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journal homepage: www.elsevier.com/locate/ympevSouth Asia supports a major endemic radiation of *Hemidactylus* geckosAaron M. Bauer^{a,*}, Todd R. Jackman^a, Eli Greenbaum^{a,d}, Varad B. Giri^b, Ansem de Silva^c^a Department of Biology, Villanova University, 800 Lancaster Avenue, Villanova, PA 19085, USA^b Herpetology Section, Collection Department, Bombay Natural History Society, Hornbill House, S.B. Singh Road, Mumbai 400 023, India^c 15/1 Dolosbage Road, Gampola, Sri Lanka^d Department of Biological Sciences, University of Texas at El Paso, 500 West University Avenue, El Paso, TX 79968, USA

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ABSTRACT

Hemidactylus geckos are a species-rich component of many tropical lizard assemblages. We sampled deeply among tropical Asian, and especially South Asian, taxa and used a multi-gene approach to establish the affinities of Indian and Sri Lankan *Hemidactylus* and to evaluate the monophyly of previously proposed taxa within the genus. There is only weak support for the monophyly of tropical Asian *Hemidactylus* as a whole, but two strongly supported subclades were retrieved: the *bowringii* group is a predominantly East Asian clade that reaches South Asia only peripherally; the *brookii* group is a morphologically diverse clade that represents a previously unrecognized, species-rich (25 species), chiefly South Asian radiation. Deep genetic divergences support the specific recognition of three Sri Lankan taxa previously regarded as subspecies of mainland forms and validate *H. subtriedrus* as a species distinct from *H. triedrus*. Unlike several other vertebrate groups, Sri Lankan *Hemidactylus* do not represent a single insular radiation. Rather, each of six Sri Lankan species reached the island independently from different continental sources. There have been extensive Quaternary land connections between India and Sri Lanka but sister-species pairs of *Hemidactylus* on the two land masses diverged from one another much earlier, probably in the mid-Miocene.

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1. Introduction

Hemidactylus is one of the most species-rich gekkonid lizard groups, with at least 90 species currently considered valid (Carranza and Arnold, 2006; Giri and Bauer, 2008). Members of the genus occur throughout the tropics and subtropics of Asia, Africa, and the Pacific as well as in Mediterranean Europe, and northern South America. Likewise, they have become widely established elsewhere through anthropogenic means (Kluge, 1969; Vences et al., 2004; Kraus, 2009). *Hemidactylus* was considered by Kluge (1967) as an expanding dominant group of geckos, and indeed *H. garnotii*, *H. frenatus*, *H. turcicus*, and *H. mabouia* are among the most widely distributed of all gekkonids and have been implicated in the competitive exclusion of native, or other introduced, geckos in areas of the world to which they have been introduced (Petren et al., 1993; Case et al., 1994; Petren and Case, 1996).

The wide distribution of these *Hemidactylus* spp., however, masks the fact that most species in the genus have highly restricted ranges. This is most evident in the Horn of Africa and adjacent parts of East Africa where a minimum of 40 species have been

recorded (Sindaco et al., 2007). The second most diverse area of the world for *Hemidactylus* is South Asia, particularly India and Sri Lanka. Smith (1935) included 14 species in his enumeration of the fauna of British India. Since then several additional taxa have been described from the region (Deraniyagala, 1953; Grandison and So-man, 1963; Sharma, 1981; Shukla, 1983; Giri and Bauer, 2008; Giri, 2008; Giri et al., 2009; Mahony, 2009), the genera *Teratolepis*, *Cosymbotus*, *Davidogecko*, and *Lophopholis* have been synonymized with *Hemidactylus* (Loveridge, 1947; Bauer and Russell, 1995; Carranza and Arnold, 2006; Zug et al., 2007; Bauer et al., 2008), *H. parvimaculatus* has been raised to specific status (Bauer et al., in press), and *H. persicus* has been recorded for the first time from the Republic of India (Vyas et al., 2006). On the other hand the occurrence of *H. karenorum* in India has been questioned (Zug et al., 2007; Mahony and Zug, 2008) as has the validity of *H. subtriedrus* and *H. mahendrai* (Smith, 1935; Zug et al., 2007). Nonetheless, the South Asian *Hemidactylus* fauna includes approximately 30 species (Table 1).

Carranza and Arnold (2006) recently used data from the cytochrome *b* and 12S rRNA mitochondrial genes to erect a hypothesis of relationships among representative geckos of the genus *Hemidactylus*. These authors identified five major clades within the genus *Hemidactylus* and demonstrated that the genera *Cosymbotus* (two species, tropical Asia) and *Briba* (monotypic, Brazil) were embedded within *Hemidactylus*. In their analysis each clade was

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Table 1
Distribution and previous and current allocation of described species of South Asian *Hemidactylus* to clades and species groups within the genus. Parenthetical listings indicate implied placement of taxa that have undergone recent taxonomic revision and associated name changes. Dashes indicate that these taxa were not sampled or allocated. Asterisks (*) indicate allocation of unsampled taxa based on inferred relationships to species sampled in this study. South Asia is here defined as including India, Pakistan, Bangladesh; Sri Lanka, Nepal, Bhutan, and the Maldive Islands.

