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The identity and probable origin of the *Hemidactylus* geckos of the Maldives

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The Maldives are coral reef islands of Holocene origin with no endemic terrestrial herpetofauna. The few species that have been reported from the region have affinities with Sri Lanka, south and south-east Asia, and are considered relatively recent introductions by humans. Recent collections of *Hemidactylus* geckos from the Maldives allowed us to identify and reconstruct the probable origin of this genus on the islands. We combine mitochondrial DNA (ND2) sequence data for the new collections with published sequences to reconstruct evolutionary relationships. The two species of *Hemidactylus* in the Maldives are *H. frenatus* and *H. parvimaculatus,* with affinities to south-east Asia and Sri Lanka, respectively. Suggestive of multiple introductions, each species included multiple haplotypes, only one of which was previously recorded (in Sri Lanka); other haplotypes showed similarities to records from south-east Asia. Unravelling the colonisation patterns of house geckos in the Maldives requires a more complete knowledge of the natural variation across the range of the widely distributed source species.

Keywords: Hemidactylus brookii; *Hemidactylus frenatus*; *Hemidactylus parvimaculatus*; human commensal; India; Sri Lanka

INTRODUCTION

With a maximum elevation of 2.4 m above sea level, the Maldives are the lowest-lying nation in the world, and its 26 atolls occupy a land area of 298 km^2. In addition to the threat of sea level rise with climate change, the islands are strongly influenced by human settlement and, in the last 45 years, by the expansion of tourism infrastructure. Given the lack of topographical relief and its uniform monsoonal climate, the vegetation is dominated by strand vegetation and human-associated plants (Fosberg, 1957). The Maldives are coral reef islands of Holocene origin and it is unclear how long each island has been land-positive (Kench et al., 2005). In combination with the small land area and low habitat diversity of the country, it is expected that the terrestrial herpetofauna is depauperate. There are no endemics, and all recorded reptiles show affinities with south Asia, and especially Sri Lanka (Moutou, 1985); it has been presumed that most, if not all of the species present arrived via either recent over water dispersal or by anthropogenic means. Indeed, Fosberg (1957) stated that there was no Maldivian (Dhivehi) word for lizard, suggesting that they are recent arrivals. The names *hoanu* (gecko) and *bondu* (lizard) are currently used in the Maldives, although it is uncertain if these words are autochthonous or imported from another language.

To date, no comprehensive survey has been conducted on the herpetofauna of the Maldives (Hameed, 2002), with several authors having reported on the constituent species. Laidlaw (1903) listed eight terrestrial reptile species based on an extended expedition: *Calotes versicolor*, *Hemidactylus frenatus*, *H.gleadowi*, *Lygosoma albopunctata*, *Aspidura trachyprocta*, *Lycodon aulicus*, *Indotyphlops braminus*, and *Melanochelys trijuga thermalis*. Deraniyagala (1956), who recorded no snakes, added *Eutropis carinata* to this list and treated *H. gleadowi* as *H. brookii*. Subsequent authors have added no further species to the Maldivian reptile fauna. Indeed, in the most recent summaries (Das, 1994, 1996) only eight terrestrial species are listed (*Aspidura trachyprocta* being excluded). Although Moutou (1985) followed Laidlaw (1903) in listing *L. aulicus* for the Maldives, Philips (1958) cited *Lycodon aulicus capucinus*. This subspecies was recognised as distinct, and is now regarded as occurring in the Maldives (Das, 1994, 1996; David & Vogel, 1996). Its position in a recently described *L. aulicus* + *L. capucinicus* clade, that lacked sampling from India or Java (the type localities of the nominate forms) (Siler et al., 2013) is, however, unknown.

