

## Cryptic variation and recent bipolar range expansion within the Stumped-Toed Gecko *Gehyra mutilata* across Indian and Pacific Ocean islands

Sara Rocha<sup>1,2,3,5</sup>, Ivan Ineich<sup>4,6</sup>, D. James Harris<sup>1,2,7</sup>

<sup>1</sup> CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, Campus Agrário de Vairão, 4485-661 Vairão, Portugal

<sup>2</sup> Departamento de Zoologia e Antropologia, Faculdade de Ciências, Universidade do Porto, Praça Gomes Teixeira, 4099-002, Portugal

<sup>3</sup> Departamento de Bioquímica, Genética e Inmunología, Facultad de Biología, Universidad de Vigo, Vigo 36310, Spain

<sup>4</sup> Muséum national d'Histoire naturelle, Département de Systématique et Evolution, Section Reptiles, CP n° 30 - 25 Rue Cuvier, 75005 Paris, France

<sup>5</sup> E-mail: sara.rocha@mail.icav.up.pt

<sup>6</sup> E-mail: ineich@mnhn.fr

<sup>7</sup> E-mail: james@mail.icav.up.pt

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### Abstract

With an impressively wide distribution, *Gehyra mutilata* is present on almost all Indian and Pacific Ocean islands and in large regions of Southeast Asia and Indonesia. Mitochondrial sequence data (~500 bp) from individuals covering large parts of its (mainly insular) distribution reveals deep cryptic variation and strong geographic structure, with two well differentiated lineages. Molecular data also reveals that the wide Indian and Pacific insular distribution of *Gehyra* is very recent and, at least across the Indian Ocean islands, most probably the result of human-aided dispersal, as no variation within this lineage was found. Further research is needed to determine geographic patterns of variation across Southeast Asia, the level of genetic variation, and possible mechanisms of speciation. If recognized as distinct taxa, the binomen *Gehyra insulensis* should be resurrected, and applied to the 'Pacific lineage'.

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### Introduction

Geckos of the genus *Gehyra* (Gray, 1834) are some of the most prominent and widespread geckos within the

Australasian and Pacific regions. *Gehyra mutilata* (Wiegmann, 1834) is widespread throughout the Pacific basin, large regions of Southeast Asia, Indonesia and the Indian Ocean. It also occurs in Mexico and it is known to have been introduced in California (USA) and in the French Guiana (Ineich and de Massary, 1997). It occurs in both natural forests and disturbed garden or urban areas and it is the least studied widespread gecko in the world, with little information available on genetic or morphological variation across its distribution.

Fisher (1997) examined allozyme variation within this species across some Southeast Asian (Thailand, Philippines) and Pacific (from Belau to Hawaii) localities and found that 1) samples across the Pacific showed no genetic variation for the loci surveyed, and 2) there were fixed differences at three loci between a group consisting of the Pacific and two southern Asian populations (the 'southern mainland type', sensu Fisher, 1997) and a second group of four southern Asian populations (the 'northern mainland type', sensu Fisher, 1997). Both groups were present in the Philippines and in Thailand, although sympatry was not found. Fisher (1997) interpreted his results as indicating that the source of the Pacific populations was probably southern Asia and pointed to a recent, possibly human-mediated, range expansion, but the lack of variation at these markers prevented assessment of alternative dispersal hypotheses. Indian Ocean populations were not studied, despite the fact that they are considered to