Species	Distribution in South Asia [and elsewhere]	Carranza and Arnold (2006)	Zug et al. (2007)	This study
<i>H. aaronbaueri</i>	ENDEMIC: India, Maharashtra	—	—	<i>brookii</i> group*
<i>H. albofasciatus</i>	ENDEMIC: India, Maharashtra	—	—	<i>brookii</i> group*
<i>H. anamallensis</i>	ENDEMIC: India, Tamil Nadu	—	<i>bowringii</i> group	<i>brookii</i> group
<i>H. aquilonius</i>	Nepal; Eastern India; Bangladesh [Myanmar; China]	(Tropical Asian clade)	(<i>bowringii</i> group)	<i>bowringii</i> group
<i>H. brookii</i>	India; Pakistan; Nepal; Bangladesh; Bhutan; [Myanmar; Southeast Asia; Indonesia; southern China]	Tropical Asian clade	<i>brookii</i> group	<i>brookii</i> group
<i>H. depressus</i>	ENDEMIC: Sri Lanka	—	<i>bowringii</i> group	<i>brookii</i> group
<i>H. flaviviridis</i>	Pakistan; Northern India; Nepal; Bangladesh; [Northeastern Africa; Middle East]	Tropical Asian clade	<i>bowringii</i> group	<i>bowringii</i> group
<i>H. frenatus</i>	India; Sri Lanka; Pakistan; Bangladesh; Bhutan; Maldives; [Tropical Asia; Tropical Pacific]	Tropical Asian clade	<i>bowringii</i> group	<i>bowringii</i> group
<i>H. garnotii</i>	Northeastern India; Nepal; Bhutan; Bangladesh; [Tropical East Asia, Tropical Pacific]	Tropical Asian clade	<i>bowringii</i> group	<i>bowringii</i> group
<i>H. giganteus</i>	ENDEMIC: Peninsular India	—	<i>bowringii</i> group	<i>bowringii</i> group
<i>H. gracilis</i>	ENDEMIC: Peninsular India	—	—	<i>bowringii</i> group*
<i>H. gujaratensis</i>	ENDEMIC: India, Gujarat	—	—	<i>bowringii</i> group*
<i>H. hunae</i>	ENDEMIC: Sri Lanka; south India?	—	(<i>bowringii</i> group)	<i>bowringii</i> group
<i>H. imbricatus</i>	ENDEMIC: Pakistan	—	—	<i>bowringii</i> group
<i>H. karenorum</i>	Bangladesh?; India, Assam?; [Myanmar]	Tropical Asian clade	<i>bowringii</i> group	<i>bowringii</i> group
<i>H. lankae</i>	ENDEMIC: Sri Lanka	—	(<i>bowringii</i> group)	<i>bowringii</i> group
<i>H. leschenaultii</i>	Pakistan; India; Sri Lanka; [Oman]	—	<i>bowringii</i> group	<i>bowringii</i> group
<i>H. maculatus</i>	ENDEMIC: Peninsular India	—	<i>bowringii</i> group	<i>bowringii</i> group*
<i>H. mahendrai</i>	ENDEMIC: India, Uttar Pradesh	—	syn. <i>H. brookii</i>	<i>bowringii</i> group (validity unconfirmed)
<i>H. parvimaculatus</i>	ENDEMIC: Sri Lanka; India, Tamil Nadu; [introduced in Mascarene Islands, Seychelles]	(Tropical Asian clade)	(<i>bowringii</i> group)	<i>bowringii</i> group
<i>H. persicus</i>	Pakistan; India, Gujarat; [Middle East]	Arid clade	—	Arid clade
<i>H. platyurus</i>	Nepal; India; Bangladesh; Bhutan; Sri Lanka?; [Southeast Asia, Indoaustralian Archipelago]	Tropical Asian clade	<i>bowringii</i> group	<i>bowringii</i> group
<i>H. porbandarensis</i>	ENDEMIC: India, Gujarat	—	<i>brookii</i> group?	<i>bowringii</i> group*
<i>H. prashadi</i>	ENDEMIC: Peninsular India	—	<i>bowringii</i> group	<i>bowringii</i> group
<i>H. reticulatus</i>	ENDEMIC: Peninsular India	—	<i>bowringii</i> group	<i>bowringii</i> group
<i>H. robustus</i>	Pakistan (probably introduced); [Northeastern Africa; Arabia; Middle East]	Arid clade	—	Arid clade
<i>H. satarensensis</i>	ENDEMIC: India, Maharashtra	—	—	<i>bowringii</i> group*
<i>H. scabriceps</i>	ENDEMIC: Sri Lanka; India, Tamil Nadu	—	—	<i>bowringii</i> group*
<i>H. subtriedrus</i>	ENDEMIC: Peninsular India	—	syn. <i>H. triedrus</i>	<i>bowringii</i> group*
<i>H. treutleri</i>	ENDEMIC: India, Andhra Pradesh	—	—	<i>bowringii</i> group*
<i>H. triedruso</i>	ENDEMIC: India; Pakistan	—	<i>bowringii</i> group	<i>bowringii</i> group
<i>H. turcicus</i>	Pakistan?; [Mediterranean Basin]	Arid clade	—	Arid clade

moderately—to well-supported, but there was no support for the interrelationships of these groups. The groups they identified included two with few included taxa—the *H. angulatus* clade and *H. mabouia* clade, and three more-or-less geographically circumscribed, more species-rich clades—the African-Atlantic clade (comprising Neotropical, Macaronesian, and central and southern African taxa exclusive of those in the *H. angulatus* and *H. mabouia* groups), the Arid clade (comprising North and Northeastern African, Mediterranean, and Middle Eastern species), and the Tropical Asian clade (South and Southeast Asian/Pacific species).

Carranza and Arnold's (2006) taxon sampling was geographically broad, but far from complete (32 of ~90 species). Among the Asian taxa occurring east of Iran they included all three chiefly Middle Eastern/Mediterranean species—*H. turcicus*, *H. persicus*, and *H. robustus*. However, with respect to chiefly tropical Asian forms, they sampled only seven species of the more than 30 occurring east of the Indus River (Zug et al., 2007; Bauer et al., 2008)—*H.* (formerly *Cosymbotus*) *platyurus*, *H. bowringii*, *H. garnotii*, *H. frenatus*, *H. flaviviridis*, *H. karenorum*, and *H. brookii*. All of these, with the possible exception of *H. karenorum* (see Mahony and Zug, 2008), occur in India, although all have extensive non-Indian Asian distributions. Thus, none of the many species of geckos endemic to India

and Sri Lanka were sampled and their position within the genus remains uncertain.

The tropical Asian taxa sampled by Carranza and Arnold (2006) fell into two well-supported subclades named by Zug et al. (2007) as the *bowringii* complex ("*H. bowringii*" [= *H. aquilonius* and *H. thaynei*], *H. garnotii*, *H. karenorum*, *H. platyurus*) and the *brookii* complex (*H. brookii*, *H. frenatus*, *H. flaviviridis*). Zug et al. (2007) questioned whether these clades encompassed all of the additional species that Carranza and Arnold did not sample and if synapomorphies existed that might be used to assign previously unsampled taxa to the appropriate clade. Based on trunk scalation, tail ornamentation, subdigital lamellae, and preloacal-femoral pores, they tentatively allocated *H. anamallensis*, *H.* (formerly *Cosymbotus*) *craspedotus*, *H. depressus*, *H. giganteus*, and *H. leschenaultii* to the *bowringii* complex and *H. maculatus*, *H. prashadi*, *H. reticulatus*, and *H. triedrus* to the *brookii* complex. Additional species of *Hemidactylus* were not evaluated by Zug et al. (2007), although subsequently described and resurrected species formerly included in *H. bowringii* (*H. aquilonius*, *H. berdmorei*, *H. thaynei*; McMahan and Zug, 2007) may be assumed to be allocated to the former complex.

The goal of our study was to incorporate the endemic South Asian *Hemidactylus* into the existing framework of *Hemidactylus*

phylogeny, to use molecular data to test Zug et al.'s (2007) tentative allocation of South Asian species to the morphologically defined *H. bowringii* and *H. brookii* groups, and to evaluate the robustness of Carranza and Arnold's Tropical Asian clade to the addition of South Asian species. We also wanted to determine if South Asian *Hemidactylus* constituted a monophyletic group and if there is evidence for a Sri Lankan subclade within a South Asian radiation.

2. Materials and methods

2.1. Sampling

Han et al. (2004) and Feng et al. (2007) demonstrated that *Hemidactylus* shares a 21-bp deletion in the nuclear gene *c-mos* with the genera *Agamura*, *Crossobamon*, *Cyrtodactylus*, and *Geckoella*. Based on this, and on preliminary results from a broad-scale phylogenetic analysis of all gekkotan genera (Bauer, Jackman, and Greenbaum, unpublished) that identifies *Cyrtodactylus* as the sister-group of *Hemidactylus*, we used *Cyrtodactylus ayeyawardensis* from Myanmar, *C. consobrinus* from Peninsular Malaysia, and *C. loriae* from Papua New Guinea as outgroups for our analyses.

