



The Global and Western Indian Ocean Dispersal of House Geckos From Asia Using Historical and Mitochondrial DNA Perspectives

Sara Rocha^{1†}, Alexandra Trinks^{2,3†}, D. James Harris⁴, Greger Larson^{5*} and Anthony S. Cheke⁶

¹ Phylogenomics Lab, Universidade de Vigo, Vigo, Spain, ² Institute of Pathology, Charité – Universitätsmedizin Berlin, Corporate Member of Freie Universität Berlin and Humboldt-Universität zu Berlin, Berlin, Germany, ³ BIH Biportal Single Cells, Berlin Institute of Health at Charité – Universitätsmedizin Berlin, Berlin, Germany, ⁴ CIBIO/InBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, Universidade do Porto Vairão, Vairão, Portugal, ⁵ The Palaeogenomics and Bio-Archaeology Research Network, Research Laboratory for Archaeology and History of Art, University of Oxford, Oxford, United Kingdom, ⁶ Independent Researcher, Oxford, United Kingdom

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*Correspondence:

Greger Larson
greger.larson@arch.ox.ac.uk

† These authors have contributed
equally to this work

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Seven species of house geckos occur across the scattered islands of the Indian Ocean. Two of these, *Hemidactylus frenatus* and *H. parvimaclatus* are both widespread and possess distribution profiles that suggest pre-European, or perhaps natural dispersal to some islands. Of these, only *H. frenatus* currently has sufficient molecular data to begin exploring dispersal patterns. This species is one of the most successful reptile colonists, as demonstrated by its global, pantropical distribution. While in some areas, such as Australia and continental South America, its dispersal patterns are both recent and well-known, early historical records of *Hemidactylus* in the Indian Ocean islands suggest earlier and/or potentially non-human-mediated dispersals. Here, we reviewed the historical literature and combined those reports with an assessment of mitochondrial DNA diversity of a global sampling of *H. frenatus* samples that included modern and museum specimens. Our results corroborate previous studies and demonstrate the relatively high diversity within this species' native range in Southeast Asia. In addition, the phylogenetic analysis suggests both a potential cryptic species complex, as well as global geographic structuring of different *H. frenatus* mitochondrial lineages. This has important implications for many comparative studies of this complex. Frequent and ongoing dispersals and colonizations complicate the identification of potentially older migration patterns. Further assessments including additional samples and analyses of additional genetic markers are necessary to disentangle older from more recent dispersals within this intriguing species.

Keywords: *H. frenatus*, house gecko, phylogenetics, evolution, human-mediated dispersal

INTRODUCTION

As the global human population has grown, so have the number of plant and animal species that we have collectively translocated beyond the boundaries of their natural distributions. These range expansions, combined with population and range contractions of many endemic native species have led to a generalized pattern of global biotic homogenization (Olden et al., 2004), and this

phenomenon has accelerated with the commensurate increase in international shipping, human travel, and cargo movement (Mooney and Cleland, 2001). Importantly, determining whether a species's distribution has been influenced by people is not always straightforward since long-distance, non-human-mediated dispersal has been demonstrated in a wide range of species (de Queiroz, 2005). The majority of studies that have focused on range expansions resulting from human-mediated transport have often done so with a view toward using these taxa as a proxy for understanding human migration pathways and trade networks. As a result, they have focused on those specific taxa that have been most closely interwoven into human societies, and on which people have become most reliant.

In addition to the common domestic animals (Frantz et al., 2019; Perri et al., 2021) and plants (da Fonseca et al., 2015), as well as animals introduced as game, numerous additional commensal species have also dispersed as a result of their association with people but in a less deliberate fashion. Classic animal examples include rats, mice and house shrews (*Suncus murinus*), all of which have been the subject of genetic (Duplantier et al., 2002; Tollenaere et al., 2010; Aplin et al., 2011; Brouat et al., 2014; Ohdachi et al., 2016) and archeological (Cucchi et al., 2020) studies investigating their dispersal beyond their native distributions, including across the Western Indian Ocean (Cheke, 2010). A comprehensive survey of taxa whose current distributions have been manipulated by people in Island Southeast Asia, for example, revealed scores of animal species that have been transported between islands over the past 10,000 years (Heinsohn, 2003). Likewise, movements of both wild, commensal and domesticated animals and plants across and around the Indian Ocean from Asia to East Africa and Madagascar have also been reviewed (Boivin et al., 2013).

Here, we explored the patterns of transport and dispersal using commensal geckos, a somewhat neglected species in animal movement studies, despite the fact that they are widespread and easily transported (Jones et al., 2013). Although there are more than 165 species within the genus *Hemidactylus* (Agarwal et al., 2021), the majority are restricted to small-ranging habitats in South Asia. Approximately 10 species, including the house geckos *H. mabouia* from Africa and the Asian *H. frenatus*, have achieved intercontinental distributions (Weterings and Vetter, 2018), while *H. parvimaclatus* reached many Indian Ocean islands. However, because the review by Weterings and Vetter (2018) regarding invasive *Hemidactylus* did not re-assess older identifications, the Indian Ocean distributions are not reliable for '*H. mabouia*' or '*H. brookii*' (= *H. parvimaclatus*).