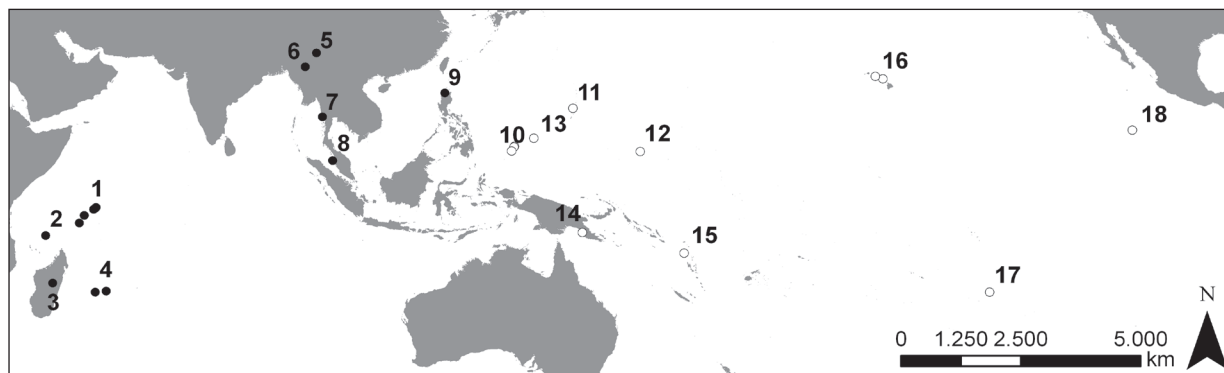


Fig. 1. Sampling localities: Seychelles (1); Aldabra (2); Madagascar (3); Mascarenes (4); Myanmar (5-7); Malaysia (8); Luzon, Philippines (9); Palau (10); Mariana (11); Caroline (12, 13); Papua New Guinea (14); Vanuatu (15); Hawaii (16); French Polynesia (17) and Clipperton Atoll (18) (see Appendix 1 for exact location and details on origin of the samples). Localities harbouring different mtDNA lineages (see results) are colour coded (black versus white dots).

have been introduced throughout this region (Cheke, 1984). It has been assumed (de Massary, 1992; I. Ineich quoted in Glaw and Vences, 1994) that *Gehyra* populations of Indonesia and from the western Indian Ocean islands are distinct from those of Oceania, and that *G. insulensis* should be resurrected and used as the proper designation for some or all Pacific populations. Faster evolving mtDNA data could provide increased

resolution regarding genetic variation of *G. mutilata* across the Pacific and could help in assessing the source and mechanisms related to the origin of Indian Ocean islands populations.

It is important to assess the mechanisms explaining the presence of this species in oceanic islands; introduced reptiles can have varied negative impacts on native species, including predation, competition for food, basking sites and other resources, hybridisation and spread of diseases and parasites, and they may alter the habitat of native species or disrupt ecosystem dynamics. All these processes are especially dangerous when they occur on islands, where the number of endemic species is generally higher and ecosystems are more vulnerable to introductions (Shine *et al.*, 2000). Furthermore, it is on islands that introductions are more frequent and that invasive species have a higher probability of successful establishment (Kraus, 2003). Indeed, several examples exist of strong negative impact of introduced reptiles in island systems (Cogger *et al.*, 1983; Powell *et al.*, 1990; Petren and Case, 1996; Cole *et al.*, 2005).

Our main goal was to assess the origins and genetic variation of Indian Ocean populations of *Gehyra mutilata*. By comparing them to other southern Asian and Pacific populations, we could assess their putative distinctiveness and better understand previously hypothesised dispersal mechanisms (Fisher, 1997).