Another uncertainty in the Maldivian reptile fauna regards the geckos. Moutou (1985) followed Philips (1958) in recognising *Hemidactylus frenatus* and *H. brookii*, whereas the geckos were listed simply as *Hemidactylus* (no species given) by Klausewitz (1958), "house geckos" by Hourston (1972), and "Palmgeckos"

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Figure 1. Colour and pattern variation of *H. frenatus* (**A-C**) and *H. parvimaculatus* (**D-F**) from the Maldives



Figure 2. Habitats where both species of *Hemidactylus* were observed on Huraa Island: **A** – palm forest; **B** – local houses

and "Hausgeckos" by Reichholf (1985). *Hemidactylus brookii* was also listed by Das (1994, 1996, 2002), recently replaced by *H. parvimaculatus* (Das & Das, 2017).

The instability in the identity of one of the two *Hemidactylus* is a reflection of the confusing taxonomic history of the *H. brookii* group. Bauer et al. (2010a, b), based on molecular phylogenetic evidence as well as morphological differences, elevated the Sri Lankan subspecies *H. b. parvimaculatus* Deraniyagala, 1953 to specific status, and showed its presence in Mauritius and part of peninsular India. Vences et al. (2004) and Rocha et al. (2005) had earlier identified low mtDNA differences between these populations and those from the Comoros, Réunion and Rodrigues. Deso et al. (2103) argued that putative *H. brookii* from Desroches in the Amirantes Group in the Seychelles were also referable to *H. parvimaculatus*. Thus, the majority of the island groups in the Indian Ocean that had previously been believed to harbor *H. brookii* have been demonstrated to support populations of *H. parvimaculatus*. Both Bauer et al. (2010a) and Deso et al. (2013) speculated that this species would also be present on the Maldives, but this has yet to be confirmed. The only explicit statements of the occurrence of *H. parvimaculatus* from the Maldives are in Rösler and Glaw (2010, citing Bauer et al., 2010a) and Das & Das (2017).

Despite a range of recent studies (Rösler & Glaw, 2010; Mahony, 2011; Kathriner et al., 2014; Lajmi et al., 2016), the identity of *H. brookii* as well as the

Table 1. Accession numbers, voucher references and localities for samples used in phylogenetic analyses. Accession numbers in bold are sequences generated in this study.

