malabo, Bioko island, Equatorial Guinea (CAS207977)	DQ120218/DQ120389		E1708.12
<i>H. haitianus</i>	91	Matanzas, Matanzas province, Cuba	DQ120217/DQ120388		HhaitiS
<i>H. haitianus</i>	92	Matanzas, Matanzas province, Cuba	DQ120216/DQ120387		HhaitiL
<i>H. modestus</i>	93	Kijido District, Rift Valley Province, Kenya (CAS198934)	DQ120215/DQ120386		E1109.7
<i>H. foudaii</i>	94	Gebel Elba, Egypt	DQ120214/DQ120385		E612.22
<i>H. citernii</i>	95	Somalia (CAS227535)	DQ120213/DQ120384		E7014.2
<i>H. citernii</i>	96	Somalia (CAS227534)	DQ120212/DQ120383		E7014.1
<i>H. pumilio</i>	97	Firmihin, Haghier, Socotra island, Yemen	DQ120211/DQ120382		E912.7
<i>H. granti</i>	98	Firmihin, Haghier, Socotra island, Yemen	DQ120210/DQ120381		E912.4
<i>H. dracaenaculus</i>	99	Diksam, Socotra island, Yemen	DQ120209/DQ120380		E912.1
<i>H. macropholis</i>	100	11 km SE of Bosasso, Bari Region, Somalia (CAS227511)	DQ120208/DQ120379		E7014.10
<i>H. yerburii</i>	101	Najran, Saudi Arabia	DQ120207/DQ120378		E1109.12
<i>H. mabouia</i>	102	Lake Nabugabo, Masaka District, Uganda (CAS202428)	DQ120206/DQ120377		E609.20
<i>H. mabouia</i>	103	Watamu, Kilifi District, Kenya (CAS186501)	DQ120205/DQ120376		E609.14
<i>H. mabouia</i>	104	Praia da Pipa, Rio Grande do Norte, Brazil	DQ120204/DQ120375		E609.9
<i>H. mabouia</i>	105	Península de Jobos, Puerto Rico (CAS200755)	DQ120203/DQ120374		E1109.1
<i>H. mabouia</i>	106	Península de Jobos, Puerto Rico (CAS200754)	DQ120202/DQ120373		E609.24
<i>H. mabouia</i>	107	Cocoa Beach, Trinidad	DQ120201/DQ120372		E609.19
<i>H. mabouia</i>	108	Cocoa Beach, Trinidad	DQ120200/DQ120371		E609.18
<i>H. mabouia</i>	109	Exu, Pernambuco, Brazil	DQ120199/DQ120370		E609.13
<i>H. mabouia</i>	110	Praia da Pipa, Rio Grande do Norte, Brazil	DQ120198/DQ120369		E609.8
<i>H. mabouia</i>	111	Genipabu, Rio Grande do Norte, Brazil	DQ120197/DQ120368		E609.6
<i>H. mabouia</i>	112	Pocone, Mato Grosso, Brazil	DQ120196/DQ120367		E609.4
<i>H. mabouia</i>	113	Pocone, Mato Grosso, Brazil	DQ120195/DQ120366		E609.3
<i>H. mabouia</i>	114	Pocone, Mato Grosso, Brazil	DQ120194/DQ120365		E609.2
<i>H. mabouia</i>	115	Chapada dos Guimarães, Mato Grosso, Brazil	DQ120193/DQ120364		E609.1
<i>H. mabouia</i>	116	Iguazu, Argentina	DQ120192/DQ120363		E509.22
<i>H. mabouia</i>	117	Pigeon Point, Tobago	DQ120191/DQ120362		E1109.9
<i>H. mabouia</i>	118	Pigeon Point, Tobago	DQ120190/DQ120361		E1109.8
<i>H. mabouia</i>	119	Coast Prov. Kilifi District, Kenya (CAS186500)	DQ120189/DQ120360		E509.21
<i>H. mabouia</i>	120	Vila dos Remédios, Fernando de Noronha, Brazil	DQ120188/DQ120359		E609.12
<i>H. mabouia</i>	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.		Specimen code
			cytb	12S	
<i>H. mabouia</i>	122	São Vicente, Cape Verde islands, Cape Verde	DQ120186/DQ120357		32HbouSV