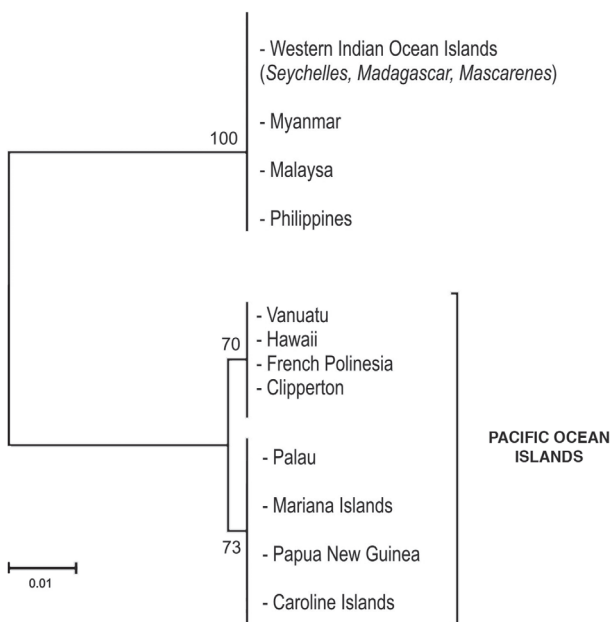


Fig. 2. ME tree for the 517bp data matrix (complete gap deletion option) with bootstrap values shown alongside the branches. The two haplotypes from the Pacific Ocean clade and the two main clades are separated by two and 53 mutational steps, respectively.

## Material and methods

Specimens were collected during fieldtrips across the Indian Ocean and Pacific Islands and additional sam-

ples obtained from museums (see Fig. 1 and Appendix 1 for locality details).

Genomic DNA was extracted following a standard high-salt protocol (Sambrook *et al.*, 1989) and part of the 16s rRNA gene (517 bp) was amplified and sequenced using primers 16sA-L and 16sB-H (Palumbi *et al.*, 1991). Amplification conditions are described in Harris *et al.* (1998). Amplified fragments were directly purified with ExoSap-IT (Amersham-Pharmacia Biotech) and sequenced on an ABI 3730xl automated capillary DNA sequencer and aligned with available *Gehyra* sequences from GenBank. Generated sequences are deposited in GenBank under accession numbers FJ613425-FJ613473 and the full alignment is available on the TreeBASE website ([www.treebase.org/treebase](http://www.treebase.org/treebase); study accession number = S2324). As the pattern of genetic variation was clear, evolutionary history was inferred using the Minimum Evolution method (Rzhetsky and Nei, 1992), with the evolutionary distances computed using the Maximum Composite Likelihood method (Tamura *et al.*, 2004) and presented in units of number of base substitutions per site. One thousand bootstrap replicates (Felsenstein, 1985) were performed to estimate nodal support. The ME tree was searched for using the Close Neighbor Interchange (CNI) algorithm (Nei and Kumar, 2000) at a search level of 2. The Neighbor Joining algorithm (Saitou and Nei, 1987) was used to generate the initial tree. Due to the shorter size of some of the sequences (Genbank sequences DQ857338/Madagascar; DQ270549 and AY517559/Mauritius), positions containing gaps and missing data were eliminated from the dataset ('complete gap deletion' option), leaving a total of 318 positions in the final dataset, from which the ME tree topology was inferred. Phylogenetic analyses were conducted in MEGA4 (Tamura *et al.*, 2007). Additionally, a haplotype median-joining network (Bandelt *et al.*, 1999) was obtained using NETWORK4.5 (Fluxus Engineering, Suffolk, UK), in which the shorter sequences were excluded, indels of more than 1bp were coded as single events, and the full fragment length (517 bp) was considered.

## Results

From a total of 53 individuals analysed from the Indian Ocean islands (24), Southeast Asia (14), East (6) and West (9) Pacific Islands, sequencing of the 16s rRNA partial fragment revealed three haplotypes, belonging

to two strongly differentiated lineages, and with a remarkable geographic structure. Southern Asian (Myanmar, Malaysia and Luzon, Philippines) and Indian Ocean islands individuals exhibited the same haplotype, with around 10% sequence divergence from the 'Pacific lineage', which harbours two closely related haplotypes (Fig. 2).

There were 55 variable positions, 53 of them diagnostic for the two clades, including four indels of variable (1-10 bp) size. In every case alignment was unambiguous and no 'gappy' region was excluded from the analysis. GenBank sequences from Madagascar and Mauritius had considerable 5' or 3' missing data regions, thus restricting the comparable fragment size including all sequences to 334 bp. As they were identical to all other Indian Ocean islands samples for the available sequence fragment (in total 418 bp for DQ857338/Madagascar; 495 bp for DQ270549/Mauritius; and 499bp for AY517559/Mauritius), they were excluded from the haplotype network construction, so that all the differences within the full length of the sequenced fragment could be represented.