Our ingroup included representatives of the major clades of *Hemidactylus* identified by Carranza and Arnold (2006). Within this group we sampled representatives of Carranza and Arnold's five major clades, as well as *H. fasciatus*, which they sampled but did not include in their named clades. For South Asian taxa we included representatives of all of the species they sampled (although following McMahan and Zug, 2007, their sample of "*H. bowringii*" actually included *H. aquilonius* and *H. thayene* and ours included only the former species) as well as *H.* (formerly *Cosymbotus*) *craspedotus*, *H. imbricatus* (formerly *Teratolepis fasciata*), *H. leschenaultii*, *H. giganteus*, *H. triedrus*, *H. maculatus*, *H. prashadi*, *H. depressus*, and an undescribed species from Rajasthan. In the case of taxa with putatively endemic Sri Lankan subspecies (*H. maculatus hunae*, *H. triedrus lanake*, *H. brookii parvimaculatus* [recently elevated to specific status, Bauer et al., in press]), both the nominate Indian forms and the Sri Lankan representatives were sampled. For several additional taxa, *H. gracilis*, *H. reticulatus*, *H. albofasciatus*, *H. subtriadrus*, sequences for only a subset of the genes used in this study could be obtained (the relationships of some of these taxa to other *Hemidactylus* have been discussed by Bauer et al., 2008). South Asian species and their associated clade membership and predicted species-complex allocation based on Carranza and Arnold (2006) and Zug et al. (2007), respectively, are listed in Table 1. Data for all samples sequenced are provided in Table 2.

2.2. Molecular methods

Genomic DNA was isolated from 95% to 100% ethanol-preserved tail or liver samples with the Qiagen DNeasy tissue kit (Valencia, CA, USA). We used double-stranded PCR to amplify 3101 aligned bases of mitochondrial (*ND2*, *cyt b*) and nuclear (*RAG1*, *PDC*) gene sequence data with 12 different published primers (Macey et al., 1997; Groth and Barrowclough, 1999; Bauer et al., 2007; Greenbaum et al., 2007). As noted above, *ND2* and *RAG1* were lacking for *Hemidactylus reticulatus*; *cyt b*, *RAG1*, and *PDC* were lacking for *H. gracilis* and *Teratolepis albofasciatus*; and *RAG1*, *PDC* and the mitochondrial tRNAs were not available for *H. subtriadrus*.

Amplification of 25 μ l PCR reactions was executed on an Eppendorf Mastercycler gradient thermocycler. Amplification of genomic DNA occurred with an initial denaturation step of 95 °C for 2 min, followed by denaturation at 95 °C for 35 s, annealing at 50 °C for 35 s, and extension at 72 °C for 95 s with 4 s added to the extension per cycle for 32 cycles for mitochondrial DNA and 34 cycles for nu-

clear DNA. When necessary, annealing temperatures were adjusted to increase or to decrease specificity on a case by case basis, and products were visualized with 1.5% agarose gel electrophoresis. Target products were purified with AMPure magnetic-bead solution (Agencourt Bioscience) and sequenced with either the Big-Dye[®] Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems) or the DYEnamic[™] ET Dye Terminator Kit (GE Healthcare). Sequencing reactions were purified with CleanSeq magnetic-bead solution (Agencourt Bioscience) and analyzed with an ABI 3700 automated sequencer. The accuracy of sequences was ensured by incorporating negative controls and sequencing complementary strands.

2.3. Phylogenetic analyses

Sequences were aligned using Geneious Pro 4.6 software (Biomatters, Auckland, New Zealand) and adjusted by eye, and protein-coding genes were translated to amino acids with MacClade (Maddison and Maddison, 1992) to confirm conservation of the amino acid reading frame and to check for premature stop codons.

Phylogenetic relationships among the samples were assessed with maximum parsimony, maximum-likelihood, and Bayesian optimality criteria. Data from all four genes (*RAG1*, *PDC*, *ND2*, and *cyt b*) were combined for a single analysis including all South Asian samples, except those with significant missing data (see above), and representatives of each of the clades identified by Carranza and Arnold (2006). The approximate phylogenetic positions of *Hemidactylus albofasciatus*, *H. reticulatus*, and *H. gracilis* were estimated on the basis of data presented elsewhere (Bauer et al., 2008).

Maximum parsimony (MP) analyses were conducted in PAUP[®] 4.0b10 (Swofford, 2002). The heuristic search algorithm was used with the following conditions: 25 random-addition replicates, tree bisection-reconnection branch swapping, and gaps treated as missing data. We used nonparametric bootstraps (1000 pseudoreplicates) to assess node support in resulting topologies. The Akaike Information Criterion (AIC) in ModelTest 3.06 (Posada and Crandall, 1998) was used to find the model of evolution that best fit the data for subsequent maximum-likelihood (ML) and Bayesian-inference (BI) analyses. In the ML analysis, the GTR + Γ + I model was used in GARLI 0.951 (Zwickl, 2006) with simultaneous tree and parameter estimations.

Partitioned Bayesian analyses were conducted with MrBayes 3.1 (Ronquist and Huelsenbeck, 2003) with default priors. Separate models were estimated for each gene and codon position of protein-coding genes (Brandley et al., 2005). A total of 10 partitions were made: *RAG1*, three codons; *PDC*, three codons, *ND2* and *cyt b*, three codon positions; and mitochondrial tRNAs. Analyses were initiated with random starting trees and run for 2,000,000 generations; Markov chains were sampled every 100 generations. Convergence was checked by plotting likelihood scores against generation, and 112 trees were discarded as "burn in." Two separate analyses with two independent chains were executed to check for convergence of log likelihoods in stationarity (Huelsenbeck and Ronquist, 2001). Both analyses ended with the standard deviation of split frequencies less than 0.01 (0.002 for both). The results of the Bayesian analyses were examined using AWTY (Nylander et al., 2008) to compare split frequencies between the separate analyses, to examine the cumulative split frequencies, and to compare tree distances both within and between analyses in order to ensure that the Bayesian analyses had reached convergence.

2.4. Hypothesis testing

Maximum-likelihood Shimodaira–Hasegawa (SH) tests (Shimodaira and Hasegawa, 1999) were used in PAUP[®] 4.0b10 (Swofford, 2002) to compare hypotheses of relationships. Parameters for the

Table 2
 List of samples used in this study. Multiple samples of a species from a single country are numbered in the "Locality" column to correspond to Fig. 1. Collection abbreviations: ADS, Ansiem de Silva field series; AMB, Aaron M. Bauer field series; BNHS, Bombay Natural History Society; Mumbai; CAS, California Academy of Sciences; EBG, Eli B. Greenbaum field series; JFBM, James Ford Bell Museum, University of Minnesota, St. Paul; FK, Fred Kraus field series; FMNH, Field Museum of Natural History, Chicago; ID, Indraneil Das field series; JB, Jon Boone private collection (Tulsa); JS, Jay Sommers private collection (Kansas City); KU, University of Kansas Natural History Museum, Lawrence; LLG, L. Lee Grismer field series; LSUMZ, Louisiana State University Museum of Zoology, Baton Rouge; MVZ, Museum of Vertebrate Zoology, University of California, Berkeley; MZUSP, Museu de Zoologia da Universidade de São Paulo; TNHC, Texas Natural History Collection, Austin; WRB, William R. Branch (Port Elizabeth); YPM, Yale Peabody Museum, New Haven. ADS and AMB specimens are pending accession in the National Museum of Sri Lanka, Colombo.