Hemidactylus frenatus is the most widely introduced gecko in the world (Weterings and Vetter, 2018), and though native to tropical Asia and the Indian subcontinent, it has been identified on islands and continents spanning the globe (McKay and Milenkaya, 2020). Adaptations that permit this species to establish populations in new locations include: the females' ability to store viable sperm for up to a year (Yamamoto and Ota, 2006); their hardshelled eggs' resistance to immersion in seawater (Hsu et al., 2021) and the capability to reproduce year-round in tropical zones (McKay and Phillips, 2012). Furthermore, they lay eggs in crevices in objects, and are therefore often accidentally

transported in cargo or baggage (Weterings and Vetter, 2018, ASC pers. obs.). These features also increase their potential to remain undetected and undamaged in transit in the past on both ancient sailing vessels and on modern shipping containers. None of these characters alone, however, explain why this species, and others such as *H. mabouia* and *H. parvimaclatus*, but not their numerous congeners, have been such successful colonists.

While the spread of *H. frenatus* throughout the Pacific was first described in association with troop and supply movements during World War II (Case and Bolger, 1991), this species has also been suggested as a proxy to understand older human movements, at least across the Indian Ocean (Cheke, 2010; Boivin et al., 2013). The observation that distinct haplogroups coexist across some of these islands (Rocha et al., 2010), together with their curious distribution on remote atolls suggests they may have arrived in a series of different events (Cheke, 2010). Given the modern widespread distribution of gecko species within tropical and subtropical ecotones, commensal geckos in general, and *H. frenatus* specifically, represent excellent models to investigate the unintentional human-mediated movement of a widespread commensal reptile. One of the problems hindering the genetic approach to understanding the spread of geckos is the use of different markers in independent studies, which precludes efforts to comprehensively and simultaneously analyze all the available data.

Here, in order to characterize the distribution of specific house gecko populations, we applied two different approaches. First, we established both the time frame and geographic distribution of house geckos in the Indian Ocean by reviewing the historic literature and early descriptions and collections of geckos in the region. We then extracted DNA and sequenced a 463 bp fragment of the mitochondrial cytochrome *b* gene from 111 museum and modern specimens of the most widespread and genetically diverse house gecko species, derived from over 70 locations representing 36 countries (**Supplementary Table 1**). Using the obtained sequence alignment, we constructed phylogenetic trees and assessed the geographic partitioning of the individuals assigned to well-supported clades. These combined approaches, including the increased resolution afforded by genetic signatures, allowed us to identify specific populations and lineages of Asian house geckos across their global and Indian Ocean distributions. These data also allowed us to discuss the results in light of human-mediated movement of taxa writ large.

RESULTS AND DISCUSSION

Historical Accounts of the Distribution of Commensal Geckos in the Indian Ocean

In addition to *H. frenatus*, six other species of house geckos, mostly small gray or brown, largely facultatively anthropophilic animals, inhabit the historically uninhabited remote islands of the Indian Ocean. None of the volcanic islands of Mascarenes and Comoros, nor the continental fragments (Madagascar and the granitic Seychelles), much less the numerous atolls of the western Indian Ocean (**Figure 3**), have been connected to any continent for upward of 60 million years, and therefore either natural or



FIGURE 1 | An image of seven geckos drawn by Charles Alexandre Lesueur in 1803. The *Hemidactylus parvimaclatus* from Coëtivy is bottom right (Cheke, 2009). Although it is a female without preano-femoral pores, the pattern of tubercles and the undertail scalation detailed in the side-sketch closely match photographs and details for *parvimaclatus* in Mahony's (2011) review of *brookii* group geckos.

human-mediated over water dispersal are necessary to explain their distribution.

Of the seven, two, *Hemidactylus platycephalus* and the *H. mabouia-mercatorius* complex are Afro-Malagasy species (Rocha et al., 2010), which historically were merged within the polyphyletic umbrella species '*H. mabouia*' (Louette et al., 2004; Rocha et al., 2010; Agarwal et al., 2021). Of these, only *H. mercatorius* seems to have spread beyond the immediate area (Madagascar, Comoros, Aldabra group, Farquhars), to the granitic Seychelles and, unexpectedly, to Platte, but only recently via human agency (Gerlach, 2007; Rocha et al., 2009a). For example, although Boulenger (1909) reported "*H. mabouia*" on Mahé in 1905 (specimen confirmed by Cheke (1984) as *H. mercatorius*), it probably did not establish a population since it was not detected again there until 1995, and in 2002 on Frégate (Gerlach, 2007). Platte, a low coral island, is infrequently visited by zoologists, and it is possible that *H. mercatorius* may have been

long established. *H. parvimaclatus* was initially misidentified as *H. mercatorius* (Vinson and Vinson, 1969) in the Mascarenes, but true *mabouia/mercatorius* was absent in the Mascarenes (Cheke and Hume, 2008; Cole, 2008) until discovered in Réunion in 2010, with molecular data suggesting their recent introduction from either the Comoros, the Seychelles or the East African coast (Sanchez et al., 2012), the most likely of these being Mayotte (Comoros), also still a French territory.

Of the other five species, one is Pacific, and four are Asian in origin, but with differing dispersal histories. *Lepidodactylus lugubris* is a parthenogenic Pacific species with apparently endemic Indian Ocean clones (Ineich, 1999), which suggests a long-established natural dispersal via drift. This species is also the least associated with humans, and only occurs on the most easterly of the islands including Rodrigues, the Chagos group, and Coëtivy (Gerlach, 2007; Cheke and Hume, 2008; Cole, 2009). Boulenger (1909) reported specimens of *L. lugubris* collected in 1905 from both Mahé and Praslin in the granitic Seychelles, but it has not been reported since (Gerlach, 2007), and no specimens exist in the United Kingdom Natural History Museum collections (Cheke, 1984), so this record may have been made in error. *L. lugubris* does occur sympatrically in houses in Rodrigues with three other gecko species (ASC pers. obs.), and it has also recently been found on St. Brandon/Cargados Carajos (Nik Cole, pers. comm. to ASC, 2020), directly in the path of the South Equatorial Current (New et al., 2005).

