ORIGINAL ARTICLE

The hills are alive with geckos! A radiation of a dozen species on sky islands across peninsular India (Squamata: Gekkonidae, *Hemiphyllodactylus*) with the description of three new species

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Abstract

Sky Islands are high-elevation environments that are separated by warmer, low elevations, forming natural patches of unique montane habitat that often persist through changing climates. Peninsular India was ancestrally forested and has gradually become more arid since at least the Oligocene, and open landscapes have dominated since the middle-late Miocene. Mesic forests today are largely restricted to coastal mountains and some other montane habitats. A mitochondrial phylogeny and fossil-calibrated timetree of Indian *Hemiphyllodactylus* reveal an Indochinese origin and an endemic radiation with 12 species-level lineages, where a single species was known, that diversified in the Oligocene-Miocene across montane forest habitats in the Eastern Ghats and south India. The phylogeny also suggests the discontinuous Eastern Ghats mountain range encompasses two distinct biogeographic entities: north and south of the Pennar/Krishna-Godavari River basins. This study highlights the deep history of the region and the importance of montane habitats as islands of unique biodiversity that have persisted through millions of years of changing climates. We describe three new species: *Hemiphyllodactylus arakuensis* sp. nov., *H. jnana* sp. nov. and *H. kolliensis* sp. nov. from montane habitats above 1000 m. The montane habitats of these species are emerging hotspots of reptile endemism, and this study emphasizes the need for systematic biodiversity inventory across India to uncover basic patterns of diversity and distribution.

Keywords Biogeography · Divergence dating · Eastern Ghats · Systematics · Western Ghats

Introduction

The mountains in the tropics have more narrowly distributed species than at temperate latitudes was first proposed by Janzen (1967), in part based on the observations that lower latitudes have less climatic variability in space and time (McCain 2009). Species on tropical mountains do in fact tend

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to have narrower elevational ranges and thermal tolerances, amongst the drivers of the high richness and endemism in tropical montane habitats (Ghalambor et al. 2006; Deutsch et al. 2008; McCain 2009). Montane habitats form a natural system of 'sky islands', climatically similar regions that are physically isolated from each other by warmer, lower elevations. These upland habitats can act as refugia for cool-adapted or forest-restricted species through cycling climates and often harbour lineages with a deep evolutionary history (e.g. Joshi and Karanth 2010; Tolley et al. 2011; Bell et al. 2010; Grismer et al. 2015).

Temperature has an even more overriding effect on tropical squamates than habitat changes (Frishkoff et al. 2015), and upslope displacement has been documented with recent warming (Raxworthy et al. 2008). Tropical forest lizards, thermoconformers in particular, are especially sensitive to warm temperatures (Addo-Bediako et al. 2003; Deutsch et al. 2008; Tewksbury et al. 2008; Huey et al. 2009). Most gekkonids are nocturnal thermoconformers, one genus with a largely montane distribution separating deeply divergent

lineages (paleoendemics; sensu Tolley et al. 2011; Grismer et al. 2015) is *Hemiphyllodactylus* Bleeker, 1860; Agarwal 2016. The genus includes 28 described species patchily distributed across a vast area including peninsular India and Sri Lanka, extending through the Andaman and Nicobar Islands and mainland Southeast Asia east from Myanmar into Vietnam, Laos, Thailand and peninsular Malaysia up until the South Pacific (Zug 2010; Chandramouli et al. 2012; Grismer et al. 2018a, b; Sung et al. 2018). Excluding six insular species in Hong Kong, Palau, the Philippines and Sumatra, the remaining 22 *Hemiphyllodactylus* species are from montane (~600–1700 m), forested habitats in mainland Southeast Asia and India-Sri Lanka (Zug 2010; Grismer et al. 2013, 2015, 2018a, b; Nguyen et al. 2014; Tri et al. 2014; Sukprasert et al. 2018; Sung et al. 2018) including a number of paleoendemics (Tolley et al. 2011; Grismer et al. 2015). *Hemiphyllodactylus* are relatively small geckos (snout to vent length 31–62 mm, only six species exceeding 50 mm), and as previously noted, are relatively inconspicuous in colour pattern and often occur at low densities with local distributions and are consequently poorly known and rarely collected (Zug 2010; Grismer et al. 2013, 2015, 2018a, b). Zug (2010) provided a comprehensive review of the taxonomy and nomenclature of the genus and described two species, taking the number of valid *Hemiphyllodactylus* species to nine. Including the elevation of three subspecies to species level, 19 new species have been named since Zug (2010)—more than tripling the species diversity in *Hemiphyllodactylus*. This resurgence in species descriptions is a combination of extensive sampling in mainland Southeast Asia and mitochondrial sequences for all described species (Heinicke et al. 2011; Grismer et al. 2013, 2015, 2018a, b; Sukprasert et al. 2018).