Sample	Museum No.	Locality	GenBank Accession Numbers			
			cyt b	ND2	RAG1	PDC
<i>Cyrtodactylus ayeyarwadyensis</i>	CAS 216446	Myanmar: Rakhine State, vic. Kanthaya Beach	EU268380	EU268348	EU268287	EU268317
<i>Cyrtodactylus consobrinus</i>	LLG 4062	Malaysia, Sarawak, Niah Cave	EU268381	EU268349	EU268288	EU268318
<i>Cyrtodactylus lorae</i>	FK 7709	Papua New Guinea, Milne Bay Province, Bumisi, N slope of Mt. Simpson	EU268382	EU268350	EU268289	EU268319
<i>Hemidactylus angulatus</i>	EBG 746	Guinea, Daniah River at Koulele River	HM559588	HM559620	HM559686	HM559653
<i>Hemidactylus angulatus</i>	MVZ 245438	Nigeria, Togo Hills, Nkwanta	EU268399	EU268367	EU268306	EU268336
<i>Hemidactylus aquilonius</i>	CAS 206649	Myanmar, Sagaing Division, Alaungdaw Kathapa Natl. Park	EU268405	EU268373	EU268312	EU268342
<i>Hemidactylus aquilonius</i>	CAS 228109	China, Yunnan Province, Nujang District, Lituku	EU268406	EU268374	EU268313	EU268343
<i>Hemidactylus brasiliensis</i>	MZUSP 92493	Brazil, Piauí, Parque Nacional Serra das Confusões	EU268383	EU268351	EU268290	EU268320
<i>Hemidactylus brookii</i>	CAS 229632	Myanmar (1), Tanintharyi Division	GQ375295	GQ458051	GQ375313	GQ375307
<i>Hemidactylus brookii</i>	CAS 206638	Myanmar (2), Mandalay Division	EU268407	GQ458054	EU268314	EU268344
<i>Hemidactylus brookii</i>	CAS 208159	Myanmar (3), Yangon	GQ375294	GQ458052	GQ375312	GQ375306
<i>Hemidactylus brookii</i>	LLG 6755	Malaysia (1), Pulau Pinang, Empangon Air Hitam	EU268398	EU268366	EU268305	EU268334
<i>Hemidactylus brookii</i>	LLG 6754	Malaysia(2), Pulau Pinang, Empangon Air Hitam	EU268397	EU268365	EU268304	EU268334
<i>Hemidactylus craspedotus</i>	LLG 5613	Malaysia (1), Pulau Pinang, Empangon Air Hitam	HM559586	HM559618	HM559684	HM559651
<i>Hemidactylus depressus</i>	AMB 7481	Sri Lanka (1), Matale	HM559593	HM559625	HM559691	HM559658
<i>Hemidactylus depressus</i>	AMB 7440	Sri Lanka (2), Dumbulaya	HM559591	HM559623	HM559689	HM559656
<i>Hemidactylus depressus</i>	AMB 7445	Sri Lanka (3), Ritigala	HM559592	HM559624	HM559690	HM559657
<i>Hemidactylus depressus</i>	AMB 7524	Sri Lanka (4), Galle	HM559594	HM559626	HM559692	HM559659
<i>Hemidactylus depressus</i>	ADS 69A	Sri Lanka (5), Kuruwelotha	HM559590	HM559622	HM559688	HM559655
<i>Hemidactylus depressus</i>	ADS 29A	Sri Lanka (6), Galkotte	HM559589	HM559621	HM559687	HM559654
<i>Hemidactylus fasciatus</i>	CAS 207777	Equatorial Guinea, Bioko Island, 3.6 km N of Luba	EU268403	EU268371	EU268310	EU268340
<i>Hemidactylus fasciatus</i>	WRB no number	Gabon, Rabi	EU268402	EU268370	EU268309	EU268339
<i>Hemidactylus flaviviridis</i>	CAS 228540	United Arab Emirates, Dubai	HM559595	HM559627	HM559693	HM559660
<i>Hemidactylus flaviviridis</i>	FMNH 245515	Pakistan, Punjab Province	EU268387	EU268355	EU268294	EU268324
<i>Hemidactylus flaviviridis</i>	ID 7626	India (1), Rajasthan, Kuldihara	EU268388	EU268356	EU268295	EU268325
<i>Hemidactylus flaviviridis</i>	ID 7640	India (2), Rajasthan, Jaisalmer	HM559596	HM559628	HM559694	HM559661
<i>Hemidactylus frenatus</i>	AMB 7420	Sri Lanka (1), Rathegala	EU268391	EU268359	EU268298	EU268328
<i>Hemidactylus frenatus</i>	AMB 7411	Sri Lanka (2), Pidipitiya	EU268389	EU268357	EU268296	EU268326
<i>Hemidactylus frenatus</i>	LLG 6745	Malaysia (1), Pulau Pinang, Empangon Air Hitam	EU268390	EU268358	EU268297	EU268327
<i>Hemidactylus frenatus</i>	LLG 4871	Malaysia (2), Pahang, Bukit Bakong	GQ375289	GQ458049	GQ375308	GQ375301
<i>Hemidactylus frenatus</i>	TNHC 62814	Philippines, Luzon Id., Albay Prov., Mt. Malinao	—	HM559630	HM559696	HM559663
<i>Hemidactylus frenatus</i>	CAS 229633	Myanmar, Tanintharyi Div., Kaw Thauing Dist.	—	HM559629	HM559695	HM559662
<i>Hemidactylus garnotii</i>	CAS 223286	Myanmar (1), Rakhine State, Taung Gok Township, Ma Ei Ywa Ma Village	EU268395	EU268363	EU268302	EU268332
<i>Hemidactylus garnotii</i>	CAS 215549	Myanmar (2), Sagaing Div., Mon Ywa Dist.	HM559597	HM559631	HM559697	HM559664
<i>Hemidactylus garnotii</i>	CAS 222276	Myanmar (3), Mon State, Kyaihto Township, Kyait Hti Yo Wildlife Sactuary	EU268396	EU268364	EU268303	EU268333
<i>Hemidactylus giganteus</i>	JB 03	India (captive specimen)	HM559598	HM559632	HM559698	HM559665
<i>Hemidactylus gracilis</i>	BNHS 1592	India, Maharashtra, Pune	—	EU268379	—	—
<i>Hemidactylus greffi</i>	CAS 219044	São Tome and Principe, São Tome Island, Praia da Mutamba	EU268401	EU268369	EU268308	EU268338
<i>Hemidactylus haitianus</i>	AMB 4189	Dominican Republic (1), Santo Domingo	HM559600	HM559634	HM559700	HM559667
<i>Hemidactylus haitianus</i>	AMB 4188	Dominican Republic (2), Santo Domingo	HM559599	HM559633	HM559699	HM559666
<i>Hemidactylus hunae</i>	AMB 7416	Sri Lanka, Pitakumbura	HM559606	HM559640	HM559706	HM559673
<i>Hemidactylus imbricatus</i>	JFBM 2	Pakistan (1; captive specimen)	EU268386	EU268354	EU268293	EU268323
<i>Hemidactylus imbricatus</i>	JS 11	Pakistan (2; captive specimen)	EU268385	EU268353	EU268292	EU268322
<i>Hemidactylus karenorum</i>	CAS 210670	Myanmar, Mandalay Division, Kyaukpadaung Township, Popa Mt. Park	EU268394	EU268362	EU268301	EU268331
<i>Hemidactylus lamkae</i>	AMB 7453	Sri Lanka, nr. Medavachchiya	HM559615	HM559648	HM559714	HM559681
<i>Hemidactylus leschenaultii</i>	AMB 7443	Sri Lanka, Polonnaruwa	HM559601	HM559635	HM559701	HM559668
<i>Hemidactylus leschenaultii</i>	JB 05	India (captive specimen)	HM559602	HM559636	HM559702	HM559669
<i>Hemidactylus longicephalus</i>	CAS 218939	São Tomé et Principe, São Tomé	HM559603	HM559637	HM559703	HM559670
<i>Hemidactylus mabouia</i>	AMB 8301	South Africa, Limpopo Prov., nr. Huntleigh	HM559604	HM559638	HM559704	HM559671

