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ARTICLE

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Abstract: We reassess the systematics of *Hemidactylus scabriceps*, a recently rediscovered and poorly known gecko, and elucidate its phylogenetic position using molecular data for the first time. Contrary to previous speculations prompted by its morphological resemblance to other terrestrial *Hemidactylus*, our phylogenetic analyses recovered *H. scabriceps* to be a part of a clade consisting of the large-bodied, rock-dwelling *Hemidactylus* – the *H. prashadi* group. *Hemidactylus scabriceps* also shows high levels of intraspecific genetic divergence, indicative of cryptic diversity. We also confirm the synonymy of the monotypic genus *Lophopholis* (erected for *H. scabriceps*) with *Hemidactylus*. We elaborate on the morphology of the type specimen and other recent voucher specimens, and compare it with sister species and other ground-dwelling *Hemidactylus* in peninsular India. Species distribution of this ‘outlier’ clade member has been modeled using MaxEnt. These exercises confirm that it is primarily a smooth-scaled, plain-dwelling, terrestrial species unlike other members in its clade. This unexpected pattern of genetic alliance and contrasting body form plus habitat associations further underscores the unstudied complexity of peninsular India’s geological history. Historical denudation of rock formations could have driven evolution of some of these otherwise rupicolous, scansorial gekkonids into smaller terrestrial lizards.

Keywords: Clade member, distribution modeling, habitat associations, Indian dry zone, morphology, phylogenetic position, rock dwelling.

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भारतीय वन्यजीव संस्थान
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INTRODUCTION

Hemidactylus Oken, 1817 is one of the most speciose gekkonid genera in the world, with about 150 congeners currently recognized, of which around 34 are found in India (Carranza & Arnold 2006; Giri & Bauer 2008; Bauer et al. 2010; Uetz & Hošek 2018; Chaitanya et al. 2018). The Indian *Hemidactylus* are part of a tropical Asian radiation, and consist of five major clades - *H. prashadi*, *H. flaviviridis*, *H. brookii*, *H. frenatus* and *H. platyurus* groups (Bansal & Karanth 2010). Of these, the *H. brookii* group encompasses all the thus-far sampled ground-dwelling *Hemidactylus* that are found in central and peninsular India (Bansal & Karanth 2010; 2013). Previous studies show that the ground dwelling clade of geckos are sister to *H. brookii*, the clade that consists of five currently recognized terrestrial species namely *H. reticulatus* Beddome, 1870, *H. albofasciatus* Grandison & Soman, 1963, *H. satarensis* Giri & Bauer, 2008, *H. imbricatus* Bauer, Giri, Greenbaum, Jackman, Dharne & Shouche, 2008, *H. gracilis* Blanford, 1870 (Bansal & Karanth 2010). *Hemidactylus scabriceps* was considered to be closely related to the ground-dwelling *Hemidactylus* due to its superficial morphological similarities such as a reduced subdigital scansorial apparatus, imbricate tail scales, reduced subcaudal scales and a terrestrial lifestyle (Bauer et al. 2010). Similar assumptions were made for *Dravidogecko anamallensis* (Günther, 1875) which was later resolved and found to be sister to the Indian *Hemidactylus* radiation (Bansal & Karanth 2013). In the past, *H. scabriceps* has been misidentified on many occasions with other marginally co-occurring terrestrial congeners such as *H. reticulatus*, despite its distinctive scalation (Ganesh et al. 2017).

Annandale (1906) originally described this species as *Teratolepis scabriceps* based on its imbricate scalation, as the second congener next to *T. fasciatus* (currently *H. imbricatus*, after Bauer et al. 2008). Later, a new monotypic genus *Lophopholis* was erected by Smith & Deraniyagala, 1934 to accommodate this species as it was considered quite unique (Smith 1935). Parker & Taylor (1942) reassigned the species back to *Teratolepis* along with various other African geckos such as *H. isolepis* and *H. ophiolepis*, attributing this generic transfer to the imbricate scalation. Due to the similarity of *H. scabriceps* with other oriental *Teratolepis* and *Hemidactylus* geckos, it was called the 'Oriental imbricate-scaled *Hemidactylus*'. Subsequently, the generic allocation of this species was debated and later the genus *Lophopholis* was synonymized with *Hemidactylus* by Loveridge (1947). Furthermore, Bauer et al. (2008) synonymized the genus

Teratolepis with *Hemidactylus* based on a multilocus molecular phylogeny and mentioned the possible close relationship of *H. scabriceps* with *H. imbricatus* (Image 5), along with other small-bodied, ground-dwelling endemic geckos such as *H. albofasciatus*, *H. gracilis* and *H. reticulatus*, which themselves are genetically-tested clade members (Bansal & Karanth 2010).

Since its description, *H. scabriceps* was not re-sighted for 104 years till an uncollected specimen was reported from Mayiladuthurai in the Coromandel Coastal Plains (Ganesh & Chandramouli 2010). More recently, Ganesh et al. (2017) dug up some obscure publications reporting this species under a wrong name, described a series of preserved specimens including its hemipenal morphology, provided natural history notes and mapped its locality based on newer fieldwork. *Hemidactylus scabriceps*, however, still remains an intriguing gecko for both Indian and Sri Lankan herpetologists due to its assumed rarity and unknown phylogenetic relationships, since it is underrepresented and poorly sampled (Bauer et al. 2010). In this paper, we provide for the first time data on its phylogenetic position, elaborate on its morphology, habitat associations and distribution.

MATERIALS AND METHODS

Specimens of *H. scabriceps* were opportunistically collected from three ecoregions: Coimbatore plateau, Thanjavur delta and Kalakad foothills, abutting Western Ghats in peninsular India. The specimens were deposited in the collections of BNHS (Bombay Natural History Society, Mumbai), IISc - CES (Indian Institute of Science, Bengaluru - Center for Ecological studies), and IISER (Indian Institute of Science, Education and Research, Thiruvananthapuram). Tissue samples were collected from the tail tips and liver of the specimens and sent for molecular analysis and sequencing at the Indian Institute of Science (IISc), Bengaluru and Osmania University, Hyderabad. The geographic coordinates of the localities were obtained from Garmin 62 GPS. Other comparative materials, including the type specimens, were examined at the Natural History Museum, London (BMNH).

Morphological analysis

Morphological and meristic data were collected following methods described by Giri & Bauer (2008) and Mahony (2009) with Mitutoyo™ digital calipers (to the nearest 0.1mm). The following measurements were taken from collected specimens and the museum types: snout vent length (SVL; from tip of snout to vent), trunk

length (TRL; distance from axilla to groin measured from posterior edge of forelimb insertion to anterior edge of hind limb insertion), body width (BW; maximum width of body), crus length (CL; from base of heel to knee); tail length (TL; from below vent to tip of tail), tail width (TW; measured at widest point of tail near the tail base); head length (HL; distance between retroarticular process of jaw and snout-tip), head width (HW; maximum width of head), head height (HH; maximum height of head, from occiput to underside of jaws), forearm length (FL; from base of palm to elbow); ear length (EL; longest dimension of ear); orbital diameter (OD; greatest diameter of orbit), nares to eye distance (NE; shortest distance between anterior most point of eye and nostril), snout to eye distance (SE; distance between anterior most point of eye and tip of snout), eye to ear distance (EE; distance from anterior edge of ear opening to posterior corner of eye), internarial distance (IN; distance between nares), interorbital distance (IO; shortest distance between left and right supraciliary scale rows). Scale counts and external observations of morphology, meristic characters were made using a Wild M5 dissecting microscope.

Species distribution modeling

Species distribution modeling was carried out using MaxEnt v.3.3 (Phillips et al. 2006), which is based on maximum entropy modeling. MaxEnt, a machine learning program that estimates the probable species distribution based on constraints of the environment. It uses presence-only data for prediction and studies show that it has good success rate for small sample sizes compared to other SDMs (Elith et al. 2006; Wisz et al. 2008). We have considered 21 environmental variables - the 19 bioclimatic layers, one topographic layer representing elevation (Hijmans et al. 2005) and one vegetation layer-NDVI (NRSC, ISRO). The 13 location points used in the model were obtained from the recent collections, literature which includes historical points Adayar (13.0012°N & 80.2565°E), and Maricukatte (8.588°N & 79.933°E). The environmental layers were derived from globally interpolated datasets observed from climate stations around the world. All the layers are of approximately 1,000m resolution, clipped for the Indian subcontinent including Sri Lanka and projected on WGS84 Lat-Long map datum. The layers were subjected to a multicollinearity test and 10 bioclimatic variables that were least correlated (Pearson's correlation coefficient $r < 0.85$) were selected for the distribution modeling.