Species	Voucher	GenBank accession number	Locality
Hemidactylus parvimaculatus	ADS 36	GQ458053	Sri Lanka, Kartivu
H. parvimaculatus	AMB 7466	GQ458056	Sri Lanka, Mampuri
H. parvimaculatus	AMB 7475	GQ458055	Sri Lanka, Kandy
H. parvimaculatus	CES/14/174	MH454766	India, Visakhapatnam District, Araku
H. parvimaculatus	DJ3428	**MK559032**	Maldives, Huraa Island
H. parvimaculatus	DJ3429	**MK559033**	Maldives, Huraa Island
H. parvimaculatus	DJ3430	**MK559034**	Maldives, Huraa Island
H. parvimaculatus	DJ3431	**MK559035**	Maldives, Huraa Island
H. frenatus	AMB 7411	EU268357	Sri Lanka, Pidipitiya
H. frenatus	AMB 7420	EU268359	Sri Lanka, Anuradhapura District, Ritigala
H. frenatus	CAS 229633	HM559629	Myanmar, Tanintharyi Div., Kaw Thaung Dist
H. frenatus	CES G088	**MK559036**	India, Tripura, Rowa
H. frenatus	CES G115	**MK559037**	India, Assam, Kohora
H. frenatus	DJ1138	**MK559038**	Costa Rica, Cahuita
H. frenatus	DJ1150	**MK559039**	Costa Rica, Cahuita
H. frenatus	DJ1220	**MK559040**	Vietnam, Cuc Phuong NP
H. frenatus	DJ1252	**MK559041**	Vietnam, Cuc Phuong NP
H. frenatus	DJ1259	**MK559042**	Vietnam, Son Trach
H. frenatus	DJ1264	**MK559043**	Vietnam, Son Trach
H. frenatus	DJ1279	**MK559044**	Vietnam, Bach Ma NP
H. frenatus	DJ3432	**MK559045**	Maldives, Viligilimathidhahuraa Island
H. frenatus	DJ3433	**MK559046**	Maldives, Huraa Island
H. frenatus	DJ3434	**MK559047**	Maldives, Huraa Island
H. frenatus	DJ3435	**MK559048**	Maldives, Huraa Island
H. frenatus	DJ3436	**MK559049**	Maldives, Huraa Island
H. frenatus	DJ3437	**MK559050**	Maldives, Huraa Island
H. frenatus	DJ3438	**MK559051**	Maldives, Huraa Island
H. frenatus	DJ3439	**MK559052**	Maldives, Huraa Island
H. frenatus	DJ3440	**MK559053**	Maldives, Huraa Island
H. frenatus	DJ3445	**MK559054**	Maldives, Viligilimathidhahuraa Island
H. frenatus	DJ640	**MK559055**	Malaysia, Tanah Rata, Malaysia
H. frenatus	LSUHC 4871	GQ458049	Malaysia, Pahang, Bukit Bakong
H. frenatus	LSUHC 6745	EU268358	Malaysia, Pulau Pinang, Empangon Air Hitam
H. frenatus	TNHC 62814	HM559630	Phillippines, Luzon Id., Albay Prov., Mt. Malinao
H. frenatus	USNM 579075	KM975949	Timor-Leste, E of Baucau
H. frenatus	USNM 579429	KM975950	Timor-Leste, Com
H. gleadowi	CES/11/014	MH454761	India, Karnataka, Bagalkot
H. malcolmsmithi	CES/11/065	MH454765	India, Himachal Pradesh, Sujanpur
H. cf. *malcolmsmithi*	CAS 252886	KM975948	USA, Louisiana, New Orleans
H. murrayi	CAS 206638	GQ458054	Myanmar, Mandalay Division
H. murrayi	CAS 208159	GQ458052	Myanmar, Yangon
H. murrayi	CAS 229632	GQ458051	Myanmar, Tanintharyi Division
H. murrayi	LSUHC 6754	EU268365	Malaysia, Pulau Pinang, Empangon Air Hitam
H. murrayi	LSUHC 6755	EU268366	Malaysia, Pulau Pinang, Empangon Air Hitam
H. murrayi	USNM 579430	KM975941	Timor-Leste, Com
H. murrayi	USNM 579441	KM975942	Timor-Leste, Com
H. murrayi	USNM 579442	KM975943	Timor-Leste, Com
H. murrayi	USNM 579443	KM975944	Timor-Leste, Com
H. murrayi	USNM 579728	KM975945	Timor-Leste, Dili
H. murrayi	USNM 579729	KM975946	Timor-Leste, Dili
H. murrayi	USNM 581298	KM975947	Timor-Leste, Dili
H.murrayi	ZRC 2.6167	GQ458050	Borneo, Sarawak, Loagan Bunut National Park
H. treutleri	CES/14/216	MH454770	India, Telangana, Hyderabad
H. flaviviridis	ID 7640	HM559628	India, Rajasthan, Jaisalmer
H. giganteus	JB03	HM559632	Captive