Hemiphyllodactylus aurantiacus (Beddome, 1870), the sole representative of the genus in peninsular India (Bauer & Das 1999; Zug 2010), was described from Yercaud, Tamil Nadu at an elevation of ~1200 m in the Shevaroys (Fig. 1; Beddome 1870). The species was considered a subspecies of the widely distributed *Hemiphyllodactylus typus* Bleeker, 1860 (Smith 1935), though relatively recent topotypical collections and molecular sequence data confirm its specific status (Bauer and Das 1999; Heinicke et al. 2011). *Hemiphyllodactylus aurantiacus* is poorly represented in collections, with scattered distributional records from mid-high elevation forests (~600–1400 m) across south India including the Shevaroys and other isolated massifs, the southern Western Ghats and the southern Mysore Plateau (Smith 1935; Daniels 1994; Daniels and Kumar 1998; Aengals 2013; Ganesh and Arumugam 2016), as well as the northern Eastern Ghats from both the Mahendragiri and Nallamala Hills (Sanyal et al. 1993; Chetri and Bhupathy 2010; Javed et al. 2010) (Fig. 1). The single Sri Lankan record is based on a specimen labelled as originating from Hambonota, Sri Lanka, which may not have originated on the island (Zug 2010).

As part of herpetological surveys and ongoing work on lizards across the Eastern Ghats and south India from 2009 to 2018, the research community based out of the Centre for Ecological Sciences and National Centre for Biological Sciences in Bangalore, and colleagues studying Indian biodiversity have accumulated a small collection of *Hemiphyllodactylus* from across montane habitats broadly spanning the known Indian range of the group. Given the high diversity and endemicity of the genus in other parts of its range (e.g. see Grismer et al. 2013, 2015, 2018a, b) and the isolated nature of the Indian montane localities, we expected to see some genetic structure. We sequenced the mitochondrial gene ND2 and used a fossil-calibrated timetree and biogeographic analyses to establish the timing and geographic origin of Indian *Hemiphyllodactylus* and to evaluate species diversity. Sequence data reveals a deep split between populations in the northern Eastern Ghats and those in south India, with a dozen species level lineages distributed between the two clades. Here, we describe three new species, *Hemiphyllodactylus jnana* sp. nov. and *Hemiphyllodactylus kolliensis* sp. nov. from south India and *Hemiphyllodactylus arakuensis* sp. nov. from the northern Eastern Ghats. We also discuss the implications for Indian biogeography based on *Hemiphyllodactylus* diversity and distribution.