MaxEnt program with following changes was used in the model: auto feature for environmental variables was

selected. The random test percentage was set to 20%, making the training percentage 75%. The regularization multiplier and maximum number of background points for sampling was kept at 1 and 10,000 respectively. With subsampling as replicating model, 15 replicates were used. Maximum iterations were set to 5,000, with 10^{-5} as convergence threshold with threshold rule of 10 percentile training presence as it relatively better at predicting suitable habitat for endemic species (Escalante et al. 2013). The logistic output of the model shows the suitability of the habitat, graded over a range of 0 to 1.

Molecular analysis

Genomic DNA was isolated from 95–100 % ethanol preserved liver tissue sample using phenol: chloroform: isoamyl alcohol reagent (25:24:1 v/v) as described by Sambrook & Russell (2001). Two partial mitochondrial markers, cytochrome *b* (cyt *b*) and NADH dehydrogenase 2 (ND2) along with two nuclear markers, Recombination Activation Gene 1 (RAG-1), Phosducin (PDC) were used to infer the phylogeny of *H. scabriceps* (see Agarwal et al. 2011). These molecular markers were useful for resolving the phylogenetic relationships at deeper nodes. Primers and PCR conditions used were as described in Bauer et al. (2008). PCR products were purified and sequences were obtained commercially from Bioserve Biotechnologies, Hyderabad, India. All PCR amplifications were carried out in 25µL reaction volumes, with 12.5µL of the 2X PCR master mix (Thermo Scientific), 0.5µL forward primer, 0.5µL reverse primer (10 pm/ µL concentration each) and 2µL template DNA added and the final volume was adjusted with nuclease-free water. Reactions were carried out with Thermo Scientific Mastercycler gradient thermocycler. The sequence integrity was analyzed by BLAST tool (Altschul et al. 1997), processed and submitted to NCBI GenBank under the accession numbers given in Table 3 (Appendix 1).

Phylogenetic analysis

The mitochondrial genes cyt *b* (379 bp), ND2 (981 bp) and the nuclear genes PDC (400 bp) and RAG-1 (1000 bp) sequences of representative members of major, well supported *Hemidactylus* groups - *H. flaviviridis*, *H. brookii*, *H. prashadi* and *H. frenatus* (Bansal & Karanth 2010, 2013; Murthy et al. 2015; Giri et al. 2017; Chaitanya et al. 2018) were downloaded from GenBank (accession numbers listed in Table 3 in the appendix). Sequences were aligned with default gap penalties using ClustalW (Thompson et al. 1994) in MEGA 7.0. (Tamura et al.

2011). Protein-coding genes were translated to amino acids to check for the reading frame and premature stop codons. Uncorrected pairwise distances were calculated using the inbuilt program in MEGA.

Sequences of the members of the *H. brookii* sensu lato group that were published prior to the revisions of the group (Mahony 2011; Lajmi et al. 2016) were labeled as *H. brookii* due to the inability to trace and identify the specimens from which the sequences were derived. The same revision, however, shows that the group including the ground-dwelling *Hemidactylus* is monophyletic and is sister to the *H. frenatus* group. Hence, the *H. brookii* epithet is used here indicating individuals that may represent *H. murrayi*, *H. gleadowi*, *H. treutleri*, *H. kushmorensis* or *H. parvimaculatus* (Lanfear et al. 2012).

We used Partition Finder 2.1.1 to pick the partitions and best substitution model for the analysis. The concatenated gene dataset (cyt *b*, ND2, PDC and RAG1) comprise a total of 2760 bp. We built a maximum likelihood (ML) tree in RAxML HPC 7.4.2 through RAxMLGUI v1.3.1 (Silvestro & Michalak 2012) by running ML + thorough bootstrap for 10 runs and 1000 repetitions.

RESULTS

Molecular phylogeny and relationships

Our tree (Image 1) recovered *H. scabriceps* as member of a clade containing *H. triedrus* of peninsular Indian plains, *H. lankae* of Sri Lankan plains, *H. maculatus* of the northern Western Ghats, *H. prashadi* of central Western Ghats, *H. acanthopholis* and *H. vanam* of southern Western Ghats, *H. hunae* of Sri Lankan hill tracts, *H. graniticulus* of southern Eastern Ghats, *H. sushilduttai* and *H. kangenerensis* of northern Eastern Ghats and Chota Nagpur plateau, and more closely with *H. depressus* of Sri Lanka.

From a broader perspective, the ML analyses on the concatenated dataset with sequence lengths of 2760 bp yielded a tree (Image 1) of similar topology to previous studies (Chaitanya et al. 2018). Comparing tree topologies from prior works corroborated the integrity of our trees. *Davidogecko anamallensis* is sister to all Indian *Hemidactylus* that consists of four well-supported groups, *H. flaviviridis*, *H. brookii*, *H. prashadi* and *H. frenatus* (Bansal & Karanth 2010; 2013). As previously known, *H. brookii* sensu lato is sister to the *H. frenatus* group; while *H. scabriceps* falls within the *H. prashadi* group (support seen in tree). The relationship of *H. scabriceps* with other rock-dwelling Indian and Sri

Lankan *Hemidactylus* is strongly supported in our tree.

From a species-specific viewpoint, the pairwise distance matrix revealed 6% divergence in the cyt *b* gene between the two individuals of *H. scabriceps* sampled from different localities (Thanjavur and Coimbatore). The genetic distance between *H. scabriceps* and other species of the *H. prashadi* and *H. brooki* clades are given in Table 1. The high genetic divergence between the populations sampled may indicate that *H. scabriceps* could be a potential species complex that requires further study.

Morphology and body configurations (n=7, in mm) (Images 2 & 3)

A small-sized *Hemidactylus* (30.1–41.3); head short (9.6–13.8); distinct from neck; head broader (4.3–7.4) than high (3.9–6.9); forehead flat; snout (3.5–4.6) longer than orbital diameter (1.0–2.7); snout concave; covered with heterogeneous granular scales; scales on head keeled; small warty scales on parietal region intermixed with granular scales; scales largest on canthal region, size similar to tubercles on parietal region; pupil vertically elliptical with sharp crenellated edges, supraciliaries large when compared to scales on canthal region; pointed posteriorly; becoming smaller and less pointed towards posterior; spinose posteriorly; nostrils close to snout-tip (2.8–3.0), moderately wide (1.3–2.7), fairly close to eye (2.3–3.5); ear opening small (0.2–1.5); orbital diameter slightly smaller than orbit to ear distance; eyes distant from each other (1.4–3.8); rostral large; subrectangular to pentagonal in shape; in contact with nostril and the 1st supralabial, medial groove dorsally, extending more than half the length of the rostral depth; supralabials 7/7 (left/right); infralabials 6/6 (left/right); mental triangular; two pairs of post mentals, inner pair in contact with mental and each other, outer pair not in contact with each other; a pair of smaller chin shields in contact with the outer postmentals followed by elongated shields in two rows in contact with the infralabials; no chin shields posterior to the postmentals; a row of smaller, slightly elongated scales with slightly pentagonal scales wedged in the intersection of the postmental scales; gular covered with small granular scales; trunk of moderate size (13.1–20.7); body slightly depressed, oval in cross-section, dorsolateral fold weak to indistinct; dorsum covered with mildly keeled, imbricate scales with no tubercles; granular scales from head gradually changing into sub-imbricate scales on nape and imbricate scales towards torso; mild keels on dorsal scales distinct, gradually disappearing towards ventral scales, scales at paravertebral line comparatively smaller than other