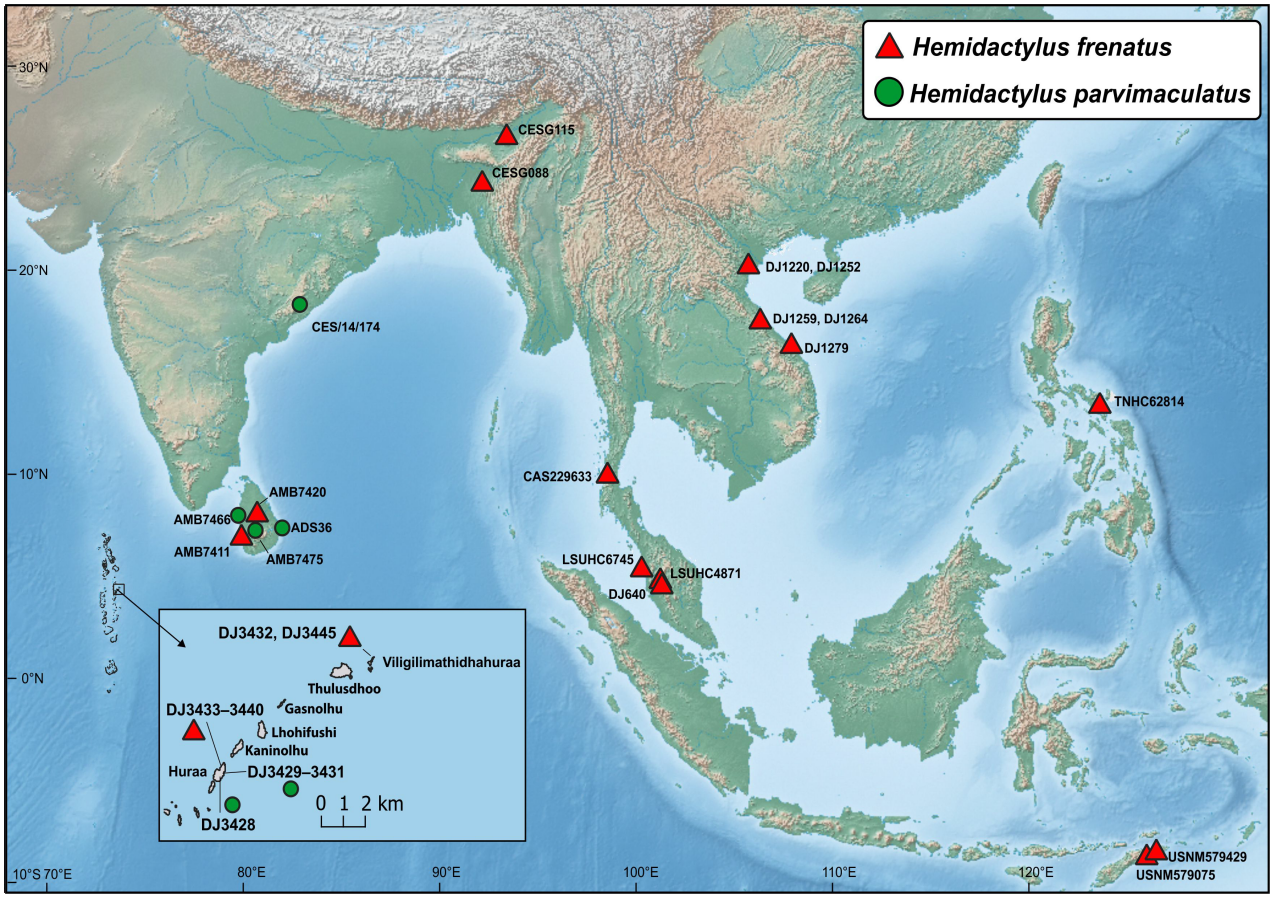


Figure 3. Map of south and south-east Asia showing sample locations for *H. frenatus* and *H. parvimaculatus*. Inset shows sample locations in the Maldives. Voucher number is given next to symbols, referenced in Table 1.

partitioning of the *H. brookii* group remain not yet fully resolved. With the elevation of several nominal taxa from synonymy, including *H. gleadowi* Murray, 1884 (Mahony, 2011) and *H. malcolmsmithi* (Constable, 1949) (Agarwal et al., 2018), and the description of several new species (Mahony, 2009; Mirza & Raju, 2017), the identity of the Maldives brookii-like geckos warrant an explicit clarification. A visit by one of us (DJ) to the Maldives in 2015 provided an opportunity to obtain further material of *Hemidactylus* geckos in order to ascertain the identity of the resident *H. brookii*. *Hemidactylus frenatus* were also collected in order to identify the potential source population(s) from which the other species of Maldivian house gecko was derived.