Parthenogenic *Hemiphyllodactylus typus*, only found in the Mascarenes, is not usually associated with buildings (Grégory et al., 2007) and was first reported in 1948 (Vinson and Vinson, 1969; Deso et al., 2020). Two studies (Grégory et al., 2007; Deso et al., 2020) however, suggested that given the difficulty in observing this species, it may have escaped notice and be native in the Mascarenes, especially since it appears to favor the native forest habitat. This narrative would require oceanographically difficult cross-equatorial drifting. Another Asian gecko species, *Gehyra mutilata*, is widespread in the Indian Ocean, but lacks sufficient genetic variation in this region to identify its geographical origins (Rocha et al., 2009b). *G. mutilata* is strictly commensal and is unlikely to have survived on islands where the human presence was only fleeting. Therefore, even if cross-ocean mariners introduced the species unintentionally, a temporary human stopover would not be sufficient for the species to maintain a presence. In fact, this species failed to establish a population on Aldabra until there was a permanent human presence at a research station (Cheke, 1984; Gerlach, 2007).

The final two species, *Hemidactylus frenatus* and *H. parvimaclatus*, are both facultative commensals, with distributions, histories and genetic signatures that warrant further investigation. Both of these species, common in southern India and Ceylon/Sri Lanka (Daniel, 2002; Das and de Silva, 2005), have long-term established populations in the Maldives where *H. frenatus* was likely introduced on multiple occasions (Agarwal et al., 2019). When the first faunal collections were made in the Maldives by the Stanley Gardiner expedition of 1899-1900, *H. frenatus* was widespread throughout, but *parvimaclatus* (as '*H. gleadowii*') was only collected on Hulule, Male Atoll (Laidlaw, 1902). People from Sri Lanka are known

to have settled on numerous occasions, so the presence of *H. parvimaclulatus* is not unexpected, and *H. frenatus* could also have arrived from long-standing trading (Maloney, 1980; Litster, 2016) with ports to the east.

The Maldives are long-inhabited islands, possibly from 1400 BCE (Maloney, 1980; Jaufar, 2019), though Litster (2016, 2020) is more cautious about BCE dates, suggesting probable early stopover use, if not settlement. The oldest confirmed direct radiocarbon date is remarkably late, 249–393 CE, evidently after the cowry-shell (*Monetaria moneta*) trade for currency was well-established. While they could be the source of gecko populations elsewhere, it is the presence of geckos on further-flung islands first encountered by humans more recently, in the last 1,500 years, mostly the last 500, that concern us here.

Hemidactylus parvimaclulatus

Hemidactylus parvimaclulatus is part of the Indo-Asian *H. brookii* complex, and was only recognized as a separate species in 2010; the natural range of the species being the island of Sri Lanka and also southern India (Bauer et al., 2010). Although not reported in Mauritius until 1818 (Cheke and Hume, 2008) (as '*H. brookii*'), and still absent from the granitic Seychelles (Gerlach, 2007), it was collected on then uninhabited isolated sand cay of Coëtivy in 1803. Coëtivy, discovered in 1771 (Lionnet, 1972), was first settled in 1811 (de Froberville, 1848), though it had been visited on various occasions by Seychellois and French/Mauritians (Toussaint, 1967) seeking free coconuts and turtles. This specimen was illustrated in a remarkable watercolor of seven geckos by Baudin expedition artist Charles-Alexandre Lesueur (Collection Lesueur, Muséum du Havre MS 78-115; reproduced in Cheke (2009); **Figure 1**); the species was also collected in 1905 on the remote atoll of Desroches in the Amirantes (Boulenger, 1909; as *H. brookii*), and was still present in 1981 (Gardner, 1986).

Its presence on these isolated low islands is anomalous, and is unlikely to result from natural drift (it would be a unique cross-equatorial case of sea drift in the Indian Ocean). It is also unlikely to have been brought from Mauritius, whence the Seychelles and their outer islands were settled, as it would have shown up on the much more populated main granitic islands, where it is still absent (Gerlach, 2007; Rocha et al., 2009a). It is therefore possible that it arrived via Austronesian cross-ocean mariners traveling via Sri Lanka or the Maldives - the species does not occur in these travelers' source areas (Sumatra, Borneo). The species was not found on Desroches in 2005 despite targeted searches (Rocha et al., 2009a) - only *frenatus*, absent in 1905, (Boulenger, 1909 contra Gerlach, 2007) but present in 1981 (Cheke, 1984; Gardner, 1986) was identified, nor has it been rediscovered on Coëtivy (Cheke, 1984; Gardner, 1986). A more likely source is the Maldives: Maldivian folklore recounts tales of boats lost at sea ending up in remote islands, so, although the islands are not specifically named (apart from Chagos; Romero-Frias, 1999; Romero-Frias, 2012), this could be the source of *H. parvimaclulatus* on Desroches and Coëtivy.

One story, *Hoiivavai* (= Chagos in Maldivian; Litster, 2016), was based on a 17th century BCE case of a fishing vessel wrecked in the Chagos, and its crew rescued to tell the tale (Romero-Frias,

2012). Although some Portuguese ships had been wrecked on the northern Chagos banks in the mid-late 16th century, they were traders heading for the East Indies and back (Wenban-Smith and Carter, 2016), so would have been unlikely to have carried *parvimaclulatus*. The same applies to the first known deliberate landing on Egmont in 1605 by an English party traveling east (Wenban-Smith and Carter, 2016). There is no evidence of any European landing on Diego Garcia until much later. *H. parvimaclulatus* also occurs on Moheli and Anjouan (Comoros) (Vences et al., 2004; Rocha et al., 2005; Hawlitschek et al., 2011), and all three Mascarenes (Vinson and Vinson, 1969; as '*H. mercatorius*'; Vences et al., 2004), but not Madagascar (Glaw and Vences, 2007).