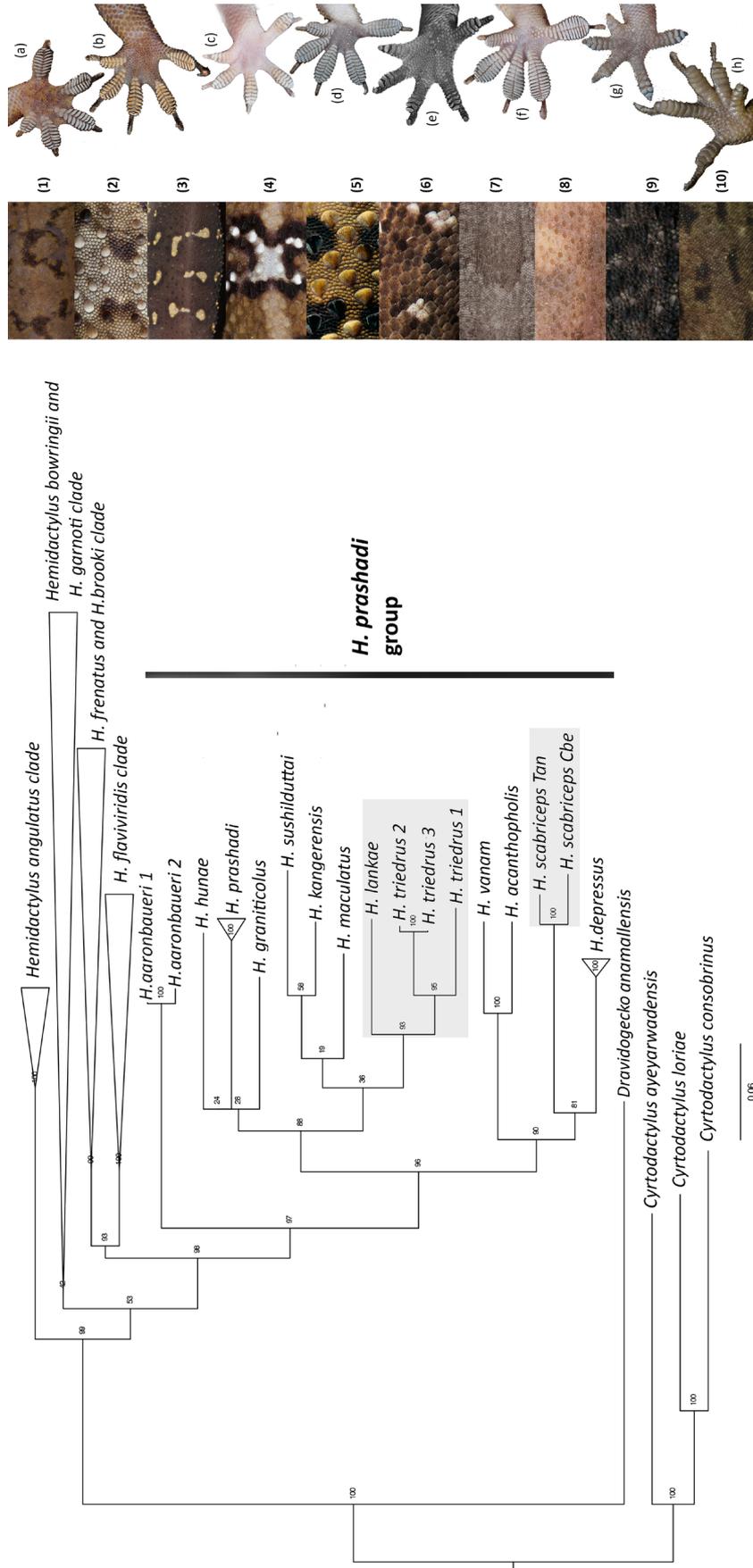


Image 1. ML tree constructed using *cyt b*, ND2 mitochondrial sequences and RAG1, PDC nuclear sequences representing the Indian groups of *Hemidactylus*. Bootstrap support values are mentioned in the nodes. Specimens of *Hemidactylus scabriceps* are suffixed with the location collected from (Cbe-Coimbatore and Tan-Thanjavur). The taxa highlighted in grey denote the plains dwelling taxa. A visual comparison of dorsal scale images of representative clades are as follows: (1) *H. depressus*, (2) *H. graniticolus*, (3) *H. prashadi*, (4) *H. triedrus*, (5) *H. maculatus*, (6) *H. scabriceps*, (7) *H. prashadi*, (8) *H. brookii*, (9) *H. gracilis*, (10) *D. anamallensis*. A visual comparison of Lamellar morphology of representative clade members as follows: (a) *H. depressus*, (b) *H. prashadi*, (c) *H. triedrus*, (d) *H. maculatus*, (e) *H. scabriceps*, (f) *H. graniticolus*, (g) *H. brookii*, (h) *H. gracilis*, (i) *D. anamallensis*

Table 1. Percentage values of uncorrected pairwise divergence (*p*-distance) for the *cyt b*, RAG-1, PDC and ND2 genes between the closely related congeners of *H. scabriceps* and morphologically similar members of *H. prashadi* and *H. brookii* clades. The percentage divergence of *cyt b* gene between the two specimens of *H. scabriceps* used in this study is 6.3 %.

Pairwise genetic distance with <i>H. scabriceps</i> from Coimbatore	ND2 distances	RAG-1 distances	PDC distances	<i>cyt b</i> distances
<i>H. scabriceps</i> (Tanj)*	-	0.4	2.1	6.3
<i>H. prashadi</i>	13.8	1.4	2.5	15.3
<i>H. maculatus</i>	17.5	2.5	2.5	15.3
<i>H. kangerensis</i>	-	-	-	18.8
<i>H. depressus</i>	8.8	1.8	3.8	18.2
<i>H. vanam</i>	-	1.4	2.5	19.3
<i>H. sushilduttai</i>	-	-	-	17.0
<i>H. graniticulus</i>	-	1.8	3.0	19.3
<i>H. hunae</i>	15.0	1.8	3.0	21.6
<i>H. triedrus</i> ^	11.2	2.2	2.1	18.8
<i>H. lankae</i> #	11.2	2.2	2.5	18.2
<i>H. acanthopholis</i>	12.5	1.8	3.0	19.9
<i>H. reticulatus</i>				24.4
<i>H. albofasciatus</i>				19.9
<i>H. gracilis</i>		4.7	5.5	22.2
<i>H. imbricatus</i>	21.3	3.9	6.4	22.7
<i>H. parvimaculatus</i>	16.2	3.6	5.1	21.1

Foot notes: * - intraspecific distance; ^ - syntopic clade-member in peninsular India; # - syntopic clade-member in Sri Lanka.

dorsal scales; ventral scales imbricate till femoral region; slightly smaller, rounded sub-imbricate scales posterior to femoral region; preanofemoral pores 2–4 on each side separated by 1–2 pore-less scales; forelimbs slender, covered with small, imbricate scales reducing in size and sub-imbricate to granular scales ventrally, forelimbs moderate, crus (5.4–6.7) longer than forearm (4.0–5.1); hindlimbs slender, covered with imbricate scales both ventrally and dorsally; dorsal part of manus and pes covered with small granular scales; digits short, free, with interdigital webbing absent, a distinct short curved claw present in all the digit tips; all digits with initial few lamellae divided, other lamellae fused; lamellar formula of manus 4-6-5-5-5 and pes 5-7-8-8-5; basal lamellae narrow; tail fairly long, (21.2–43.2) subequal to body length, robust and thickset in width (3.2–4.9); blunt at tip, round in cross section, covered with imbricate scales subequal to size of scales on dorsum, tubercles absent; dorsum light brown with dark brown bands extending from above the dorsolateral fold region sometimes forming 'x's along the body from nape to vent region with large white spots or scales sometimes forming

Table 2. A comparison of synapomorphic morphological characters that is convergent to *H. scabriceps* with the ground-dwelling *Hemidactylus* clade and the *H. prashadi* clade. Note the commonly shared characters of *H. scabriceps* with both the ground dwelling *Hemidactylus* and the *H. prashadi* clade.