METHODS

We sampled 14 Maldivian *Hemidactylus* (Fig. 1) from natural vegetation (palm trees) and buildings (Fig. 2) from three localities on two islands including four from the *H. brookii* group (Fig. 1D-F) and 10 *H. frenatus* (Fig. 1A-C), besides eight *H. frenatus* from south-east Asia and two from Costa Rica (Table 1, Fig. 3). Blood or muscle samples were either preserved in 96 % ethanol or frozen after collection, and stored at -25 or -80 °C. We used the Qiagen DNeasy® Blood and Tissue Kit for DNA extraction and targeted up to 1041 nucleotides of the protein-coding mitochondrial gene ND2 using the primers L4437 and H5934 (Macey et al., 1997; flanking tRNAs excluded) for PCR amplification (following Bauer et al., 2010a, b) and sequencing (performed by Macrogen Inc.; Seoul, South Korea and Amsterdam, Netherlands; http://www.macrogen.com). These sequences were combined with published ND2 sequences for *H. frenatus* and for the *H. brookii* group excluding the morphologically unique ground-dwelling clade (Mahony, 2011; Lajmi et al., 2016), with *H. flaviviridis* and *H. giganteus* as outgroups (Table 1). Sequences were aligned using ClustalW (Thompson et al., 1994) in Mega 5.2 (Tamura et al., 2011) and translated to check for stop codons. A maximum likelihood phylogeny was constructed using the codon partitioned dataset with the GTR+G model, 10 independent ML runs and 1000 rapid bootstraps through raxmlGUI 1.5 (Silvestro & Michalak, 2012) that implements RAxML HPC 8.1.2 (Stamatakis, 2014). Uncorrected genetic distances (*p*-distances) were calculated in MEGA 5.2 with the pairwise deletion option. Museum abbreviations are as follows: ADS, Anslem de Silva field series; AMB, Aaron M. Bauer field series (now deposited in the National Museum, Colombo, Sri Lanka); CAS, California Academy of Sciences, San Francisco; CES, Centre for Ecological Sciences, Bangalore, India; DJ, Daniel Jablonski field series; ID, Indraneil Das field series; JB, Jon Boone private collection; LSUHC, La Sierra University Herpetological Collection; TNHC, Texas Natural History Collection, Austin; USNM, United States National Museum, Washington D.C.; ZRC, Lee Kong Chian Natural History Museum (formerly Raffles Museum of Biodiversity Research), Singapore.