Methods

Phylogenetic analysis

Genomic DNA was extracted from liver or tail tissues stored in ethanol using the Qiagen DNeasy extraction kit for 18 samples from 16 localities across peninsular India, including the type locality of *Hemiphyllodactylus aurantiacus* (Table S1; Fig. 1). A partial fragment of the mitochondrial ND2 gene (756–1041 nucleotides) was amplified with the primers MetF1 and H5934 and sequenced using MetF1 (Macey et al. 1997). Sequences were obtained commercially from the NCBS sequencing facility and Medauxin, Bangalore. Published ND2 sequences for all described and a few unnamed divergent lineages of *Hemiphyllodactylus* were obtained from GenBank and trees rooted with *Gehyra* spp. (following the results of Heinicke et al. 2011; Table S1). MEGA 5.2.2 (Tamura et al. 2011) was used to align sequences and calculate uncorrected percentage pairwise sequence divergence (Table S2). A maximum likelihood (ML) phylogeny was constructed using the codon-partitioned ND2 data and the GTR + G model in RA × ML HPC 7.4.2 (Stamatakis 2006) implemented through the raxmlGUI 1.3 (Silvestro and Michalak 2012), with 10 independent ML runs and support assessed with 1000 rapid bootstraps.
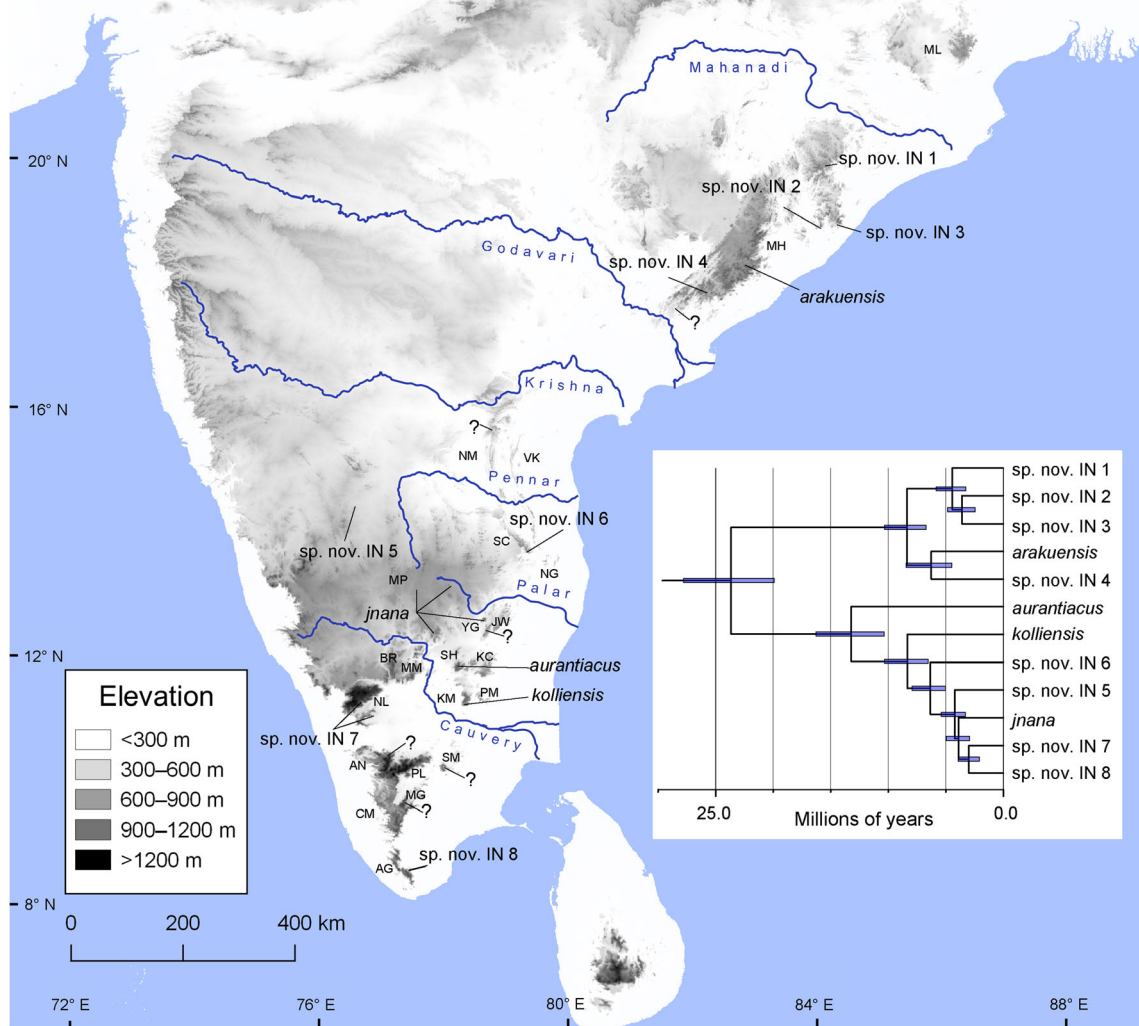
Fig. 1 Distribution of *Hemiphyllodactylus* in peninsular India, and inset, timetree for Indian *Hemiphyllodactylus* with 95% HPD indicated by bars at nodes. Lines on the map indicate localities sampled in this study, '?' indicates unsampled published records (from Sanyal et al. 1993; Daniels 1994; Daniels and Kumar 1998; Javed et al. 2010; Ganesh and Arumugam 2016), major east-flowing rivers marked in blue. Mountain ranges are marked by two capital letters, AG, Agasthyamalai; AN, Anaiamalai; BR, Biligirirangana Hills; CM, Cardamamom; JW, Jawadhi Hills; KC, Kalrayan-Chitteri; KM, Kollimalai; MG, Meghamalai; MH, Mahendragiri; ML, Malaygiri; MM, Male Mahadeshwara; MP, Mysore Plateau; NG, Nagari; NL, Nilgiris; NM, Nallamala; PL, Palani; PM, Pachamalai; SC, Seshachalam; SH, Shevaroy; SM, Sirumalai; VK, Velikonda; YG, Yelagiri