Species	Series of white spots/dotted line	Series of black stripes in the infralabials and gular
<i>H. scabriceps</i>	Present	Present
<i>H. prashadi</i>	Present	Absent
<i>H. parvimaculatus</i>	Present	Absent
<i>H. maculatus</i>	Present	Absent
<i>H. kangerensis</i>	Present	Absent
<i>H. sushilduttai</i>	Present	Absent
<i>H. graniticulus</i>	Present	Absent
<i>H. hunae</i>	Present	Absent
<i>H. triedrus</i>	Present	Absent
<i>H. lankae</i>	Present	Absent
<i>H. acanthopholis</i>	Present	Absent
<i>H. reticulatus</i>	Absent	Present
<i>H. albofasciatus</i>	Absent	Present
<i>H. gracilis</i>	Absent	Present
<i>H. imbricatus</i>	Absent	Present

stripes across the body found; smaller white and black spots intermixed with the light brown parts of the body; head covered with dark and light-colored spots, labials characterized with a black patch forming a stripe pattern throughout the labials, sometimes extending into stripes in the gular region; venter dirty white, rarely with small black dots; mental shields with small black blotches; manus and pes darker beneath.

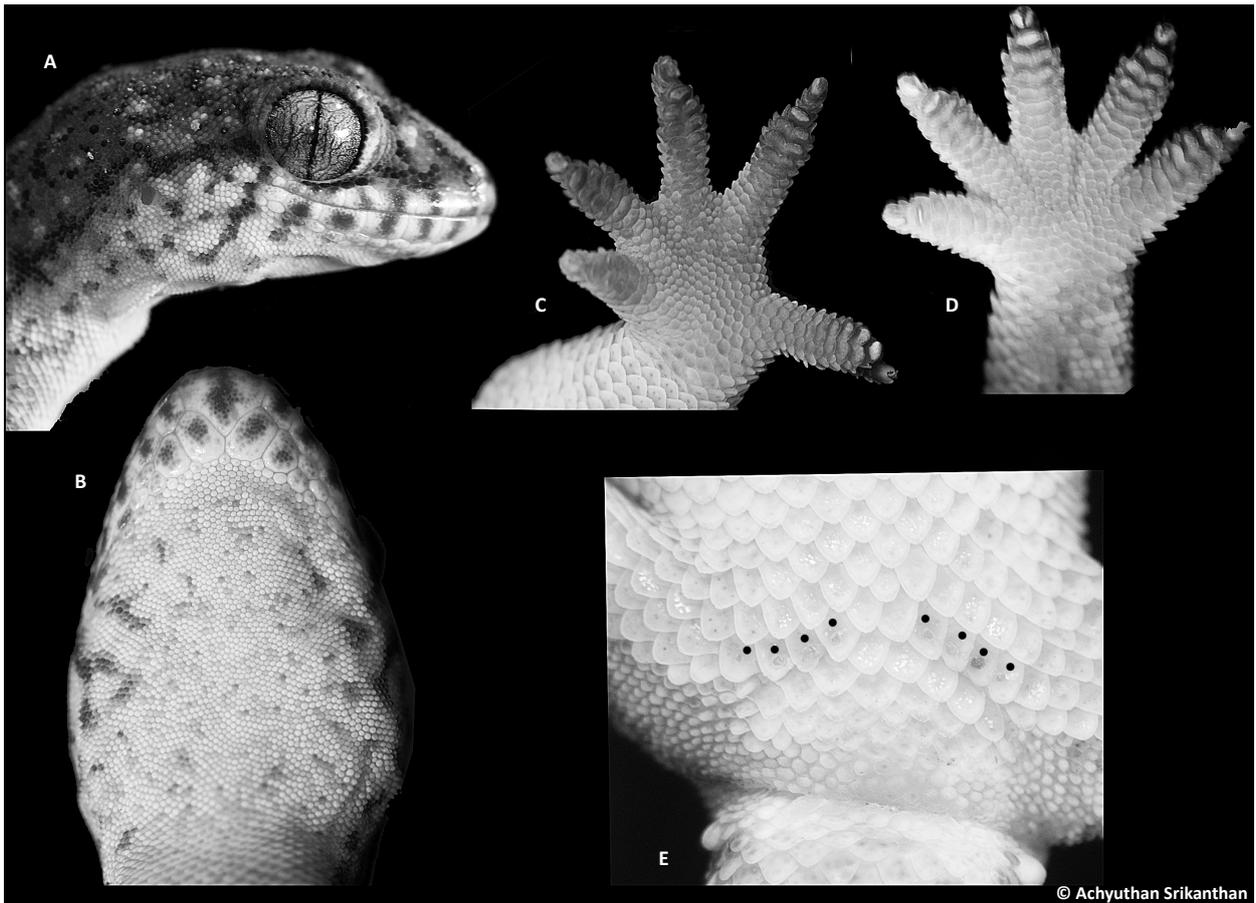
Distribution and niche modeling

Hemidactylus scabriceps has so far been recorded from the dry, low-elevation plains of Tamil Nadu ranging from 10 to 380 m (Image 4). In the Coromandel Coastal Plains this species is known from Adayar (in Madras) near Palar Bay, southwards to Mannampandal near Cauvery Delta, further down in Ramanathapuram and Thoothukudi north and south of the Palk Strait, respectively. Apart from the earlier records we sighted this species from Thitai (11.083°N & 77.031°E; 44m) in Thanjavur Delta region, Kalapatti (11.083°N & 77.0317°E, 385m) further westwards in the Coimbatore Plateau, south in Pottal (8.644°N & 77.484°E, 77m) just east of Tirunelveli foothills and Mariccukatte (Marichchukkaddi) in Sri Lanka (8.580°N & 79.946°E).

The input for species distribution modeling are nine least correlated bioclim variables, altitude and NDVI layers with 13 sample locations of the species. The



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Image 2 & 3. (Above) Image (in life) of BNHS 2421 (Below) (A) Head lateral showing labials and eye, (B) Mentum, (C) Lamellae of the left manus, (D) Lamellae of the left pes and (E) Preanal pores of BNHS 2421

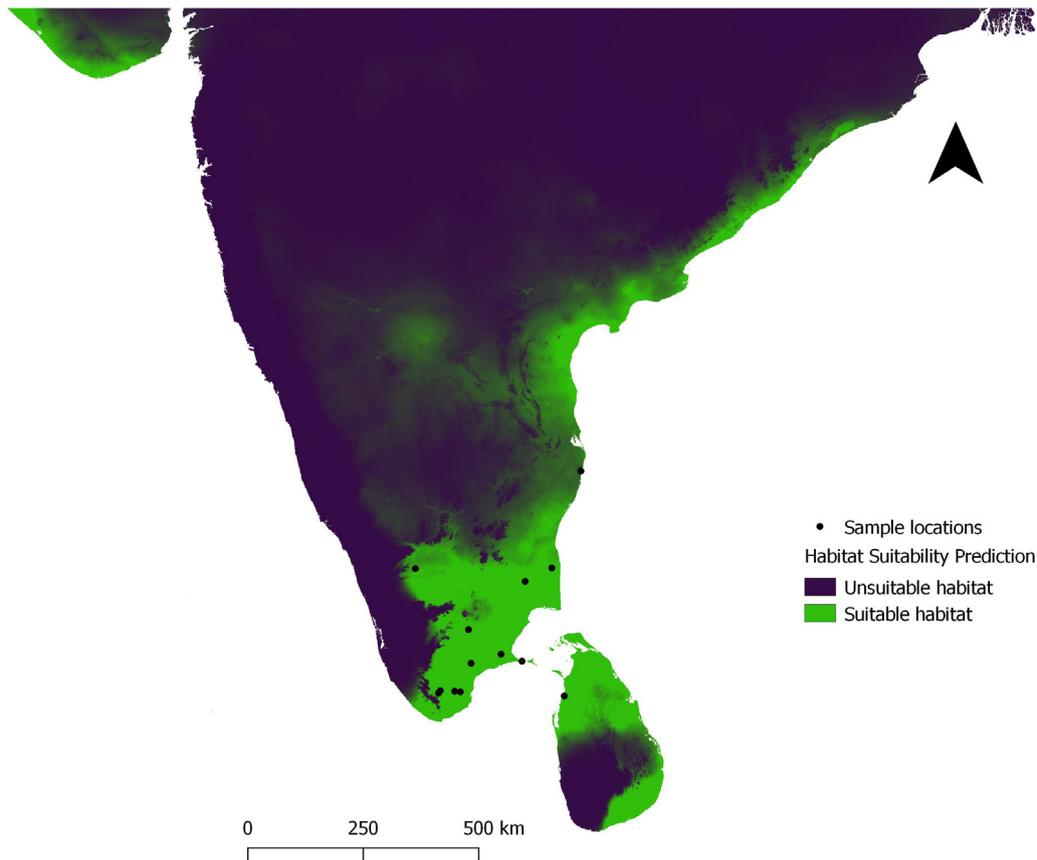


Image 4. Habitat Suitability Map projected based on MaxEnt modeling of *H. scabriceps* occurrences (both previously published and new) in India and Sri Lanka, revealing dry-zone plains (green shade) abutting Coromandel Coast, Cauvery flood-plains and dry peneplain of Sri Lanka as its realised range.