<i>H. mabouia</i>	123	São Vicente, Cape Verde islands, Cape Verde	DQ120185/DQ120356		31HbouSV
<i>H. mabouia</i>	124	Monroe Co. Florida, USA (CAS174850)	DQ120184/DQ120355		E609.23
<i>H. mabouia</i>	125	Monroe Co. Florida, USA (CAS174849)	DQ120183/DQ120354		E609.22
<i>H. mabouia</i>	126	Rukungiri District, Uganda (CAS201744)	DQ120182/DQ120353		E609.21
<i>H. mabouia</i>	127	Vila dos Remedios, Fernando de Noronha, Brazil	DQ120180/DQ120351		E609.11
<i>H. mabouia</i>	128	Genipabu, Brazil	DQ120179/DQ120350		E609.7
<i>H. mabouia</i>	129	Genipabu, Brazil	DQ120178/DQ120349		E609.5
<i>H. mabouia</i>	130	Malabo, Bioko island, Equatorial Guinea (CAS207978)	DQ120177/DQ120348		E1708.13
<i>H. mabouia</i>	131	Vila dos Remedios, Fernando de Noronha, Brazil	DQ120188/DQ120359		E609.10
<i>H. robustus</i>	132	Safaga, Egypt	DQ120176/DQ120347		E612.20
<i>H. robustus</i>	133	Abu Dhabi, United Arab Emirates	DQ120175/DQ120346		E1008.17
<i>H. robustus</i>	134	Jebel Dhanna, near Ruweis, Abu Dhabi, United Arab Emirates	AF184989/AF186117		Hturc2
<i>H. robustus</i>	135	Jebel Dhanna, near Ruweis, Abu Dhabi, United Arab Emirates	DQ120174/DQ120345		E1008.16
<i>H. oxyrhinus</i>	136	Abd al Kuri island, Socotra archipelago, Yemen	DQ120173/DQ120344		E912.6
<i>H. macropholis</i>	137	11 km NW of Bargal, Bari Region, Somalia (CAS227519)	DQ120172/DQ120343		E7014.11
<i>H. homoeolepis</i>	138	Firmihin, Haghier, Socotra island, Yemen	DQ120171/DQ120342		E912.5
<i>H. homoeolepis</i>	139	Socotra island, Yemen	DQ120170/DQ120341		E509.17
<i>H. homoeolepis</i>	140	Socotra island, Yemen	DQ120169/DQ120340		24Hhomo
<i>H. forbesii</i>	141	Abd al Kuri island, Socotra archipelago, Yemen	DQ120168/DQ120339		E912.3
<i>H. persicus</i>	142	4.5 km N. of Tanuf, Wilayat Nizwa, Oman (CAS227614)	DQ120167/DQ120338		E7014.13
<i>H. persicus</i>	143	4.5 km N. of Tanuf, Wilayat Nizwa, Oman (CAS227612)	DQ120166/DQ120337		E7014.12
<i>H. turcicus</i>	144	Dair al Khaf, Jordan (voucher in National Museum, Prague)	DQ120165/DQ120336		E28104.10
<i>lavadeserticus</i>					
<i>H. turcicus turcicus</i>	145	Wadi al Burbeyath, Jordan (voucher in National Museum, Prague)	DQ120164/DQ120335		E28104.8
<i>H. turcicus turcicus</i>	146	Erzin, Turkey	DQ120163/DQ120334		E2505.2
<i>H. turcicus turcicus</i>	147	Andalucía, Spain	DQ120162/DQ120333		E1008.13
<i>H. turcicus turcicus</i>	148	Islet of Marathi, near Patmos, North Dodekanese, Greece	DQ120161/DQ120332		E1008.9
<i>H. turcicus turcicus</i>	149	Iraklio, Crete, Greece	DQ120160/DQ120331		E1008.8
<i>H. turcicus turcicus</i>	150	Crete, Greece	DQ120159/DQ120330		E612.23
<i>H. turcicus turcicus</i>	151	Kos island, Greece	DQ120158/DQ120329		E1008.6
<i>H. turcicus turcicus</i>	152	Near Gafsa, Tunisia	DQ120157/DQ120328		E2505.18