<i>Hemidactylus mabouia</i>	YPM 14798	USA, Florida, Monroe Co., Little Torch Key	HM559639	HM559705	HM559672
<i>Hemidactylus maculatus</i>	BNHS 1516	India, Maharashtra, Raigad Dist., Zirad	HM559641	HM559707	HM559674
<i>Hemidactylus palaichthus</i>	LSUMZ 12421	Brazil, Roraima State	EU268368	EU268307	EU268337
<i>Hemidactylus parvimaculatus</i>	AMB 7475	Sri Lanka (1), Kandy, 7°15'36"S, 80° 37'11"E	Q458055	Q375309	Q375302
<i>Hemidactylus parvimaculatus</i>	AMB 7466	Sri Lanka (2), Mampuri, 7°59'38"S, 79°44'33"E	Q458056	Q375311	Q375304
<i>Hemidactylus parvimaculatus</i>	ADS 36	Sri Lanka (3), Kartivu, 7°22'35.6"S, 81° 58'59.0"E	Q458053	Q375310	Q375303
<i>Hemidactylus persicus</i>	CAS 227612	Oman, Wilayat Nazwa, 4.5 km N. of Tanuf, Wadi Tanuf	EU268377	EU268316	EU268346
<i>Hemidactylus platyrus</i>	KU 304111	Philippines, Lubang Id., Occidental Mindoro Prov., Lubang Barangay Paraiso	HM559619	HM559685	HM559652
<i>Hemidactylus prashadi</i>	JB 30	India (1; captive specimen)	HM559644	HM559709	HM559676
<i>Hemidactylus prashadi</i>	JB 02	India (2; captive specimen)	HM559643	HM559708	HM559675
<i>Hemidactylus reticulatus</i>	AMB 5730	India, Tamil Nadu, Vellore	—	—	EU268347
<i>Hemidactylus robustus</i>	MVZ 234374	Iran, Lorestan Province, 99 km SW (by road) of Khorram Abah	HM559644	HM559710	HM559677
<i>Hemidactylus robustus</i>	MVZ 248437	Pakistan (1), Thatta District, 40 km S of Mipur Sakro	EU268376	EU268315	EU268345
<i>Hemidactylus robustus</i>	FMNH 245519	Pakistan (2), Baluchistan Province, Gwadar Division, Makran District	EU054287	EU054271	EU054255
<i>Hemidactylus subtriedrus</i>	JB no number	India (captive specimen)	HM627909	—	—
<i>Hemidactylus triedrus</i>	JB 08	Pakistan (captive specimen)	HM559650	HM559716	HM559683
<i>Hemidactylus triedrus</i>	JB 09	India (captive specimen)	HM559649	HM559715	HM559682
<i>Hemidactylus turcicus</i>	LSUMZ H-1981	USA, Louisiana, Baton Rouge	EU268360	EU268299	EU268329
<i>Hemidactylus sp.</i>	ID 7647	India (1), Rajasthan, Pokhran	HM559647	HM559713	HM559680
<i>Hemidactylus sp.</i>	ID 7644	India (2), Rajasthan, Pokhran	HM559645	HM559711	HM559678
<i>Hemidactylus sp.</i>	ID 7645	India (3), Rajasthan, Pokhran	HM559646	HM559712	HM559679

test were estimated using the alternative topology with a GTR + Γ + I model. The test was performed using RELL bootstrap (one tailed) and 1000 bootstrap replicates.

3. Results

Overall, of the 3101 aligned bases, 1652 were variable and of these 1357 were parsimony informative. For 1638 aligned bases of mitochondrial DNA (cyt *b* and ND2) there were 1157 variable characters (1021 parsimony informative) and of the remaining 1463 bases of aligned nuclear DNA (RAG1, PDC), 336 of 495 variable sites were parsimony informative. There were 12 equally parsimonious MP trees of length 8723 and the log likelihood of the ML tree was $\ln L$ -42430.7.

The monophyly of *Hemidactylus* as a whole is well-supported, and four of the five clades reported by Carranza and Arnold (2006) were retrieved with strong support in all analyses (posterior probability (pP) 1.0, MP and ML bootstraps 100%). The Tropical Asian clade was recovered in the Bayesian and maximum-likelihood analyses (although without bootstrap support in the latter) but not in majority-rule consensus tree generated under MP. All analyses strongly supported the *H. mabouia* group and African-Atlantic clade as sister taxa, and BI and ML analyses retrieved *H. fasciatus* as the sister taxon of this group, albeit without significant support. The *H. angulatus* clade received support as the sister-group to all other *Hemidactylus* only in the Bayesian analysis (pP = 0.98). Although less well resolved, the parsimony results are fully consistent with the Bayesian topology *angulatus/fasciatus* grouping, but all of these together formed a polytomy.

The smaller clade of Tropical Asian *Hemidactylus* includes *H. garnotii*, *H. karenorum*, and *H. aquilonius* as the sister-group to the two species formerly assigned to *Cosymbotus*, *H. platyrus*, and *H. craspedotus*. The larger Tropical Asian clade includes a strictly South Asian subclade: *H. depressus* ((*H. maculatus hunae*, *H. prashadi*) (*H. m. maculatus*, (*H. t. triedrus*, *H. t. lankae*))) and a more widely distributed subclade (((*H. flaviviridis*, *H. leschenaultii*) *H. giganteus*) (*H. frenatus* (*H. brookii* (*H. parvimaculatus*, *H. imbricatus*))))). All interspecific relationships within both Tropical Asian clades were supported by posterior probabilities of 1.0 except the sister taxon relationships between *H. prashadi* and *H. maculatus hunae* ($p = 0.96$) and between *H. parvimaculatus* and *H. imbricatus* ($p = 0.88$).