Image 5. Habitat spectrum of *H. scabriceps* in India (left) rocky habitat from the most inland locality Kalapatti, Coimbatore; (right) sandy habitat of *H. scabriceps* from the most coastal locality Mandapam, Rameshwaram.

logistic output of the model shows the suitability of the habitat, graded over a range of 0–1. A binary map is created indicating suitable and unsuitable habitat for occurrence of *H. scabriceps*. A threshold of 0.3491 was

selected to classify the suitability which is the average value of the threshold rule used for the MaxEnt model. The AUC for the run/model is above 0.9 showing high goodness of fit. The AUC value of the model is 0.987

indicating that the resultant model is reliable.

The relative contribution (approx.) of the environmental variables to the MaxEnt model is as shown in Table 4. It is observed that the following variables are the major contributors to the model - bio2 (mean diurnal temperature range), bio12 (Annual Precipitation) and alt12 (altitude) signifying that the habitat most suitable for *H. scabriceps* is low altitudes, less rainfall and relatively less change in maximum and minimum temperature with annual mean temperature of approximately around 28.5°C.

As per the output of MaxEnt modeling (Image 4), *H. scabriceps* is predicted to be distributed from the far south of Tamil Nadu (including Tirunelveli and Tuticorin) northwest till about Coimbatore, northeastwards till about Madras (currently Chennai), with high possibilities of being present in dry parts of northern Sri Lanka. This species is possibly confined to this range within the dry parts of Tamil Nadu, Kerala and Sri Lanka, bound by the Western and Eastern Ghats; and the highlands in central Sri Lanka.

DISCUSSION

Hemidactylus scabriceps is a member of a clade comprising large-bodied, rock-dwelling, scansorial geckos, although it has a small terrestrial body-build and is found in low-elevation plains that are not dominated by rock formations. Our new molecular phylogenetic analyses provide a radically different and contrasting relationship for *Hemidactylus scabriceps*, as shown in Image 1. To untangle this complex interplay between morphology, habitat associations / distribution and genetic relationships, we herein elaborate on these three seemingly disparate features and discuss their dynamics in light of potential evolutionary trajectories that might have acted upon this species shaping it into what it is now.

The morphological characterization and ecological data of our new individuals are for the most part in conformity with literature reports (Annandale 1906; Smith 1935; Ganesh & Chandramouli 2010; Ganesh et al. 2017). Another important facet of morphology of *H. scabriceps* is the persistence of transverse series of white spots / dotted lines across the trunk, typical of all the known members of *H. prashadi* group and absent in *H. albofasciatus*, *H. imbricatus*, *H. reticulatus* and *H. sataransensis* (Smith 1935; Bauer et al. 2008; Giri & Bauer 2008). We postulate that the white spots and barred pattern on the back are a synapomorphy of the

H. prashadi clade, present either bold or diffuse in all of its members. Based on our phylogeny we postulate that the under-developed or rudimentary claws and digits in general, along with the partial fusion of digital lamellae of *H. scabriceps*, are ecologically derived traits consequent upon a strictly terrestrial lifestyle. Similar to the phenotypically biased taxonomic allocations that taxa from the *H. brookii* clade have had, the current study confirms that the genus *Lophopholis*, originally erected for *H. scabriceps*, is actually a synonym of *Hemidactylus* (also see Bauer et al. 2008).

We observed this species in grassland/ dry thorn scrub jungle dominated by palmyra trees, in coconut grove and paddy fields. The species is strictly nocturnal, found resting under rocks during the day, preferably on mounds of gravel under moderately large rocks. It was repeatedly observed to be in a 's' shaped position under rocks and trying to stay still and not trying to get away while the rock was disturbed. This behavior was also observed in *H. reticulatus* (Ganesh et al. 2017; this work) and *H. sataransensis* (see Bauer & Giri 2008). It is also common for *H. scabriceps* to be found in sympatry with *H. triedrus* (Image 8). Some specimens were also found inside termite-eaten and weathered palm and coconut logs, leaves and fruits. This species was observed to be highly territorial. Two individual male specimens in the same vicinity showed territorial behavior, circling each other making chirping calls to each other (the only time the species was heard vocalizing) with a raised waving tail, stretched legs and arched body, and trying to bite at the neck of opponent male. Individuals were found to occur at quite a distance from one another (15–20 m). Thus our observations on the microhabitat associations of *H. scabriceps* along with previously published notes (Ganesh & Chandramouli 2010; Ganesh et al. 2017) do attest its strictly terrestrial lifestyle.

We found some of our adult male individuals to have either 2 or 4 pores on a single side, whereas it usually numbers 3 (Ganesh et al. 2017). Such variations in characters of diagnostic importance in gecko taxonomy, coupled with high levels (6% in cyt *b*) of inter-individual genetic divergence point out to the possibility of cryptic speciation within this complex. It is also noteworthy to highlight that though the original description (Annandale 1906) and subsequent expanded characterizations, both historical (Smith 1935) and recent (Ganesh & Chandramouli 2010; Ganesh et al. 2017) of this species still stems from Coromandel Coastal Plains population, except for the sole record of a specimen from near Madurai (see Ganesh et al. 2017).