Two clades are present in the Mascarenes (Vences et al., 2004; Rocha et al., 2005), and one extends to the Comoros, potentially indicating invasion events from different source populations. Although Austronesian and subsequent pre-European cross-ocean trading from c.800 BCE (Cheke, 2010; Boivin et al., 2013) is a possible source of the Comorian clade (with backspread to Réunion later), a post-European origin of both clades is probably more likely since the Comoros was formerly administered colonially from Réunion. There is no reason to suppose that *Hemidactylus* spp. in the Mascarenes arrived other than accidental transport post-European contact since there is no evidence of pre-European landings in this group (Cheke and Hume, 2008; Cheke et al., 2017).

Hemidactylus frenatus

The most complex and interesting case is that of the common house gecko *Hemidactylus frenatus*. Although its almost universal presence on Indian Ocean islands suggests a generalized, probably anthropogenic distribution, there are numerous anomalies within this apparently uniform pattern. Rocha et al.'s (2010) statement that this species is 'present throughout Indian Ocean islands without any signs of geographical structure' overlooked the fact that some structure is evident in both this and previous papers (Vences et al., 2004; Rocha et al., 2005) as discussed below.

House geckos tend only to be reported by naturalists, and not by mariners or explorers, so it is unsurprising that the first Indian Ocean record is not until c.1770 when Philibert Commerson's artist Paul Jossigny drew a *Hemidactylus frenatus* from Mauritius; the previously unpublished image is preserved in the Muséum National d'Histoire Naturelle in Paris (Cheke and Hume, 2008), reproduced by Bour (2015); **Figure 2**. A report (Hoffstetter, 1946) identifying some gecko subfossils as *H. frenatus* was made in error; the bones were those of the osteologically similar endemic gecko *Cyrtodactylus* (now *Nactus*) *serpensinsula* (Arnold, 2009), extinct on the Mauritian mainland, and only discovered alive on offshore islets after Hoffstetter's study. Despite intensive fossil collection across different Indian Ocean islands (Aldabra, Reunion, Mauritius, Madagascar and Seychelles), where other gekkonid species have been identified (Cheke and Hume, 2008; Hume, 2004; Hume et al., 2018) there are no known subfossils of *Hemidactylus* spp. in the Indian Ocean, suggesting that a natural and old (pre-human) colonization is unlikely.

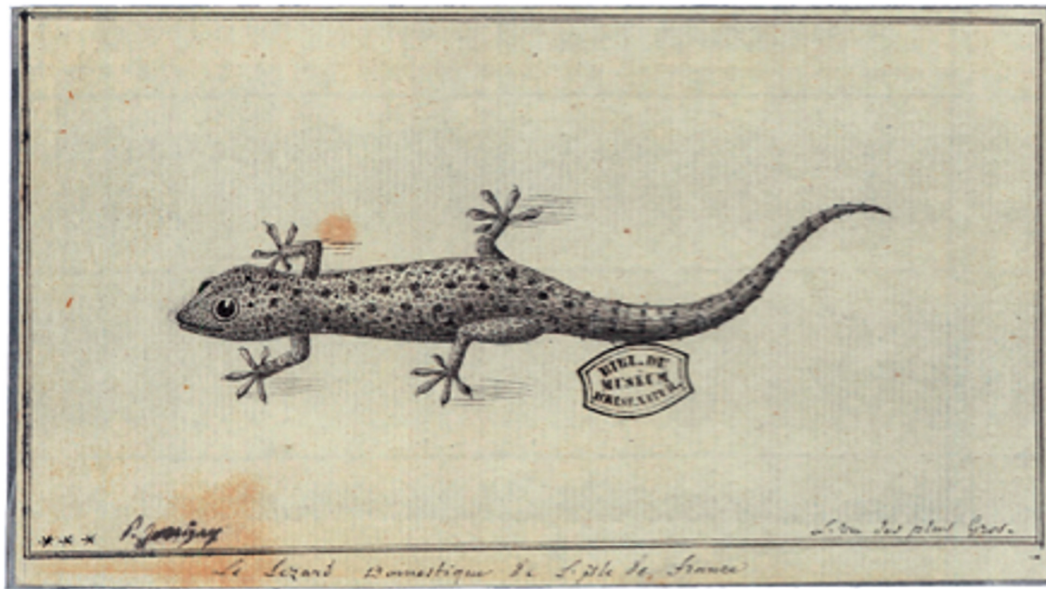


FIGURE 2 | An image of *Hemidactylus frenatus*, Mauritius. Sketch by Paul Philippe Sanguin de Jossigny c.1770 (from Bour (2015)).

The interesting aspects of *frenatus* are its curious distribution on outlying atolls and sand cays of the Seychelles (**Figure 3**) – the species is widespread on these islands which have only small agricultural (coconut) or, more recently, tourist-related settlements. Despite this, the species was absent on the much more populated, visited and biologically known granitic islands until the 1990s (Gerlach, 2007), barring a doubtful record from “the Seychelles” (island unspecified) in 1863 (Peters and von der Decken, 1869).