<i>H. turcicus turcicus</i>	153	Menorca, Balearic islands, Spain	DQ120156/DQ120327		E1008.15
<i>H. turcicus turcicus</i>	154	Chergui island, Kerkenah, Tunisia	DQ120155/DQ120326		E2505.22
<i>H. turcicus turcicus</i>	155	Chergui island, Kerkenah, Tunisia	DQ120154/DQ120325		E2505.21
<i>H. turcicus turcicus</i>	156	Chergui island, Kerkenah, Tunisia	DQ120153/DQ120324		E2505.20
<i>H. turcicus turcicus</i>	157	Chergui island, Kerkenah, Tunisia	DQ120152/DQ120323		E2505.19
<i>H. turcicus turcicus</i>	158	5 km south of Le Kef, Tunisia	DQ120151/DQ120322		E2505.17
<i>H. turcicus turcicus</i>	159	Obejo, Cordoba, Spain	DQ120150/DQ120321		E2505.6
<i>H. turcicus turcicus</i>	160	El Alquian, Almeria, Spain	DQ120149/DQ120320		E2505.4
<i>H. turcicus turcicus</i>	161	Cuevas de Almanzora, Almeria, Spain	DQ120148/DQ120319		E612.29
<i>H. turcicus turcicus</i>	162	Castillejos, Morocco	DQ120147/DQ120318		E612.26
<i>H. turcicus turcicus</i>	163	Castillejos, Morocco	DQ120146/DQ120317		E612.25
<i>H. turcicus turcicus</i>	164	South of Jendouba, Tunisia	DQ120145/DQ120316		E2505.12
<i>H. turcicus turcicus</i>	165	Qariat Arkmane, Morocco	DQ120144/DQ120315		E2505.16
<i>H. turcicus turcicus</i>	166	Qariat Arkmane, Morocco	DQ120143/DQ120314		E2505.15
<i>H. turcicus turcicus</i>	167	Barcelona city, Spain	DQ120142/DQ120313		E612.27
<i>H. turcicus turcicus</i>	168	Qariat Arkmane, Morocco	DQ120141/DQ120312		E2505.14
<i>H. turcicus turcicus</i>	169	Torregorda, Cadiz (Spain)	DQ120140/DQ120311		E1008.14
<i>H. turcicus turcicus</i>	170	Kato Gatzea, near Volos, Greece	DQ120139/DQ120310		E1008.3
<i>H. turcicus turcicus</i>	171	Erzin, Turkey	DQ120138/DQ120309		E2505.1
<i>H. turcicus turcicus</i>	172	Carmona, Sevilla, Spain	DQ120137/DQ120308		E2505.5
<i>H. turcicus turcicus</i>	173	Valdeinferno, Cordoba, Spain	DQ120136/DQ120307		E2505.8
<i>H. turcicus turcicus</i>	174	Junqueira, Portugal	DQ120135/DQ120306		E2505.9
<i>H. turcicus turcicus</i>	175	Zaframagon, Cadiz, Spain	DQ120134/DQ120305		E2505.11
<i>H. turcicus turcicus</i>	176	Gran Canaria, Canary islands, Spain	AF364319/AF363568		HturcGC
<i>H. turcicus turcicus</i>	177	Baton Rouge, Louisiana, USA (CAS175646)	DQ120133/DQ120304		E1008.20
<i>H. turcicus turcicus</i>	178	Dade Co., Florida, USA	DQ120132/DQ120303		E1008.19
<i>H. turcicus turcicus</i>	179	El Garrobo, Ayo de la Torre, Spain	DQ120131/DQ120302		E1008.12
<i>H. turcicus turcicus</i>	180	Kato Gatzea, near Volos, Greece	DQ120130/DQ120301		E1008.4
<i>H. turcicus turcicus</i>	181	Kato Gatzea, near Volos, Greece	DQ120129/DQ120300		E1008.2
<i>H. turcicus turcicus</i>	182	Las Palmas de Gran Canaria, Gran Canaria, Canary islands, Spain	DQ120128/DQ120299		E612.28
<i>H. turcicus turcicus</i>	183	Zaranikh reserve, North Sinai, Egypt	DQ120127/DQ120298		E612.21