Thus the current study describes previously

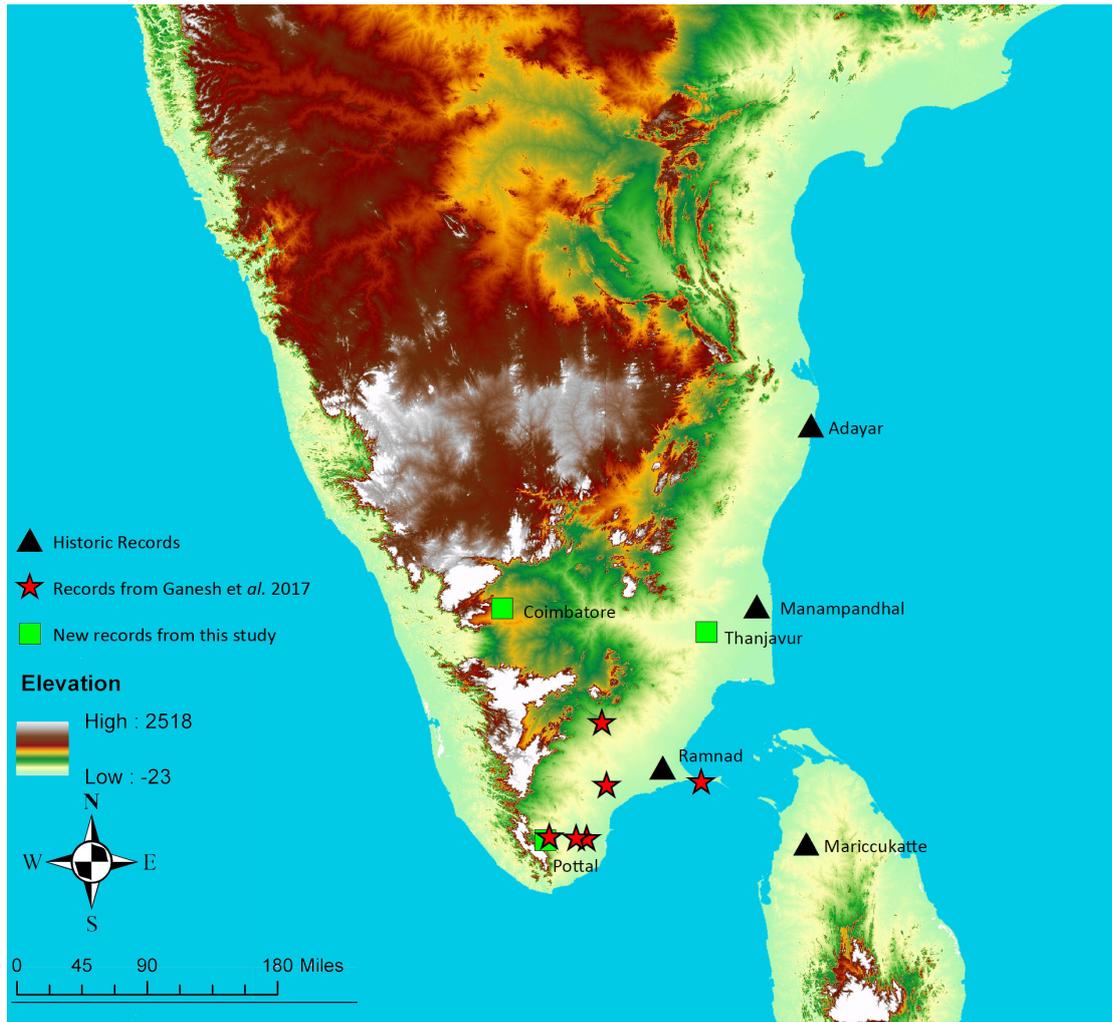


Image 6. Distribution of *H. scabriceps*. Black triangle denotes historical records before 1935 - (type locality) Ramnad by Anandale, 1906; P.E.P Deraniyagala (Mariccukatte, Sri Lanka), D.W. Devanasan (Adayar, Madras (Chennai)); red star denotes records from Ganesh et al. (2017) and green squares denote new records used in this study.



Image 7. *Hemidactylus imbricatus* (captive individual) in life, the species with which *H. scabriceps* was originally considered congeneric during its description; illustrating the homoplasy

Table 3. List of specimens used for the molecular analysis and genetic comparison with the museum numbers, localities and GenBank accession numbers. Highlighted species are the samples used in this study.

Species	Museum No.	Locality	cyt b	ND2	RAG-1	PDC
<i>Cyrtodactylus ayeyarwadyensis</i>	CAS 216446	Myanmar, Rakhine State, Than Dawe District	EU268380	JX440526	JX440685	JX440634
<i>Cyrtodactylus consobrinus</i>	LLG 4062	-	EU268381	EU268349	EU268288	EU268318
<i>Cyrtodactylus loriae</i>	FK 7709	Papua New Guinea: Milne Bay, Bunisi	EU268382	EU268350	EU268289	EU268319
<i>Hemidactylus scabriceps</i>	BNHS 2421	Kalapatti, Coimbatore, Tamil Nadu	KX902971	*	KX902973	KX902972
<i>Hemidactylus scabriceps</i>	VPC-GK-029	Tanjore, Tamil Nadu	KX902975	BankIt2106186	KX902977	KX902976
<i>Hemidactylus brasiliensis</i>	MZUSP 92493	Brazil, Piauí, Parque Nacional Serra das Confusões	EU268383	EU268351	EU268290	EU268320
<i>Hemidactylus imbricatus 1</i>	JS11	Pakistan (captive specimen)	EU268385	EU268353	EU268292	EU268322
<i>Hemidactylus imbricatus 2</i>	JFBM2	Pakistan (captive specimen)	EU268386	EU268354	EU268293	EU268323
<i>Hemidactylus flaviviridis 1</i>	FMNH 245515	Pakistan, Punjab Province	EU268387	EU268355	EU268294	EU268324
<i>Hemidactylus flaviviridis 2</i>	ID 7626	India, Rajasthan, Kuldhara	EU268388	EU268356	EU268295	EU268325
<i>Hemidactylus flaviviridis 3</i>	ID 7640	India, Rajasthan, Jaisalmer	HM559596	HM559628	HM559694	HM559661
<i>Hemidactylus frenatus 1</i>	AMB 7411	Sri Lanka, Pidipitiya 1	EU268389	EU268357	EU268296	EU268326
<i>Hemidactylus frenatus 2</i>	LLG 6745	Malaysia, Pulau Pinang, Empangon Air Hitam 2	EU268390	EU268358	EU268297	EU268327
<i>Hemidactylus frenatus 3</i>	AMB 7420	Sri Lanka, Rathegala 3	EU268391	EU268359	EU268298	EU268328
<i>Hemidactylus frenatus 4</i>	LLG 4871	Malaysia, Pahang, Bukit Bakong 4	GQ375289	GQ458049	GQ375308	GQ375301
<i>Hemidactylus frenatus 5</i>	CES07035	India, Tamil Nadu, Valparai 5	HM595655		HM622356	HM622371
<i>Hemidactylus turcicus</i>	LSUMZ H-1981	USA, Louisiana, Baton Rouge	EU268392	EU268392	EU268299	EU268329
<i>Hemidactylus karenorum</i>	CAS 210670	Myanmar, Mandalay Division, Kyaukpadaung Township, Popa	EU268394	EU268362	EU268301	EU268331
<i>Hemidactylus garnotii 3</i>	CAS 215549	Myanmar, Sagaing Division, Mon Ywa District 3	HM559597	HM559631	HM559697	HM559664
<i>Hemidactylus garnotii 2</i>	CAS 222276	Myanmar, Mon State, Kyaihto Township, Kyait Hti Yo 2	EU268396	EU268364	EU268303	EU268333
<i>Hemidactylus garnotii 1</i>	CAS 223286	Myanmar, Rakhine State, Taung Gok Township, Ma Ei Ywa 1	EU268395	EU268363	EU268302	EU268332
<i>Hemidactylus brookii 1</i>	LLG6754		EU268397.1	EU268365.1	EU268304.1	
<i>Hemidactylus brookii 2</i>	LLG6755		EU268398.1	EU268366.1	EU268305.1	
<i>Hemidactylus angulatus 1</i>	MVZ 245438	Nigeria, Togo Hills, Nkwanta	EU268399	EU268367	EU268306	EU268336
<i>Hemidactylus angulatus 2</i>	EBG 746	Guinea, Daniah River at Koulete River	HM559588	HM559620	HM559686	HM559653
<i>Hemidactylus palaichthus</i>	LSUMZ 12421	Brazil, Roraima State	EU268400	EU268368	EU268307	EU268337
<i>Hemidactylus greeffii</i>	CAS 219044	São Tome and Principe, São Tome Island, Praia da Mutamba	EU268401	EU268369	EU268308	EU268338
<i>Hemidactylus fasciatus 1</i>	WRB no number	Gabon, Rabi 1	EU268402	EU268370	EU268309	EU268339
<i>Hemidactylus fasciatus 2</i>	CAS 207777	Equatorial Guinea, Bioko Island, 3.6 km N of Luba 2	EU268403	EU268371	EU268310	EU268340
<i>Hemidactylus bowringii 1</i>			EU268405.1	EU268373.1	EU268312.1	
<i>Hemidactylus bowringii 2</i>			EU268406.1	EU268374.1	EU268313.1	
<i>Hemidactylus robustus 1</i>	MVZ 248437	Pakistan, Thatta District, 40km S of Mipur Sakro 1	EU268408	EU268376	EU268315	EU268345
<i>Hemidactylus robustus 2</i>	FMNH 245519	Pakistan, Baluchistan Province, Gwadar Division, Makran 2	HM559610	EU054287	EU054271	EU054255
<i>Hemidactylus robustus 3</i>	MVZ 234374	Iran, Lorestan Province, 99km SW (by road) of KhorramAbah 3	HM559611	HM559644	HM559710	HM559677
<i>Hemidactylus reticulatus 1</i>	AMB 5730	India, Tamil Nadu, Vellore 1	EU268410	—	—	—