SH tests corroborated the monophyly of the *bowringii* and *brookii* groups (Fig. 1; $p < 0.01$ and $p = 0.036$, respectively), whereas the tropical Asian clade was not significantly better than the best tree in which the clade was absent ($p = 0.23$). The collective monophyly of Sri Lankan members of the *brookii* group was unambiguously rejected.

4. Discussion

4.1. Non-Asian *Hemidactylus*

Our results (Fig. 1) support each of the major clades identified by Carranza and Arnold (2006), although the tropical Asian clade is retrieved only in the Bayesian analysis and is not significantly supported by the SH test. Our data also yielded consistent support for the sister-group relationship of *H. mabouia* and the African-Atlantic clade, as was also found by Rocha et al. (2005). The position of *H. fasciatus* remains problematic, as its union with the *H. mabouia*/African-Atlantic clade does not receive strong support. *Hemidactylus fasciatus* was the only member of the West African group analyzed by Carranza and Arnold (2006), and by us, and we suspect that better taxon sampling in this group may stabilize

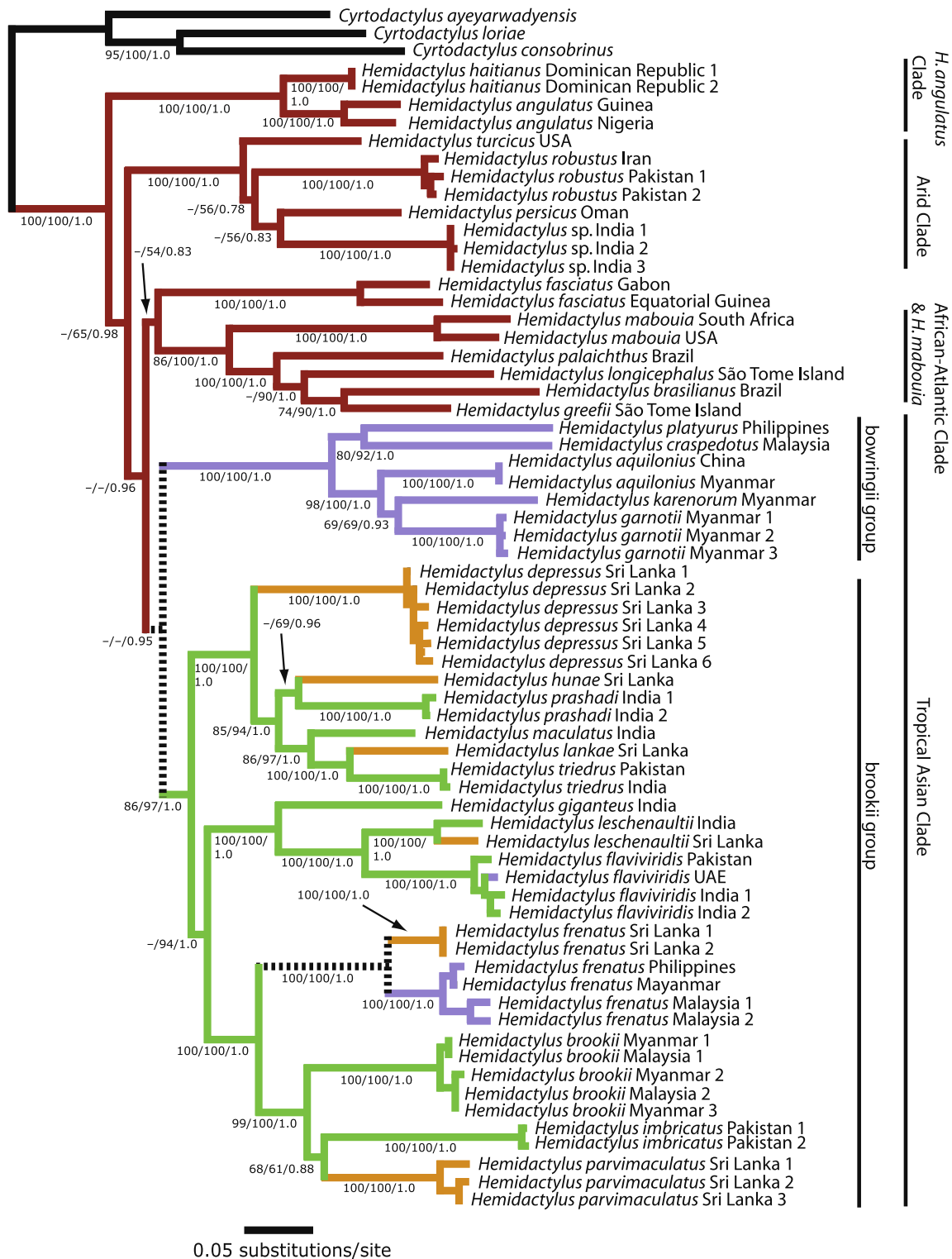


Fig. 1. Phylogeny of tropical Asian and other *Hemidactylus* geckos. Maximum-likelihood topology with parsimony bootstrap, likelihood bootstrap, and Bayesian posterior probability values indicated for each branch. Outgroup taxa indicated in black and non-tropical Asian *Hemidactylus* in red. Within the tropical Asian clade, chiefly East Asian taxa are indicated in lavender, mainland or widespread South Asian taxa in green, and Sri Lankan taxa (or samples) in orange. Basal branch colors reflect ancestral geography as reconstructed using parsimony in MacClade (Maddison and Maddison, 1992); dashed lines indicate equivocal geographic states. The *brookii* group represents a species-rich, chiefly South Asian clade which has given rise to six independent Sri Lankan lineages.

and increase support for the position of *H. fasciatus* and its presumed West African relatives.

Within the *H. angulatus* group our *H. haitianus* specimens from the Dominican Republic are identical to one from Cuba sequenced

by Carranza and Arnold (2006), a result also found by Weiss and Hedges (2007), supporting the contention that the New World colonization of this species from the Gulf of Guinea is probably from a single source area and is probably very recent, possibly in associa-

tion with the slave trade. However, the divergence (>13% uncorrected ND2) between New World and Bioko *H. haitianus* and other “*H. angulatus*” suggests the specific distinctiveness of these taxa. It is unclear if any other names in the synonymy of *H. angulatus* might also apply to the Bioko population (and thus also to New World *haitianus*), but for the time being we consider *H. haitianus* the valid name for this clade. Quite substantial differences exist also between *H. fasciatus* from Equatorial Guinea and one from Rabi, Gabon, suggesting that, like “*H. angulatus*,” this name may subsume two or more discrete biological entities, as has been proposed by Leaché and Fujita (2010).

Within the African-Atlantic clade our patterns of relationship differ slightly from those of Carranza and Arnold (2006), with *H. greefi* closest to *H.* (formerly *Briba*) *brasiliiana*, rather than *H. longicephalus*. Our additional specimens indicate substantial differentiation within *H. greefi*, *H. palaichthus*, and *H. mabouia*. The status of Indian Ocean populations within the *H. mabouia* group is convoluted and has been discussed elsewhere (Vences et al., 2004).