Specimen codes identify individuals on the phylogeny shown in Fig. 1. BEV—Laboratoire de Biogéographie et Ecologie des Vertébrés, Université 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 calibra-

tion 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).

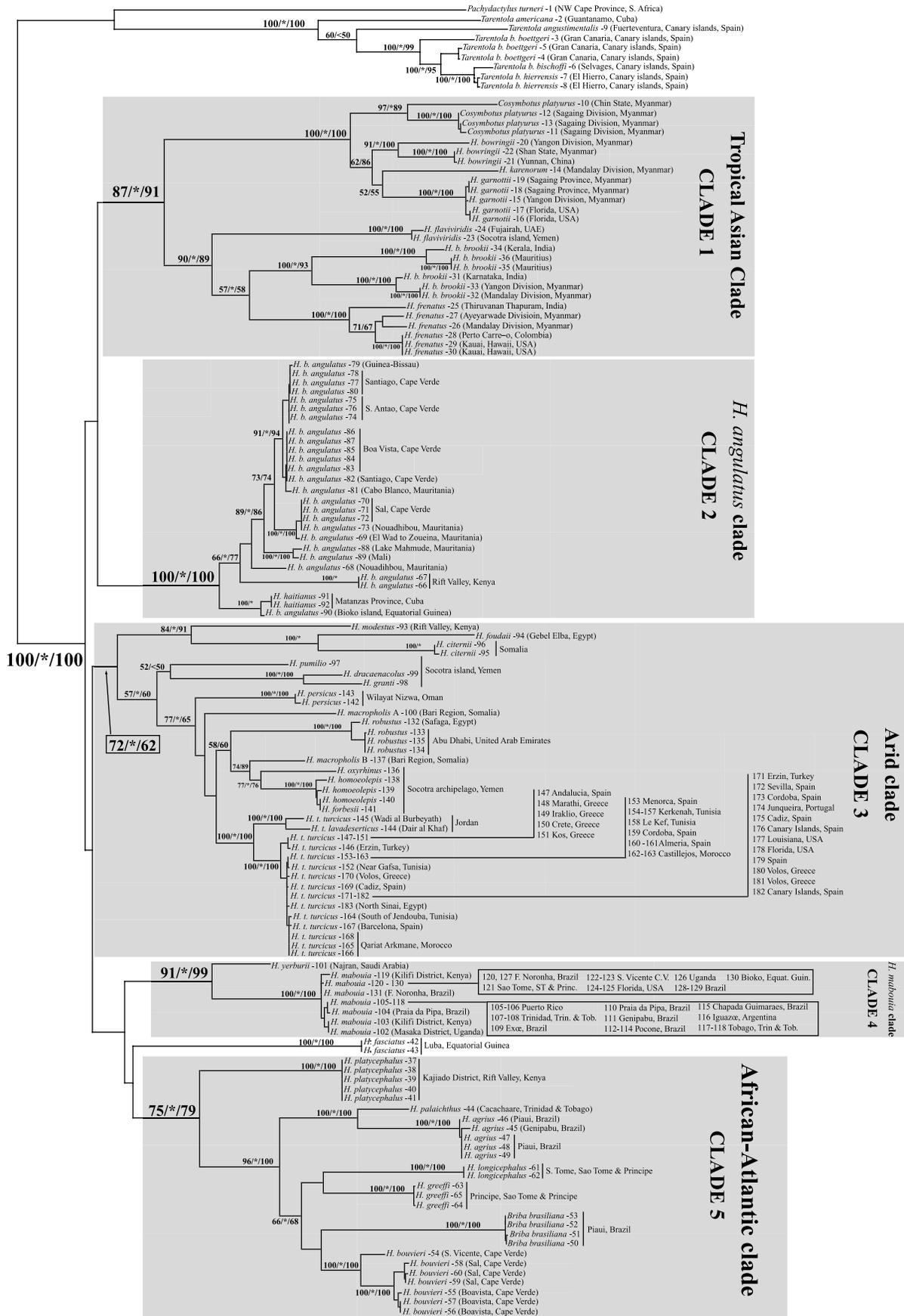
3. Results

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. bowringii*, *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 parthenogenetic species, shows only 0.8% differentiation among specimens from the Sagaing and Yangan 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.



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-

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 brasiliensis*, *H. agrius*, and *H. pal-aichthus*). 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. pal-aichthus* 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 brasiliensis* becomes *Hemidactylus brasiliensis* **comb. nov.**, while *Cosymbotus platyurus* 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. bavazonoi*, *H. barbouri*, *H. barodanus*, *H. curlei*, *H. funaeolii*, *H. isolepis*, *H. jubensis*, *H. klauberi*, *H. laevis*, *H. laticaudatus*, *H. lemuringus*, *H. matschiei*, *H. megalops*, *H. mindiae*, *H. ophiolepis*, *H. ophiolepidoides*, *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 than 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 north-east 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. bowieri* (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 *Hemi-*

dactylus 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. bowieri* (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. brasiliensis*. 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. brasiliensis* 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. brasiliensis* 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 brasiliensis* and *H. agri-*

us) 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 archipelago 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. homoeolepis* 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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