Species	Museum No.	Locality	cyt b	ND2	RAG-1	PDC
<i>Hemidactylus reticulatus</i> 2	CES07016	India, Karnataka, Pavgada 2	HM595669	—	—	—
<i>Hemidactylus reticulatus</i> 3	CES06024	India, Karnataka, Bangalore 3	HM595670	—	—	—
<i>Hemidactylus parvimaculatus</i> 1	AMB 7475	Sri Lanka, Kandy 1	GQ375290	GQ458055	GQ375309	GQ375302
<i>Hemidactylus parvimaculatus</i> 2	ADS36	Sri Lanka, Kartivu 2	GQ375291	GQ458053	GQ375310	GQ375303
<i>Hemidactylus parvimaculatus</i> 3	AMB 7466	Sri Lanka, Mampuri 3	GQ375292	GQ458056	GQ375311	GQ375304
<i>Hemidactylus craspedotus</i>	LLG 5613	Malaysia, Perak, Temengor	HM559586	HM559618	HM559684	HM559651
<i>Hemidactylus platyurus</i> 1	KU 304111	Philippines, Lubang Id., Occidental Mindoro Prov., Lubang 1	HM559587	HM559619	HM559685	HM559652
<i>Hemidactylus depressus</i> 1	ADS 29A	Sri Lanka, Galkotte 1	HM559589	HM559621	HM559687	HM559654
<i>Hemidactylus depressus</i> 2	ADS 69A	Sri Lanka, Kuruwekotha 2	HM559590	HM559622	HM559688	HM559655
<i>Hemidactylus depressus</i> 3	AMB 7440	Sri Lanka, Dumbulayala 3	HM559591	HM559623	HM559689	HM559656
<i>Hemidactylus depressus</i> 4	AMB 7445	Sri Lanka, Ritigala 4	HM559592	HM559624	HM559690	HM559657
<i>Hemidactylus depressus</i> 5	AMB 7481	Sri Lanka, Matale 5	HM559593	HM559625	HM559691	HM559658
<i>Hemidactylus depressus</i> 6	AMB 7524	Sri Lanka, Galle 6	HM559594	HM559626	HM559692	HM559659
<i>Hemidactylus giganteus</i> 1	JB03	India (captive specimen) 1	HM559598	HM559632	HM559698	HM559665
<i>Hemidactylus giganteus</i> 2	CES08013	India, Karnataka, Hampi 2	HM595657		HM622357	HM622372
<i>Hemidactylus haitianus</i> 1	AMB 4188	Dominican Republic, Santo Domingo 1	HM559599	HM559633	HM559699	HM559666
<i>Hemidactylus haitianus</i> 2	AMB 4189	Dominican Republic, Santo Domingo 2	HM559600	HM559634	HM559700	HM559667
<i>Hemidactylus leschenaultii</i> 1	AMB 7443	Sri Lanka, Polonnaruwa 1	HM559601	HM559635	HM559701	HM559668
<i>Hemidactylus leschenaultii</i> 2	JB05	India (captive specimen) 2	HM559602	HM559636	HM559702	HM559669
<i>Hemidactylus leschenaultii</i> 3	CES07041	India, Tamil Nadu, Chidambaram 3	HM595662		HM622360	
<i>Hemidactylus longicephalus</i>	CAS 218939	São Tomé et Príncipe, São Tomé	HM559603	HM559637	HM559703	HM559670
<i>Hemidactylus mabouia</i> 1	AMB 8301	South Africa, Limpopo Prov., nr. Huntleigh 1	HM559604	HM559638	HM559704	HM559671
<i>Hemidactylus mabouia</i> 2	YPM 14798	USA, Florida, Monroe Co., Little Torch Key 2	HM559605	HM559639	HM559705	HM559672
<i>Hemidactylus hunae</i>	AMB 7416	Sri Lanka, Pitakumbura	HM559606	HM559640	HM559706	HM559673
<i>Hemidactylus maculatus</i>	BNHS1516	India, Maharashtra, Raigad District, Zirad	HM559607	HM559641	HM559707	HM559674
<i>Hemidactylus prashadi</i> 1	CES07037	India, Maharashtra, Ratnagiri 1	HM595666	—	—	—
<i>Hemidactylus prashadi</i> 2	CES06170	India, Karnataka, Udupi 2	HM595667	—	—	—
<i>Hemidactylus prashadi</i> 3	CES07040	India, Karnataka, Castle Rock 3	HM595668		HM622364	HM622378
<i>Hemidactylus prashadi</i> 4	JB02	India (captive specimen) 4	HM559608	HM559643	HM559708	HM559675
<i>Hemidactylus prashadi</i> 5	JB30	India (captive specimen) 5	HM559609	HM559644	HM559709	HM559676
<i>Hemidactylus lankae</i>	AMB 7453	Sri Lanka, nr. Medavachchiya	HM559615	HM559648	HM559714	HM559681
<i>Hemidactylus triedrus</i> 1	JB09	India (captive specimen) 1	HM559616	HM559649	HM559715	HM559682
<i>Hemidactylus triedrus</i> 2	JB08	Pakistan (captive specimen) 2	HM559617	HM559650	HM559716	HM559683
<i>Hemidactylus triedrus</i> 3	CES07007	India, Karnataka, Ramnagar 3	HM595673	—	HM622365	HM622379
<i>Hemidactylus aaronbaueri</i> 1	CES08022	India, Maharashtra, Pune 1	HM595640	—	—	—
<i>Hemidactylus aaronbaueri</i> 2	CES08016	India, Maharashtra, Raigad District 2	HM595641		HM622352	HM622367
<i>Hemidactylus albofasciatus</i> 1	CES07038	India, Maharashtra, Sindhudurg District, Malvan 1	HM595642	—	—	—
<i>Hemidactylus albofasciatus</i> 2	CES08018	India, Maharashtra, Sindhudurg District, Malvan 2	HM595643	—	—	—
<i>Dravidogecko anamallensis</i>	CES08029	India, Kerala, Eravikulam,	HM595644		HM622353	HM622368

Species	Museum No.	Locality	cyt b	ND2	RAG-1	PDC
<i>Hemidactylus gracilis</i>	CES07039	India, Maharashtra, Pune	HM595660	—	HM622359	HM622374
<i>Hemidactylus persicus</i>	CES08027	India, Rajasthan, Jaisalmer	HM595665	—	HM622362	HM622376
<i>Hemidactylus yajurvedi</i> 1	CES12006	Kanker, Chhattisgarh, India 1	KT601564	—	KT601569	KT601566
<i>Hemidactylus yajurvedi</i> 2	CES12007	Kanker, Chhattisgarh, India 2	KT601565	—	KT601568	KT601567
<i>Hemidactylus treutleri</i>	CES06108	India, Telangana, Hyderabad	KU720681	—	KU720742	
<i>Hemidactylus graniticolus</i>	CES08028	India, Tamil Nadu, Nilgiri Hills	HM595664	—	HM622361	HM622375
<i>Hemidactylus vanam</i>	BNHS2329	India, Tamil Nadu, Meghamalai	MG711527.1	MG711532.1	MG711540.1	MG711535.1
<i>Hemidactylus sushilduttai</i>	ESV 112	Simhachalam, Visakhapatnam District, Andhra Pradesh, India	MF668228.1			
<i>Hemidactylus kangerensis</i>	BNHS 2486	Kanger Valley National Park, Bastar District, Chhattisgarh	KY938009.1			
<i>Hemidactylus acanthopholis</i>	CES17066	Tamil Nadu, India	MG711526.1	MG711531.1	MG711539.1	MG711534.1

*accession number pending

Table 4. Analysis of variable contributions of *H. scabriceps* Maxent model. The names of the variables are as follows: **_bio3_28 = Isothermality, _bio2_28 = Mean diurnal range, _bio1_28 = Annual mean temperature, _bio15_28 = Precipitation seasonality, _bio14_28 = Precipitation seasonality, _bio19_28 = Precipitation of coldest quarter, _bio18_28 = Precipitation of the warmest quarter, _bio8_28 = Mean temperature of the wettest quarter and _bio12_28 = Annual temperature**

Variable	Percent contribution	Permutation importance
bio2	43.5	49.3
bio12	23	26.5
alt	11.9	20.5
bio1	9.7	2.9
bio18	6.5	0
bio3	4.8	0.2
veg	0.5	0.3
bio19	0.1	0
bio14	0.1	0.1
bio8	0	0.1

unsampled populations from Coimbatore near the foothills of the Western Ghats, a different ecoregion altogether. Even here, we observed fine-scale landscape partitioning between *H. scabriceps* and the ecologically similar *H. reticulatus* (see Ganesh et al. 2017). This makes *H. scabriceps* the only member of *H. prashadi* clade to be distributed exclusively in a primarily sandy alluvial plains terrain not dominated by rock outcrops. The loose occurrence of individuals of *H. scabriceps* at some distance between each other was observed to be similar to other *Hemidactylus* species such as *H. mabouia* (see Regalado 2003). Our niche distribution model shows an indication that rivers Cauvery and Amaravathi (a tributary of Cauvery) could be geographic barriers between the Coimbatore plateau population



Image 8. A field photograph taken in Tuticorin showing syntopic sighting of *H. scabriceps* (bottom) and *H. triedrus* (top).

and the Cauvery delta and Palk Strait populations, which might explain the high genetic divergence between the individuals sampled from these distinct populations.