Patterns within the Arid clade differ slightly from Carranza and Arnold (2006), with *H. persicus* and *H. robustus* more closely related (vs. *H. turcicus* and *H. robustus*). Our new samples fall within the range of variation previously documented. However, we have added a new species from Rajasthan (description in preparation), which is more closely related to *H. persicus* than it is to other Arid clade members. This entire clade is clouded by great taxonomic confusion, and it is highly likely that many identifications in the literature are incorrect. However, as all of the other taxa occurring in Pakistan (Khan, 2006) and northwestern India (Sharma, 2002) appear elsewhere in the phylogeny, it seems that this species is truly new or, if assignable to a name in synonymy, such a name has been wrongly placed, most probably in the synonymy of *H. brookii*.

4.2. Tropical Asian clade

The two tropical Asian clades retrieved correspond to Zug et al.'s (2007) *bowringii* and *brookii* groups (Fig. 1). The *bowringii* complex is essentially an East Asian group and the affinities of its constituents have long been recognized (Boulenger, 1890). *H. karenorum* may be restricted to Myanmar (Mahony and Zug, 2008), and *H. bowringii* sensu stricto is probably restricted to southern China, eastern Indochina, Taiwan and the Ryukyus (McMahan and Zug, 2007). *H. berdmorei* occurs in extreme southern Myanmar, *H. thayene* in central Myanmar, and *H. aquilonius* in northern Myanmar and adjacent southwestern China (and presumably in Northeast India and Bangladesh). *H. garnotii* is likewise distributed chiefly in Indochina and into the tropical Pacific, whereas *H. platyurus*, widely distributed in southeast Asia, is known from South Asia from only a few doubtful records from Sri Lanka (Wickramasinghe and Somaweera, 2008). *H. craspedotus* is endemic to southeast Asia, from southern Thailand, through the Malay Peninsula to Sumatra and Borneo. Within the limits of sampling, this group is also supported by karyological data, as a $2n = 46$ karyotype is shared by *H. platyurus* and *H. bowringii*, whereas $2n = 40$ karyotype is shared by the *brookii* clade species *H. brookii*, *H. flaviviridis*, and *H. frenatus* (Das and Ota, 1998).

Our specimens of *H. garnotii* fell within the narrow range of variation reported by Carranza and Arnold (2006), and our additional *H. aquilonius* clustered with their northern Myanmar/Yunnan “*bowringii*” samples. Although Carranza and Arnold (2006) did not formally refer *Cosymbotus platyurus* to *Hemidactylus*, despite its clear placement within the tropical Asian clade, Zug et al. (2007) did take this step. As the latter authors noted, the particular relationships of *H. platyurus* to *H. craspedotus* have not been explicitly examined. Our results support the implications of previous workers (based on their inclusion of both forms in *Mimetozone*, *Platyurus*, or *Cosymbotus* to the exclusion of other *Hemidactylus*-

group species; de Rooij, 1915; Smith, 1935; Wermuth, 1965) that these two forms are sister taxa. Based on relatively deep molecular divergences between samples from Chin State and the Sagaing Division in Myanmar (Carranza and Arnold, 2006) and variation in morphology (Zug et al., 2007), taxonomic revision of *H. platyurus* may be warranted.

Carranza and Arnold's (2006) representation in the *brookii* complex was limited to three species. With our additional data it may be seen that there are three subclades within this group, one represented by *brookii*, *parvimaclatus*, and *frenatus*, as well as *H. imbricatus* and related forms (Bauer et al., 2008), one including the large, relatively smooth-bodied *H. flaviviridis*, *H. giganteus*, and *H. leschenaultii*, and one that was entirely unsampled by Carranza and Arnold (2006) and comprises exclusively peninsular Indian and Sri Lankan endemics.

Carranza and Arnold (2006) found significant differentiation between a specimen of *H. frenatus* from Thiruvananthapuram, Kerala and others from Myanmar and introduced populations from Colombia and Hawaii. Zug et al. (2007) suggested that this might warrant the reinvestigation of the validity of *H. punctatus* Jerdon, 1854 [sic]. Our samples from Sri Lanka formed a distinctive lineage closer to Myanmar and Malaysian *H. frenatus* than to the Indian sample (based on comparison on *cyt b* data only), but highly divergent nonetheless. Vences et al. (2004) found minimal divergence between Sri Lankan *frenatus* and specimens from Madagascar, the Andamans, the Comores, and the Mascarenes.

Hemidactylus parvimaclatus, formerly treated as a Sri Lankan subspecies of *H. brookii*, is deeply divergent from true *brookii*, which has a broad distribution from India (and possibly Pakistan) to parts of Indonesia (see Bauer et al., in press). In our analysis the sister-group of *H. parvimaclatus* is *H. imbricatus*, formerly *Teratolepis fasciata*. Bauer et al. (2008) identified a cluster of closely related terrestrial South Asian taxa in this group, including *H. albofasciatus*, *H. gracilis*, and *H. reticulatus*. Because of non-overlapping data sets, the pattern of relationship among these four taxa is unclear, but based on mtDNA data, they form a well-supported clade with *H. imbricatus*. Bauer et al. (2008) also suggested that *H. anamallensis* and *H. scabriceps*, neither sampled here, would prove to be allied to the *H. imbricatus* group within the *brookii* complex, chiefly on the basis of their reduced subdigital scansorial apparatus, and the recently described *H. sataransensis* is also clearly allied to this group (Giri and Bauer, 2008).

The last tropical Asian species included by Carranza and Arnold (2006) was *H. flaviviridis*, which they sampled only from the Arabian Peninsula. Our additional samples include several from Rajasthan and Pakistan, and these are only marginally divergent from the Arabian samples, consistent with the view that the distribution of this often commensal species has been influenced by human agency (Daniel, 2002). The other two species that are clearly allied to *H. flaviviridis* are *H. giganteus* and *H. leschenaultii*. *H. giganteus* is limited to peninsular India, and its sister taxon is probably a newly described species, *H. aaronbaueri*, apparently endemic to the northern Western Ghats of Maharashtra (Giri, 2008). *Hemidactylus leschenaultii* has a wide South Asian distribution and our samples, from Sri Lanka and an unknown mainland locality, differ from one another to a much lesser degree than Indian and Sri Lankan populations of *H. maculatus* and *H. triedrus*.

All remaining taxa constitute a previously unsampled clade of South Asian endemic *Hemidactylus*. These include one Indian endemic, *H. prashadi*, one Sri Lankan endemic, *H. depressus*, and two polytypic species with populations on both sides of the Palk Strait. Neither of the monotypic forms exhibited significant variation across samples, not surprisingly as the range of *H. depressus* in Sri Lanka is relatively small (Wickramasinghe and Somaweera, 2008) and the two samples of *H. prashadi* were derived from captive animals, probably ultimately from stock from a single locality.

However, there was significant divergence within the polytypic taxa, supporting the probable validity of the named Sri Lankan forms as valid species (see below).