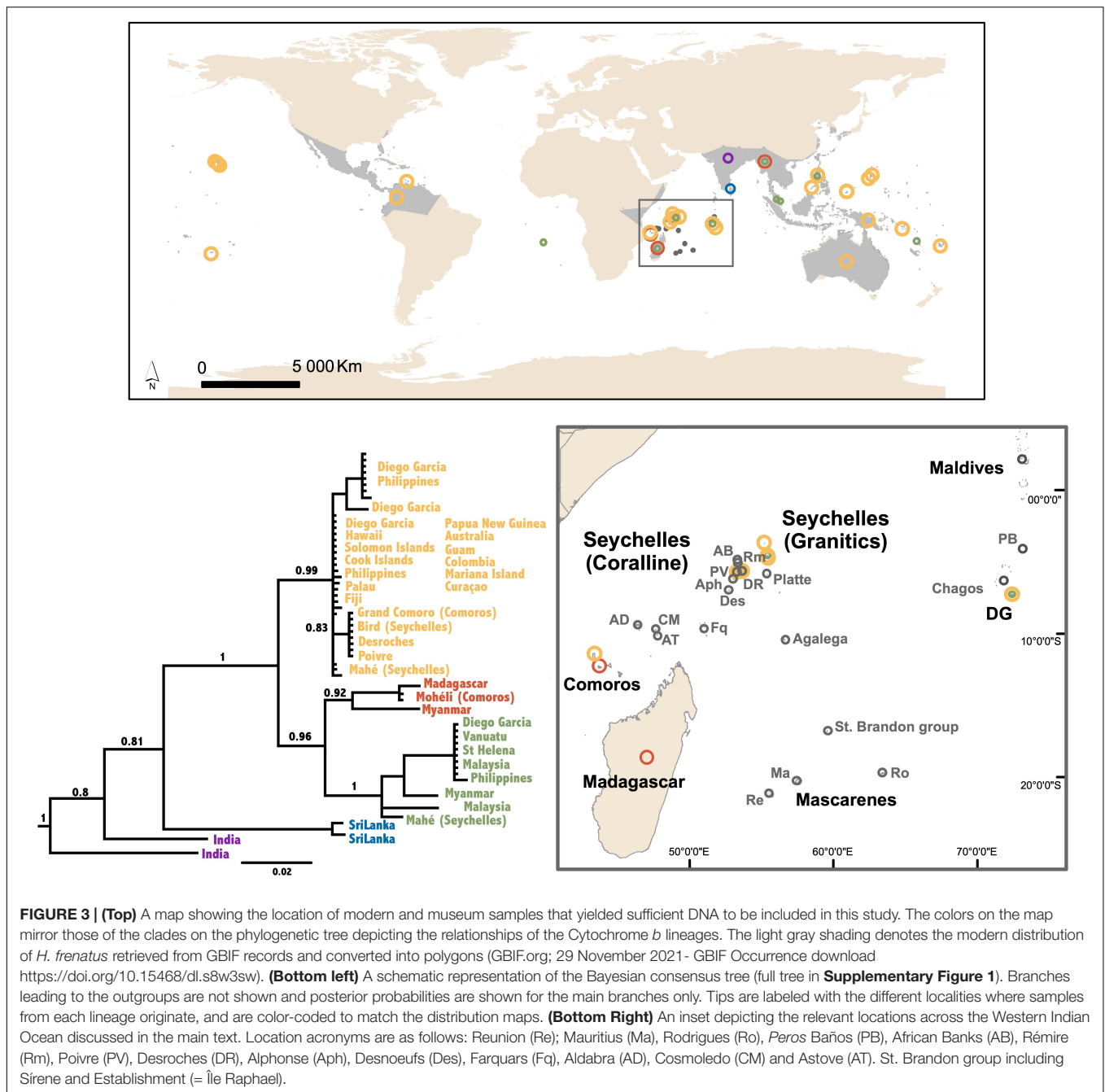
H. frenatus occurs, or occurred, on many low islands and atolls visited by the 1905 Stanley Gardiner/Percy Sladen Trust expedition (Boulenger, 1909; Cheke, 1984). There are no earlier records since, other than Rémire (Amirantes; collection in 1882; Günther, 1884), no-one had previously collected lizards on these islands. The expedition found them on Bird (central Seychelles), Poivre, Rémire and Desroches (Amirantes), Sirène and ‘Establishment’ [= Raphael] (St. Brandon), Diego Garcia, Salomon group, Peros Banhos group and possibly Egmont (Chagos), but none were identified on the granitic islands. This species has subsequently been found on several other low islands: Platte, Alphonse, Desnoeufs, African Banks (Cheke, 1984; Gerlach, 2007), Agalega (Cheke and Lawley, 1983; Webster and Cadinouche, 2013), and belatedly reconfirmed on St. Brandon (Nik Cole, pers. comm. 2020). The species was, and remains (Cheke, 1984; Gerlach, 2007), absent on more westerly atolls closer to Madagascar, where *H. mercatorius* was, and is, present (Farquhars, Aldabra, Cosmoledo, Astove) (Boulenger, 1909), and where the currents favor transport northwest from Madagascar, and at times effectively north/north-east via the SECC (Peng et al., 2015; Hawlitschek et al., 2017).

While commonly found in houses, *H. frenatus* is found living in rocks and trees on islands inhabited only by seabirds in the Amirantes’ (Gardner, 1986), leading him to agree with Cheke (1984) that this distribution was due to natural sea-drift from

the east. However, that does not explain why the drift missed the granitic islands (but hit Bird further north), and carried the geckos further west to the Amirantes. The fullest flow of the South Equatorial Current runs south of the Seychelles Bank (New et al., 2005), which might have impacted the Amirantes more than the granitics, which would also be ‘protected’ (in a sense) by the shallow bank diverting the flow around it. Unlike many of the atolls, the granitic islands have other native lizards including geckos, but pre-existing reptiles have never been known to prevent its establishment elsewhere, and *H. frenatus* is known to aggressively out compete other similarly sized geckos (e.g., Cole et al., 2005; Dame and Petren, 2006; Newbery and Jones, 2007; Csurhes and Markula, 2009).