Other ground-dwelling *Hemidactylus* occur both in the *H. prashadi* and the *H. brookii* clades. In the *H. prashadi* clade, in as far as is known, only *H. triedrus* is terrestrial and is currently known to be distributed in most of the dry zones of peninsular India including the transitional zones of the Western Ghats. From the *H. brookii* clade, *H. reticulatus* is a similarly distributed terrestrial species, closely associated with rocky habitats. *Hemidactylus gracilis* has its close affinities with black soil throughout its distribution in central India and northern peninsular India, while *H. albofasciatus* and *H. satarensis* are distributed in parts of the northern Western Ghats occupying rocky plateaus. *Hemidactylus scabriceps* occupies the dry zone of Tamil Nadu and northern Sri Lanka (rainfall <1,000mm/year), restricting itself to the grasslands of the alluvial plains and sandy

regions in Northern Sri Lanka and towards the east of Tamil Nadu and red soils towards its west in the Tamil Nadu uplands till the foothills of the Western Ghats. The rocky outcrops in Tamil Nadu (both Eastern and Western Ghats), though interrupted by *H. scabriceps* habitat, are occupied by *H. reticulatus*. Both the Western and Eastern Ghats in the west and north respectively restrict *H. scabriceps* within Tamil Nadu. Informed by our MaxEnt analysis, we hypothesize that the farthest inland locality of *H. scabriceps* disclosed herein (Coimbatore) is inhabited by this species largely because of the deep erosion of the plateau created by the Cauvery River system, engraving a low, alluvial, plains ecosystem into the table-land, much far west than in other nearby parts of the peninsula. This scenario is comparable to the Moyar Gorge being an important biogeographic barrier for terrestrial lizards such as *Sitana* sp. that are predominantly plateau dwelling (Deepak & Karanth 2018). *Hemidactylus scabriceps* also shows the contrast of shared fauna between the dry zones of Tamil Nadu and Sri Lanka (Guptha et al. 2015; Deepak et al. 2016; Deepak & Karanth 2018).

Our findings have a direct bearing on the evolutionary history of this species. The inferred trees from the current work showed strong support for the previously known groups—*H. prashadi*, *H. flaviviridis*, *H. brookii*, *H. frenatus* and *H. platyurus*. From our study, it is also revealed that *H. scabriceps* belongs to the *H. prashadi* group (recognized by Bansal & Karanth 2010). The reduced subdigital scansorial apparatus, imbricate tail scales, imbricate dorsal scales, reduced subcaudal scales and a terrestrial lifestyle are traits that seem to be visually convergent within sub-groups of *Hemidactylus* geckos both from Africa (*H. isolepis*, *H. ophiolepis*) and India (*H. imbricatus*) (Bauer et al. 2008). The ground dwelling clade of geckos that share similar traits was previously known to be sister to the *H. brookii* group of geckos and *H. scabriceps* was assumed to be related to this group (Bauer et al. 2008). Our phylogenetic analysis reveals that *H. scabriceps* is related to the large rock dwelling clade of geckos contrary to what was previously assumed prompted by morphological similarity.

The unexpected and contrasting genetic relationship of the morphologically and ecologically discordant *H. scabriceps* and *H. prashadi* group underscores the complexity of peninsular India's geological history. Previous studies on peninsular India's terrestrial lizard species have all revealed such discordant patterns of genetic alliance and eco-morphology. Agarwal & Karanth's (2015) molecular phylogenetic analyses revealed that the fat-bodied, forest-floor dwelling taxa

'*Geckoella*' is actually a part of primarily scansorial and rupicolous *Cyrtodactylus* radiation. Deepak et al.'s (2015) study on '*Brachysaura* minor' also points out a similar structure, i.e. the short body form and completely terrestrial habits of that taxon, contrary to its arboreal congeners in the genus *Calotes*, is nothing but a result of reduction in tree cover and other associated landscape changes (Stromberg 2011; Ponton et al. 2012). Similarly, the Miocene landscape changes such as aridification of the Indian sub-continent has shown large influence on lizard groups such as *Cyrtodactylus*, *Ophisops*, *Sitana* and *Sarada* in the Indian subcontinent (Agarwal & Karanth 2015; Agarwal & Ramakrishnan 2017; Deepak & Karanth 2018). Similar to the phenotypically biased taxonomic allocations the above taxa have had, the current study confirms that the genus *Lophopholis*, originally erected for *H. scabriceps*, is actually a synonym of *Hemidactylus* (also see Bauer et al. 2008).

Although previous studies on other peninsular Indian lizard taxa have revealed such unexpected yet consistent patterns of genetic and eco-morphological discordance, such an instance within the better-studied Indian *Hemidactylus* radiation (Bansal & Karanth 2010; 2013; Bauer et al. 2008, 2010) exhibiting this sharp a contrast is without precedent. This is particularly intriguing, especially when another member of the *H. prashadi* clade, *H. triedrus*, occurring in areas inhabited by *H. scabriceps* (see Smith 1935) can afford to survive in sandy low-elevation alluvial tracts without changing its body form too much. But it must be borne in mind that though *H. triedrus* occurs in plains habitat it could still scale vertical rock surfaces when such formations are present within its range, whereas *H. scabriceps* cannot (Ganesh et al. 2017; this work). Additionally, in most of the range of *H. scabriceps*, there are no other strictly-terrestrial geckoes, neither *Hemidactylus* nor other genera (Smith 1935; Somaweera & Somaweera 2009; Ganesh et al. 2017; this work), thereby throwing open prospects of an empty niche for a potential species to exploit. Thus the current work brings to light a case of so far hidden historical competition between a eurytopic (*H. triedrus*, *H. lankae*) versus a stenotopic (*H. scabriceps*) clade member. These species are geographically sympatric (Image 6), in India and Sri Lanka respectively, genetically related but morphologically very different (see Image 1). This sharp discordance amply illustrates the complex interplay of historical landscape changes, eco-morphological reactions and resource-use competition.

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Appendix 1. *Hemidactylus scabriceps* material examined

Syntype: BMNH 1946.8.22.40, adult female, Ramnad, Madras District (=Ramnad, Tamil Nadu, India), collected by Col. Annandale, 1906.
 BMNH 1920.12.14.2, adult female, Adiyar, Madras (= Chennai, Tamil Nadu, India), collected by D.W. Devanesan, 1920.
 BMNH 1933.11.24.1, adult male, Mariccukatti, Northern Province, Ceylon (= Sri Lanka), collected by P.E.P. Deraniyagala, 1934.
 CESL 503 & CESL 504, Adult male and female, Kalakad, Tamil Nadu, India, Collected by Saunak Pal, 2012.
 BNHS 2421, Adult Male, Kalapatti, Coimbatore, Tamil Nadu, India, Collected by Achyuthan, N. Srikanthan and Chethan Kumar Gandla, 2014.
 VPC-GK-029 (IISER, Thiruvananthapuram), Adult male, Thanjavur, Tamil Nadu, India, collected by Gopal Murali, 2014.



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Article

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