4.3. Hypothesis testing

Although our data support distinctive East (*bowringii* group) and South (*brookii* group) clades, Zug et al.'s (2007) allocation of unsampled taxa to Carranza and Arnold's (2006) Tropical Asian subclades is not in general supported by our data. They predicted that *Hemidactylus anamallensis*, *H. craspedotus*, *H. depressus*, *H. giganteus*, and *H. leschenaultii* would be in the *bowringii* complex and that *H. maculatus*, *H. prashadi*, *H. reticulatus*, and *H. triedrus* would be in the *brookii* complex. Although *H. craspedotus* does clearly nest within the *bowringii* group, all of the other species sampled are more closely allied to *H. brookii*. *Hemidactylus anamallensis* was not included in our analysis, but based on morphological data (Bauer and Russell, 1995; Bauer et al., 2008), we strongly suspect that it too will be a member of this clade. Our likelihood SH tests allow us to redefine the *bowringii* and *brookii* groups to include those taxa shown in Fig. 1.

4.4. Taxonomic implications

Our results have several taxonomic implications for South Asian *Hemidactylus*. First, we confirm the placement of *Cosymbotus craspedotus* in *Hemidactylus*, corroborating Zug et al. (2007). Second, in the context of our expanded data set we confirm the findings of Bauer et al. (2008) that the genus *Teratolepis* is imbedded within the *brookii* complex of *Hemidactylus*. Our results also support the elevation of *H. parvimaaculatus* to specific status within the *brookii* group (Bauer et al., in press) and provide the first evidence for deep genetic divergences between mainland Indian and Sri Lankan populations of *H. maculatus* and *H. triedrus*, both of which are represented by named subspecies in Sri Lanka (Wickramasinghe and Somaweera, 2002). As a conservative estimate of divergence time, the percent difference in ND2 when scaled to the same 1463 bases as the agamid lizard *Laudakia* (Macey et al., 1998), suggests that the split between Sri Lankan and Indian *H. leschnaultii* occurred 5.8 million years ago and that between the *H. triedrus* pair was 11.6 million years ago (0.68% divergence per lineage per million years). Divergences estimated this way are likely to be conservative given that agamid lizards show a faster overall rate of mtDNA evolution than most other lizards (Kumazawa, 2007), including gekkotans (Macey et al., 1999).

Given the high levels of divergence between Indian and Sri Lankan samples of *H. maculatus* and *H. triedrus*, comparable to those between full species pairs of other *Hemidactylus* (Fig. 1), we propose the elevation of both *H. maculatus hunae* and *H. triedrus lankae* to specific status. These geckos may be diagnosed from the nominotypic *H. m. maculatus* and *H. t. triedrus*, respectively, based on morphological features noted in their original descriptions (Deraniyagala, 1937, 1953), although ongoing research (Giri and Bauer, unpublished) suggests that Indian populations included in *H. hunae* by Deraniyagala (1937), are probably referable to an undescribed species. Further, data from the ND2 gene (not figured) reveals that *Hemidactylus subtriedrus*, the validity of which had been questioned by Smith (1935) and Zug et al. (2007), is highly divergent from its sister taxon, typical *H. triedrus*, with an uncorrected sequence divergence of 12%.

4.5. Biogeography

Bauer and Russell (1995) suggested that Indian members of *Hemidactylus* might be an old radiation that could contribute to an understanding of Indian biogeography but that this would re-

quire a more thorough knowledge of the relationships of *Hemidactylus*. Our data suggest that there is indeed a major, previously unrecognized, monophyletic South Asian group of relatively great age within the genus. This roughly corresponds to Zug et al.'s (2007) *brookii* group. Within this group is a subclade of strictly South Asian endemics (*H. depressus*, *H. maculatus*, *H. hunae*, *H. prashadi*, *H. triedrus*, *H. subtriedrus*, *H. lankae*) and two other groups, each including South Asian endemics and one or more widespread taxa. A large cluster of strict endemics (*H. imbricatus*, *H. albofasciatus*, *H. reticulatus*, *H. gracilis*, *H. parvimaaculatus* and probably *H. sataraisensis*, *H. scabriceps* and *H. anamallensis*) form the sister-group to the widely distributed *H. brookii*, which appears to have expanded out of India very recently, possibly through human agency (Bauer et al., in press). Two other, apparently closely related Peninsular Indian endemics, *H. giganteus* and *H. aaronbaueri* (Giri, 2008), are members of another subclade that also includes the widely distributed taxa *H. flaviviridis* and *H. leschenaultii*. Remaining members of Carranza and Arnold's (2006) Tropical Asian clade correspond to Zug et al.'s *bowringii* group. This East Asian clade is deeply divergent from the South Asian clade and may or may not be its sister-group. Members of this group do not, or only barely, enter India from the east.

As reflected by their minimal intraspecific uncorrected ND2 divergences (<3.9%), the few widespread members of the South Asian *Hemidactylus* clade (e.g., *H. brookii*, *H. flaviviridis*) appear to have achieved their broad distributions relatively recently (Bauer et al., in press). In contrast, divergences between Indian and Sri Lankan sister taxa are deep (at least 11.6 million years old for sister-species pairs), supporting the view that much of the Sri Lankan herpetofauna consists of endemic forms, ultimately derived from India (Pethiyagoda, 2005). Although some Sri Lankan lizard genera, e.g., *Ceratophora* (Schulte et al., 2002), *Cnemaspis* (Manamendra-Arachchi et al., 2007; Wickramasinghe and Munindradasa, 2007), and *Cyrtodactylus* (Batuwita and Bahir, 2005) and many frog groups (e.g., Meegaskumbura et al., 2002; Manamendra-Arachchi and Pethiyagoda, 2005) have apparently undergone radiations within the island, *Hemidactylus* geckos in the *brookii* group appear to have undergone several single speciation events, as has been demonstrated in groups of freshwater fishes and shrimps (Bossuyt et al., 2004).

During the Pleistocene there were prolonged periods of dry land contact across the Palk Strait, which today separates India from Sri Lanka. The strait is only 20 km wide and 10 m deep and during the last glacial maximum (~20,000 YBP) sea levels were approximately 120 m lower, yielding a 140 km wide land bridge. These connections existed for at least half of the last 500,000 years and were present as recently as 10,000 years ago (Rohling et al., 1998). As noted by Bossuyt et al. (2004) for other taxa, there is no evidence to suggest that the divergence of Sri Lankan endemic *Hemidactylus* from their Indian sister taxa dates from this period. Indeed, pairs of sister-species exhibit divergences of at least 11.6 million years ago. One reason posited for the restricted dispersal of some animals, despite the recurrent existence of a putative land corridor, is that the extensive areas of dry lowlands separating the mesic forests of the Western Ghats of India and the wet zone of Sri Lanka may have proved an insurmountable barrier (Bossuyt et al., 2004). Although this may be true for frogs and other mesic-adapted groups, it does not apply to Sri Lankan *Hemidactylus* species, none of which are forest-restricted. Indeed, the endemic species *H. hunae* and *H. lankae* are chiefly restricted to the dry zone and *H. depressus* and *H. parvimaaculatus* are broadly distributed across the island, including the dry zone (Wickramasinghe and Somaweera, 2002; Somaweera and Somaweera, 2009). Much deeper sampling of both Indian and Sri Lankan populations of species shared between the land masses (*H. frenatus*, *H. leschenaultii*) is needed to determine if their genetic substructure reveals the influ-

ence of Pleistocene land bridges, but it is clear that cladogenic patterns of the endemic Sri Lankan *Hemidactylus* reflect far older events in the history of South Asia.

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