Hemidactylus frenatus is also widespread in Madagascar (Glaw and Vences, 2007) and is present on all four Comoro islands (Louette et al., 2004; Hawlitschek et al., 2011). Unlike the oceanic high islands and atolls (Maldives excepted), these have been inhabited for well over a millennium (Crowther et al., 2016; Anderson et al., 2018b), but reptile collections, apart from one Malagasy chameleon, only date from the mid-19th century BCE (Andriamialisoa and Langrand, 2003; Hawlitschek et al., 2011). Hence, there is no historical basis for insight into the means or date of arrival of the species there. Some consider three, or all four, species of *Hemidactylus* in the Comoros to have been introduced (Vences et al., 2004; Hawlitschek et al., 2011) but given the distribution and habitat preferences (Hawlitschek et al., 2011, 2017), the evidence for *mercatorius* and especially *platycephalus* remains ambiguous.

In summary, from the seven largely commensal house gecko species that today inhabit Indian Ocean islands, only the early records of both *H. parvimaclulatus* and *H. frenatus* across some isolated islands suggest the possibility of early (pre-European) colonizations or even natural dispersals. Of these, *H. frenatus* is undoubtedly the widest distributed and most abundant across the



Western Indian Ocean (and globally), and we therefore tried to gather a comprehensive widespread set of samples that allowed for an exploration of the geographic distribution of its genetic variation, and possibly shed some light into this species's (early or modern) dispersal patterns.

Molecular Evidence for Global *Hemidactylus frenatus* Dispersal and Distribution

Several recent studies have attempted to resolve colonization patterns across parts of the range of *H. frenatus* using mtDNA

sequences. Vences et al. (2004) analyzed partial 16S rRNA sequences from individuals from Madagascar, Grand Comoro, the Andaman islands, Mauritius, Rodrigues and Sri Lanka and considered this to show “low genetic differentiation ... with no recognizable phylogeographical structure, indicating recent colonization or introductions.” Rocha et al. (2005) focused on the Comoro islands, and likewise, did not identify any notable structure with the same 16S rRNA marker.

Using partial 12S rRNA and Cytochrome *b* (CYTB) gene sequences to examine the origin of South American populations, Torres-Carvajal (2015) found no variation across Ecuador,

Colombia, Hawaii and Papua New Guinea, although these were highly distinct from lineages in Myanmar/Burma and India. Tonione et al. (2011) also identified high diversity within the tiny island of Moorea, French Polynesia, based on Cytochrome Oxidase 1 (CO1) sequences, and Agarwal et al. (2019) determined the probable origin of *H. frenatus* from the Maldives to be from Southeast Asia. Both these latter studies proposed multiple introductions, and the need for improved sampling of potential source populations to unravel colonization patterns.

At least five lineages have now been identified within *H. frenatus*, and geographic structure is present. In addition to the Indian and Sri Lankan lineages, the worldwide (Indian, Pacific and Atlantic Ocean islands) samples analyzed here fit clearly into three well-supported clades. One (red in **Figure 3**) is present in both Myanmar and the Western Indian Ocean (WIO) islands of Madagascar and Comoros (Moheli), another (green) is found both in southeast Asia (Vanuatu, Philippines, Malaysia, Myanmar) as well as across some WIO islands (Diego Garcia, the Seychelles -Mahé- and Madagascar) and also in the Atlantic Ocean island of St. Helena. The third (yellow) is also widespread across the Pacific and Indian Ocean islands.

Since we sequenced samples from the main 16S rRNA haplogroups in the Western Indian Ocean, we were able to match these three lineages of CYTB to the different haplogroups described in Rocha et al. (2010). Although structure was, unsurprisingly, previously less obvious using the more conserved locus than with CYTB, these three lineages are also reflected in 16S data. In this way, the yellow clade corresponds to 16S haplotypes H4-H7 and H10, the red clade to Comoros and Madagascar H8 and H9, and the green clade, to remaining haplotypes from Mahé (represented by H2 - sample 2MA21).

We did not sample additional South American localities, but extrapolating from Torres-Carvajal (2015), South American localities from Colombia to Ecuador (including Galapagos) all belong to the yellow lineage, which is further present also at least in Myanmar (Tonione et al., 2011). In addition, though not all lineages can be unambiguously associated with the ones in Agarwal et al. (2019), some correspondence is evident (e.g., lineage A from (Agarwal et al., 2019) with the blue lineage here, both solely in Sri Lanka). The remaining lineages are not comparable, highlighting the diversity harbored by this taxa, especially in Southeast Asia.

Given this, and the number of lineages identified in other studies with other mitochondrial loci (e.g., Tonione et al., 2011), it seems likely that additional lineages remain unidentified from Southeast Asia. With highly divergent lineages present in India and Sri Lanka, supporting their Indian origin (Bansal and Karanth, 2010), at least three of the lineages spread eastward and westward, giving rise to their modern global distribution. Contrary to its colonization across continental South America, which seems to have been recent and involved mostly a single lineage (Case and Bolger, 1991; Case et al., 1994; Torres-Carvajal, 2015), Tonione et al. (2011) identified three lineages within Moorea, a small island in French Polynesia, and similarly, Western Indian Ocean islands overall currently harbor at least three different lineages of this species.