## Discussion

As had been hypothesized based on allozyme data (Fisher, 1997), there are two cryptic lineages within *G. mutilata*. Levels of differentiation at the 16s rRNA marker (~10%) are higher or equivalent to differentiation observed between known distinct species of geckos (Jesus *et al.*, 2005; Rocha *et al.*, 2005; Weiss and Hedges, 2007).

Our data show that Western Indian Ocean populations (Seychelles, Mascarenes, Madagascar) belong to the same lineage as individuals analysed from the Philippines (Luzon Island) and mainland Asia (Myanmar and Malaysia).

Fisher (1997) observed the coexistence of two lineages in the Philippines (and Thailand) that possibly correspond to the ones that are now evident at the mtDNA level, with the Negros Island population belonging to the 'southern mainland type', also widespread across the Pacific, and the other two populations (Luzon and Camiguin) belonging to the same lineage as the two northern Thailand populations (the 'northern mainland type'). The Philippine material included in our study is from Luzon Island, which is also the type locality of *G. mutilata* (Manila), and belongs to the same clade of the remaining Southern Asia and Indian Ocean individuals. On the basis of these data,

we argue that they should all be referred to as *Gehyra mutilata* sensu stricto with *Hemidactylus peronii* Duméril and Bibron, 1836 (type locality Mauritius), *Gecko pardus* Tytler, 1865 (type localities Rangoon, Moulmein and Port Blair) and *Peropus packardii* Cope, 1869 (type locality Penang) as synonyms. Indonesian populations (on which the names *Hemidactylus platurus* Bleeker, 1859 and *Gehyra beebei* Annandale, 1913 are based) were not included in our study and their status cannot yet be assessed. If future work leads to the recognition of the Oceanian population as a separate species, priority shall be given to the name *Dactyloperus* (= *Gehyra*) *insulensis* Girard, 1857 (type locality Sandwich Islands). We suggest however, that a formal nomenclatural change be delayed pending further studies on the effective isolation of the two lineages and the geographic structure of genetic variation.

Remarkably, little or no variation was found within the ‘Indian Ocean and Southern Asia’ and ‘Pacific’ lineages, respectively, indicating a recent and fast spread of the species throughout these areas, probably from sources located in Southern Asia. The hypothesis of a recent, human-mediated, dispersal of *G. mutilata* across Indian Ocean islands is supported by the observation that records of *G. mutilata* are either recent (for Madagascar, the Mascarenes and the Seychelles - Glaw and Vences, 1994; Gerlach, 2007; Cheke and Hume, 2008) or absent (for the Comoros - Carretero et al., 2005) across this region.

Despite the near-complete absence of variation, the two haplotypes constituting the ‘Pacific lineage’ exhibit some geographic structure, being exclusive of either Western populations (comprising Palau, New Guinea and Micronesia – Mariana and Caroline) or Eastern Pacific populations (Polynesia, Vanuatu and Clipperton). This may indicate that two colonisation routes existed, although a single colonisation followed by limited gene flow would also explain the data. Interestingly, the ‘two routes’ pattern would fit Fisher’s (1997) ‘non-European’ human-mediated dispersal hypothesis involving two - Australoid and proto-Polynesian - Pacific colonisations. However, the Melanesian populations from Vanuatu, which share the Eastern and not the Western Pacific haplotype, do not fit the picture. The only specimen from Vanuatu used in this study was recently collected on Torres Islands, in northern Vanuatu, where the species was locally abundant, thus possibly reflecting a recent introduction. Previous records from Vanuatu are very scarce (only one record from a single specimen from Efate, collected in 1924 or 1925 - Medway and Marshall, 1975;

Cranbrook and Pickering, 1981) and it is possible that both Western and Eastern lineages now occur on that archipelago, the Eastern one being very recently introduced. It would be interesting to compare Fijian and Solomon Islands populations with Vanuatu to test conflicting biogeographical hypotheses for that area (Bauer, 1988).