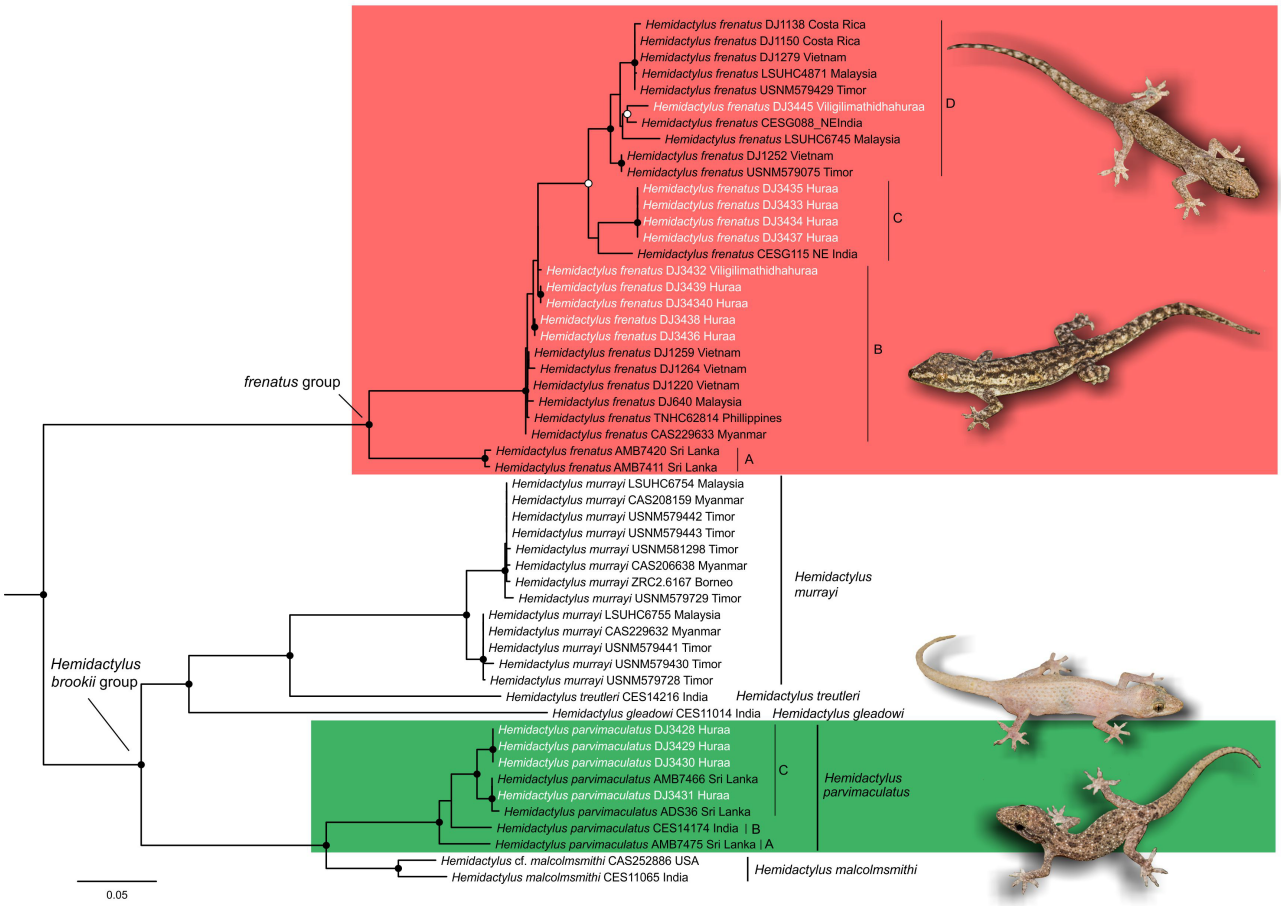


Figure 4. Maximum Likelihood phylogeny of *H. brookii* and *H. frenatus* groups with information on voucher number and country (NE India= north-east India). Samples from the Maldives are in white font and labelled by island; the *H. frenatus* group is labelled with red highlight and the *H. parvimaculatus* group by green highlight; solid black circles at nodes indicate bootstrap support >90 % and hollow circles indicate support from 80–90 %. Clades within *H. frenatus* and *H. parvimaculatus* are marked by capital letters. Representative photographs of sequenced Maldivian material.

RESULTS

The *H. brookii* and *H. frenatus* clades were each recovered with high bootstrap support (Fig. 4). The *H. brookii* complex includes *H. murrayi*, *H. treutleri*, and *H. gleadowi* in one subclade, sister to *H. parvimaculatus* + *H. malcolmsmithi*. A specimen previously identified as *H. parvimaculatus* (CAS 252886) is the divergent sister to *H. malcolmsmithi* (Fig. 4). *Hemidactylus parvimaculatus* was composed of three clades (A–C in Fig. 4). AMB 7475 from Kandy, Sri Lanka (A) is 5.5–5.7 % divergent from the rest of the clade, followed by CES14/174 from Araku, India (B) that is 4.5–4.9 % divergent from the remaining sampled individuals from the Maldives and Sri Lanka (C). The Maldivian *H. brookii* included two haplotypes in sister subclades within clade C, the first represented by a single individual (DJ3431) and identical to two individuals of *H. parvimaculatus* from Sri Lanka (AMB7466, ADS36), and the second represented by three individuals from the Maldives only (DJ 3428–3430), with a 1.8–2.3 % genetic divergence. The two Maldivian haplotypes of *H. parvimaculatus* were collected together, and the haplotype unique to the Maldives was also found at another locality 350 m away, all on Huraa Island.