As with many other widespread species of *Hemidactylus* assessed with genetic methods, including *H. mabouia* (Agarwal et al., 2021) and *H. fasciatus* (Wagner et al., 2014), *H. frenatus* appears to be a species complex. Variation between the samples from mainland India and Sri Lanka and the island populations ranges up to 14 and 11%, respectively, which is as high as the divergence between pairs of reptile (Harris, 2002) and mammalian (Allen et al., 2020) species as measured using CYTB sequences. Variation between the main lineages within the Indian Ocean islands ranges between 7.0 and 8.5%, which in some small archipelagos such as Diego Garcia (and in the Seychelles) co-occur, highlighting the intricacy of the phylogeography of *H. frenatus*.

These current patterns highlight both the high levels of diversity, particularly within the native range, and suggest a high number of colonization events required to explain their current distribution. All five primary lineages are currently found in India, Sri Lanka and/or Myanmar, but without a comprehensive sampling across this area and an increased number of markers with various levels of resolution, the timings of the different Western Indian Ocean island colonizations remain unknown. While there is yet no clear evidence for natural and old colonization events (e.g., differentiated lineages endemic from certain islands or groups), it does appear possible that this species has been transported in multiple waves, perhaps initially in pre-European times, but that these few early dispersals are now predominantly obscured by a much greater number of recent and ongoing translocations associated with modern transportation networks.

The patterns revealed here related to the three primary lineages identified allow for the development of provisional and testable hypotheses. The widespread 'yellow' lineage (**Figure 3**) occurs on scattered atolls of the coralline Seychelles. *H. frenatus*, however, was not present on the islands from which these atolls were colonized when they were first sampled in the 19th century. In addition, the yellow lineage still does not occur in Mauritius, and *H. frenatus* was only confirmed in the granitic Seychelles (Mahé) in the 1990s. Since this lineage occurs widely, both on the mainland and in the islands of Wallacea and the Pacific, it is likely to have been present in Sumatra and Borneo when the Austronesian voyagers colonized Madagascar and the Comoros. No archeological remains have been found to confirm that they crossed mid-ocean (Anderson et al., 2018a). Geckos could still have been dispersed either via shipwrecks that did not result in an archeological signature, or via lost mariners who strayed from the Maldives (Agarwal et al., 2019).

The 'red' lineage's presence in the Indian Ocean only on Madagascar and the Comoros (Rocha et al., 2010), could match the profile of Indian trade with East Africa and Madagascar/Comoros in the medieval and early modern period (Boivin et al., 2013). Specifically, the geographic distribution could be correlated with the distribution of the introduced Indian civet *Viverricula indica* found in Madagascar, Comoros, the East African islands of the Zanzibar group, and Socotra (Gaubert et al., 2017), but nowhere else in the western Indian Ocean. The third (green) lineage could correspond to more modern trade and travel (notably

to formerly isolated Diego Garcia), which may also be responsible for the yellow lineage's dispersal to Australia and the Pacific.

Higher resolution datasets, through either greater number of targeted markers such as SNPs or the retrieval of complete mitochondrial and nuclear genomes, are required to further investigate the lineage splits and chronology of these different dispersals, but the patterns presented are suggestive, and the use of these commensal species as tracers for early human movements merits further consideration. This approach would be significantly improved through denser sampling of mainland southeast Asia and the other suggested sources of all the lineages.

Furthermore, determination of dispersal patterns based on any single molecular marker, such as mtDNA, needs to be treated with caution. In Southern Europe, patterns of minimal variation in mtDNA in two unrelated gecko species conflicted with nuclear markers, suggestive of a "selective sweep" that could obscure phylogeographic history based on mtDNA (Rato et al., 2010, 2011). A higher than usual nDNA/mtDNA diversity pattern was also identified in *H. frenatus* (Tonione et al., 2011), which certainly warrants further investigation and highlights the need to interpret cautiously the phylogeographic patterns based on mtDNA.

Finally, it appears from the current data that some gecko species and lineages are significantly more amenable to human translocation, or are more efficient at establishing colonies thereafter. From the greater than 165 currently recognized species of genus *Hemidactylus*, ten have intercontinental distributions, with two that are widely present in Western Indian Ocean islands, *H. mabouia-mercatorius* complex and *H. frenatus*, among the five most widespread and invasive *Hemidactylus* (Rocha et al., 2010; Weterings and Vetter, 2018).

As noted earlier, geckos have specific characteristics that make them efficient colonizers, but the characteristics that make some species especially effective remain unknown. Several studies have suggested that thermal physiology may play a role. Thus, an investigation of thermal tolerances in widespread species, relative to those with more restricted ranges may be revealing. Clearly *H. frenatus* is able to colonize what is thought to be less optimal habitat (McKay and Milenkaya, 2020), and there is some evidence for increased cold tolerance in invasive populations (Lapwong et al., 2021). On the other hand, *H. frenatus* showed no evidence of increased boldness which is often (although not necessarily) associated with invasive species (Nordberg et al., 2021).

The identification of likely "cryptic species" within both *H. mabouia* species-complex and *H. frenatus*, however, complicates the situation, since it becomes unclear if the same lineages have been compared, or if some lineages have unique characteristics. Modeling approaches, to determine potential ranges, and the impact of climate change (e.g., Rödder et al., 2008), as well as analyses of diet, behavior and other ecological variables, may benefit from determining which lineages within these diverse species are being compared. The sequence dataset presented in this study may form a useful comparative framework for such future assessments.