Clipperton Atoll populations belong to the Eastern Pacific lineage and were generally considered as being recently introduced from Mexico (Lorvelec and Pascal, 2006). However, a natural occurrence on the atoll cannot be excluded. Likewise, the origin of Mexican populations is still under debate (Ineich and Blanc, 1987).

It is well known that *G. mutilata* is an effective island colonist possessing several morphological and ecological adaptations that facilitate successful inter-island travel (see Ineich and Blanc, 1987). It even recently recolonized Krakatau Island in Indonesia, which was completely covered by lava after an historical volcanic eruption (O’Shea and Cook, 2006) and is also present in southern Japan (Ota and Yamashita, 1985). Genetic uniformity of both lineages, across the Indian Ocean on the one hand and the Pacific on the other, is classically interpreted as proof of their recent spread through human agency (see e.g., Bruna et al., 1996). However, given that human colonisation of Pacific islands is also extremely recent (Belwood, 1997; Blust, 1995; Kirch, 1997), the hypothesis that this species was already present on the islands before man cannot be rejected with present data, i.e., colonisation can be natural, and ‘pre-human’, but still recent, and thus without time for organisms to exhibit geographical patterns of genetic variation that would allow the trace of the colonisation routes. Across most of the Pacific Islands, *Gehyra mutilata* occupies a wide range of habitats, and not only the ones related to man. It is usually not very abundant but geographically widespread and there are no clear gaps in its distribution in French Polynesia, as would be expected for a very recent ‘anthropogenic’ species (Ineich and Blanc, 1988).

Use of faster evolving genetic markers and further sampling along south-eastern territories between Myanmar and Indonesia/Papua New Guinea and comparison with proposed human migration routes should clarify this question and may possibly shed light on the causes of speciation within this apparent species complex.

The fact that *G. mutilata* is clearly a ‘newcomer’ across the major oceanic island areas is relevant for consideration of its effect on island ecosystems. As al-

ready discussed, the impact of alien species on islands can be considerable. The impact of *G. mutilata* on other Indian Ocean gecko populations is unknown. Across the Pacific this species is less abundant than many other introduced house geckos (*e.g.*, several species of the genus *Hemidactylus* Gray, 1825) but it is nowadays widespread and abundant across the Seychelles, with established populations on both coralline and granitic islands. Bringsøe (2006; see also Rösler, 2007) hypothesised that nocturnal activity of *G. mutilata* (that he considered as recently introduced) had a significant impact on, and led to nocturnal activity of some, Seychelles day geckos such as *Phelsuma sundbergi* Rendahl, 1939. We do not agree with that hypothesis and rather think that well known behavioural plasticity of island reptiles (Ineich and Blanc, 1987) better explains this recent shift of *P. sundbergi* to exploit an easily obtained and abundant food resource located around artificial lights. Across Indian Ocean islands this species seems to be rapidly spreading: earliest *G. mutilata* records date back from 1885 (1905 for the first precise locality record - Victoria, Mahé Island - Gerlach, 2007), but this species is nowadays present on almost all islands of the archipelago, including the outer ones (Gerlach, 2007). Not exclusive to urban areas, *G. mutilata* in the Seychelles can be also found in more pristine vegetation and montane areas, and it has even been observed co-existing with the native gecko *Urocotyledon inexpectata* Stejneger, 1893 at the very specific habitat/nesting sites of that species: rocks covered with empty wasp nests in which the eggs are laid (S. Rocha, *pers. obs.*, 2007). Interspecific competition may have an enormous impact on endemic gecko populations (see Cole *et al.*, 2005 and references therein), such as *Hemidactylus mercatorius* (*sensu* Vences *et al.*, 2004) on Aldabra (S. Rocha, *pers. obs.*, 2007) or *Urocotyledon inexpectata* in the granitic Seychelles, and should be the target of specific monitoring.