Hemidactylus frenatus includes four divergent clades (A–D in Fig. 4). A Sri Lankan clade (A) was 13.1–18.2 % divergent from a SE Asian sister clade (B–D). The SE Asian clade included specimens from north-east India, Malaysia, Myanmar, the Philippines, Timor and Vietnam besides Costa Rica and the Maldives. The basal splits within this clade separate a shallow polytomy (B) which included three unique Maldivian haplotypes (DJ3432; DJ3436, DJ3438; DJ3439–3440) that are 0.5–0.8 % divergent from each other and 0.5–2.1 % divergent from sequences from Malaysia, Myanmar, Philippines and Vietnam. Clade C included four individuals from Huraa Island (DJ 3433–3435, DJ 3437) that are 3.7–4.3 % divergent from a sample from Assam, India (CES G115). Clade D separated a subclade including a sample each from Vietnam and Timor. The final two subclades include almost identical haplotypes from Costa Rica, Malaysia, Timor, and Vietnam as sister to a poorly supported clade, including another unique Maldivian haplotype of *H. frenatus* that is 2.1 % divergent from a sample from Tripura, India (CES G088), and a distinct individual from Malaysia (LSUHC 6745). Huraa harbours three different haplotypes, one with affinities to north-east India and the other two assigned to clade B. One haplotype from Viligilimathidhahuraa has affinities to north-east India and another haplotype is a member of clade B.

DISCUSSION

As is the prevailing view for the colonisation of the islands by humans and predominant trade routes (Litster, 2016), *Hemidactylus* geckos on the Maldives appear to have an Indian or Sri Lankan origin, besides affinities with South-east Asia. The Maldives was a major source of cowries when they were used as currency across many parts of Asia and Africa (Litster, 2016). The cowrie trade out of the Maldives was a major driver of shipping transport across Asia and Africa, besides the import of rice and wheat from India and Sri Lanka. Maldivian cowries that date back to as early as 500 CE have been found in India (Litster, 2016) and c. 950–1200 CE in Africa (Nixon, 2008, cited in Litster, 2016). Despite records of ships coming from as far west as Arabia and the east coast of Africa (Van Mehren 1866, cited in Litster, 2016), none of the sampled Maldivian geckos have African affinities.

We sampled only two islands and recovered patterns consistent with multiple colonisation events. *Hemidactylus parvimaculatus* includes haplotypes identical to Sri Lankan samples as well as unique to the Maldives; the latter likely reflecting a lack of sampling in Sri Lanka and peninsular India (the presumed natural range of the species; Lajmi et al., 2016). Given the historical links and the fact that *H. parvimaculatus* is widely distributed across other Indian Ocean islands (Bauer et al., 2010a; Deso et al., 2013), a source population of this widely distributed species in Sri Lanka was expected.

Hemidactylus frenatus includes five unique Maldivian haplotypes, two with affinities to north-east India and the other three to South-east Asia, suggesting that more sampling is needed across South-east Asia and India-Sri Lanka to ascertain source populations. Indicative of multiple introductions on the two sampled islands, each includes multiple haplotypes of both species (Tonione et al., 2011), in contrast to South American populations of *H. frenatus* that likely originated from a single source (Torres-Carvajal, 2015). Huraa is a small densely populated island less than one kilometer long and ~500 m at its widest. It is 8.5 km SW of Viligilimathidhahuraa, which is less than one km long and <200 m wide. Viligilimathidhahuraa is largely uninhabited but less than one kilometer away from the inhabited Thulusdhoo (Fig. 3). Huraa harbors two haplotypes of *H. parvimaculatus* and three of *H. frenatus* in sympatry, whereas Viligilimathidhahuraa includes two *H. frenatus* haplotypes in sympatry.

This is the first study to use molecular data to ascertain the affinities of Maldivian terrestrial vertebrates. The revealed patterns are more complex than a simple Sri Lankan origin for all Maldives *Hemidactylus*, with one and five haplotypes unique to the Maldives for *H. parvimaculatus* and *H. frenatus*, respectively. Unravelling patterns of colonisation of house geckos in the Maldives will require a more complete knowledge of the distribution of haplotypes across the range of these widely distributed species (Tonione et al., 2011), particularly across the regions from which the source populations were derived—India, Sri Lanka and South-east Asia. Only a few, largely anthropophilic, species in the genus *Hemidactylus* are invasive, but these taxa (including *H. parvimaculatus* and *H. frenatus*, and also e.g. *H. mabouia*, *H. turcicus*) are so readily transported by humans (Carrana & Arnold, 2006) that a complex mosaic of haplotypes from disparate source populations in locations such as the Maldives is not surprising.

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