CONCLUSION

Atypical distribution patterns of *H. parvimaclatus* and *H. frenatus* on outlying atolls and sand cays of the Seychelles, coupled with an historic absence on the more populated islands are compatible with a hypothesis of early, pre-European or even natural, colonization patterns. We attempted to verify this for *H. frenatus* using analysis of CYTB sequence data from modern and museum specimens. Our results highlight high diversity across its native range, indicating that it is a potential species complex, as well as the multiple translocation events needed to explain its current distribution. Ultimately, while it was not possible to clearly define their patterns and timings without a greatly increased sampling across its native range, it remains tempting to hypothesize that they reflect the different routes and timings of human dispersals across the region, while accepting that older patterns may be obscured by frequent and ongoing recent colonization events. Increased sampling of both specimens and genomic variation is a promising way to further investigate these questions and to better understand the reasons underlying some geckos' extreme colonizing capabilities.

METHODS

Initially, 97 tissue samples of *Hemidactylus frenatus* were analyzed: 51 specimens were obtained from museum collections (Field Museum, Chicago; British National History Museum, London; Smithsonian, Washington DC), and 46 modern specimens were collected in the field by Dr. J. Chris Hillman and Solomon Pomerantz (Sealinks Project). Museum samples were mainly stored in ethanol or formalin, while the modern tissue samples were dried. To enable the data collected here to be directly compared with the phylogeographic patterns obtained by Rocha et al. (2010), 14 samples representing distinct haplogroups based on 16S rRNA sequences from this earlier work were re-extracted and included in this study. An additional 15 specimens (including two outgroups) were included from GenBank (**Supplementary Table 1**).

All samples excluding those previously analyzed by (Rocha et al., 2010) were analyzed in the facilities at the Archeology Department of Durham University. For these, DNA extractions were performed using Qiagen Microkit following the manufacturers' instructions. A 463 bp region of the mitochondrial cytochrome b was amplified and sequenced in one fragment, in 25 ul reactions (1U of Sigma Jump Start Taq (0.2 ul), 10 mM primers (0.625 ul each), 25 mM MgCl₂ (4 ul), 10* Buffer (2.5 ul) 25 mM dNTP mix (0.25 ul) with 1 ul DNA extract and made up to volume with H₂O) and annealing temperatures of 58-59°C. Due to the fact that many specimens were from museum samples, specific primers were designed (5'-3'): CTAATGATCCTCCGCAAAGC and AATCCGCCTCAAATTCCTG, based on the sequence of the whole mtDNA of *Hemidactylus frenatus* (Accession number NC_012902). For the specimens previously analyzed by Rocha et al. (2010), universal Cytochrome b primers (GluDG and Cytb2H - (Palumbi, 1996) were used to amplify a fragment that

was 417 bp, missing the last 46 bp relative to the remaining samples. Conditions were as above, but using 1U of MyTaq and the associated Mastermix Buffer, and with an annealing temperature of 50°C. These PCRs were carried out in the laboratories at CIBIO, University of Porto. Sequencing reactions were carried out using both primers by the DNA Sequencing Service at the School of Biological and Biomedical Sciences at Durham University, while those from CIBIO were purified and sequenced using a commercial company (Genewiz, Germany).

While all of the samples from Rocha et al. (2010) could be amplified, due to the known issues of extracting DNA from museum specimens, and especially those stored in formalin, (reviewed in Hykin et al. (2015), only one “old” museum sample yielded DNA, and in total only 64 samples were successfully sequenced (information detailed in **Supplementary Table 1**). Electropherograms were manually inspected and corrected, and manually aligned using both Geneious R6 version (Kearse et al., 2012) and BioEdit (Hall, 1999). All showed typical mtDNA base composition, and could be translated into expected amino acid sequences for the gene. Regarding the ingroup (*H. frenatus*), the alignment had 106 variable and 74 parsimony informative sites. New sequences were submitted to GenBank (accession numbers OL880471-OL880521).

Phylogenetic analyses were performed by construction of Bayesian trees using MrBayes version 3.2.2 (Ronquist et al., 2012). The best-fit nucleotide substitution model, selected in jModelTest2 (Darriba et al., 2012) under the AIC criterion was the HKY + G model. The analysis was run for 5,000,000 generations, with a sample frequency of 5,000 and with a burn-in period of 25%, with remaining trees used to infer a consensus tree and calculate Bayesian Posterior Probabilities. A Maximum likelihood (ML) approach was also employed to estimate a phylogeny, using PhyML 3.0 (Guindon et al., 2010), both for defining the most appropriate model of molecular evolution under the AIC criteria, and producing a phylogeny. The chosen model was again the HKY + G model, and support for the phylogenetic tree was inferred with 1,000 bootstrap replicates. The phylogenetic trees were imported to FigTree v.1.4.2 (Rambaut, 2014) for graphical visualization and editing. Two divergent species from the genus, *Hemidactylus shihraensis* and *Hemidactylus dawudazraqui*, were used as outgroups. The full resulting tree (BI consensus; complete tips labeled) with bootstraps and posterior probabilities is shown on **Supplementary Figure 1**.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author/s.

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Agarwal, I., Ceriaco, L. M. P., Metallinou, M., Jackman, T. R., and Bauer, A. M. (2021). How the African house gecko (*Hemidactylus mabouia*)

ETHICS STATEMENT

Permits for fieldwork and tissue collection were obtained from SBS (Seychelles Bureau of Standards) for Seychelles specimens (granted to SR and DJH). Permission to sample museum specimens was secured from the museums after a destructive application process.

AUTHOR CONTRIBUTIONS

ASC, and GL conceived of the study. ASC collected and analyzed historical records. SR, AT, and DJH extracted DNA and generated and analyzed mitochondrial sequences. SR, AT, GL, DJH, and ASC wrote the manuscript with contributions from all authors.

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SUPPLEMENTARY MATERIAL

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