Concerning Pacific island populations, we have found that they clearly avoid artificial lights, contrary to Indian Ocean *G. mutilata*. It is also noteworthy that they avoid humid forest habitats where they are rarely observed. Instead, they are more abundant in littoral dry forests (*e.g.*, the Tuamotu atolls in French Polynesia), even when isolated and far from human habitations, but also occur in and around houses. They shelter by day under loose bark on dead trees, and lay two adhesive eggs (sometimes in communal laying sites) in the same microhabitat. They occupy more xeric habitats than *G. oceanica* (Lesson, 1839), a more com-

mon Pacific island congener, thus explaining its colonization success on the American continent, even in Mediterranean climates such as in California, and on some remote and dry areas like Clipperton Atoll in Eastern Pacific.

Competition with other species in the Pacific islands apparently does not occur, or at least not at a significant level. The impact of *G. mutilata* on native species, if really recently introduced, seems limited. Perhaps this can be considered as evidence of its slightly 'older' arrival in the Pacific, and establishment of equilibrium with other sympatric species. The rarity of *G. mutilata* on Pacific islands compared to the initial explosive demography of *H. frenatus* Duméril and Bibron, 1836 (Case and Bolger, 1991), suggests that its current impact on other local species is not significant and that the species does not constitute a major threat to other native species.

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## Appendix

Specimens used in this study and respective locations. Sequences obtained from GenBank are identified by the accession number. Museum acronyms are BPBM: Bernice P. Bishop Museum, Hawaii, USA; CAS: California Academy of Sciences, San Francisco, USA; MNHN: Muséum National d'Histoire Naturelle, Paris, France; USNM: United States National Museum, Smithsonian Institution, Washington, USA. See also Fig. 1.

**Indian Ocean:** MA14, MA16: Beau Vallon, Mahé, Seychelles; MA21, MA22: Victoria, Mahé, Seychelles; 2MA10: Glacis, Mahé, Seychelles; 2MA16: North, Mahé, Seychelles; 2MA52: La Reserve, Mahé, Seychelles; 38713, 38714: La Passe, Silhouette, Seychelles; PL16: Anse Volbert, Praslin, Seychelles; AD1, AD25, AD26: Picard, Aldabra, Seychelles; APH8, APH9, APH11, APH12, APH13: Alphonse, Seychelles; GmDer1: Desroches, Seychelles; GmReu1, GmReu3: Réunion, Mascarenes; B-16 (DQ857338): Antananarivo, Madagascar; P-25 (DQ270549): Gorges de la Rivière Noire, Mauritius; D25 (AY517559): Mauri-

tius. **Southern Asia:** USNM-FS 499244, USNM-FS 499246: Lasam, Luzon Is., Philippines; CAS229883, CAS229884: Da Wei Dist., Taninthayi Div., Myanmar; CAS232241, CAS232242, CAS232246, CAS232250, CAS232251, CAS232253, CAS232255: Khandi Dist., Sagaing Div., Myanmar; CAS232804, CAS232809: Myitkyna Dist, Kachin St., Myanmar; K6 (AY217956): Pulau Pinang, Malaysia. **Pacific Islands:** USNM-FS 220248: Babeldaob, Airai, Palau; USNM-FS 220257: Malakal, Palau; USNM-FS 220441: Koror, Ngerbeched, Palau; USNM-FS 220541: Angaur, Palau; USNM-FS 536087: Saipan, San Vicente, Mariana Islands; BPBM 19753: Rossel Island, Damunu, Papua New Guinea; BPBM 15436: Duabo, Pini Range, Milne Bay Province, Papua New Guinea; USNM-FS 220293: Pohnpei, Kolonia, Caroline Islands; USNM-FS 224263: Yap, Colonia, Caroline Islands; 690: Torres Islands, Vanuatu; USNM-FS 221195: Oahu, Lanikai, Hawaii; USNM-FS 221051: Maui, Wailuku, Hawaii; MNHN 2007-0098: Gambier, Vahanga Island, French Polynesia; Gm1625, Gm1659: Clipperton Atoll.