Species delimitation and divergence dating

We did not use tree-based species delimitation as we had sequences for one or two individuals per population, precluding a thorough evaluation of within and between species branching patterns. Instead, we used an uncorrected ND2 sequence divergence value of 5% as suggestive of species level divergence, as has been previously applied for *Hemiphyllodactylus* and other geckos (e.g. Grismer et al. 2013). The alignment with lineages reduced to one per putative species was included in a larger gekkotan alignment for divergence dating analyses (Table S1). Starting xml files were created in BEAUTI 1.8.4 (Drummond et al. 2016) with the HKY + G model applied to the codon-partitioned ND2 data, a Yule speciation prior, relaxed uncorrelated lognormal clock models for each partition and the Diplodactylidae constrained to be sister to the rest of Gekkota (matching the ML tree). Four fossils were used as calibration points with exponential distributions and an arbitrary mean of 5—amber fossils from Myanmar (crown Gekkota, offset 99; Daza et al. 2016), New Zealand diplodactylid material (most recent common ancestor (mrca) New Zealand Diplodactylidae; offset 19; Lee et al. 2009a, b; Skipwith et al. 2016), *Pygopus hortulanus* (stem calibration for mrca *Pygopus* Merrem, offset 23; Hutchinson 1997; Jennings et al. 2003; Lee et al. 2009b) and *Sphaerodactylus dommeli* (mrca *Sphaerodactylus* Wagler, offset 20; Kluge 1995; Iturralde-Vinent and MacPhee 1996; Heinicke et al.

2011). An additional geological calibration was used, the divergence of *Phelsuma inexpectata* Mertens, 1966 on Reunion from its closest relative on Mauritius *P. ornata* Gray, 1825 (uniform prior, 0.05–5; Agarwal 2011; Gillot et al. 1994; Rocha et al. 2010). Analyses were run in BEAST 1.8.4 (Drummond et al. 2012, 2016) for 50 million generations, sampling every 5000 generations, log files examined in Tracer 1.6 (Rambaut et al. 2014) for convergence (ESS > 200) and a maximum clade credibility (MCC) tree was generated in TreeAnnotator 1.8.4 (Drummond et al. 2016) after conservatively discarding the first 25% of trees as burn-in. Original alignments, BEAST xml files or output tree files are available on request.

Biogeographic analysis

The BEAST MCC tree from the previous analysis was trimmed to include only *Hemiphyllodactylus* species, which were assigned to three subregions of the Indo-Malayan region: peninsular India, Indochina (mainland Southeast Asia, southern China) and Sundaland (Thai-Malay Peninsula south of the Isthmus of Kra, through Singapore to Borneo). We used the dispersal-extinction-cladogenesis (DEC) ML model in Lagrange 20130526 (Ree and Smith 2008) to estimate range evolution in *Hemiphyllodactylus*. The analyses were set up using the Lagrange configurator (http://www.reelab.net/lagrange/configurator), with a maximum of two ancestral areas allowed and no dispersal constraints. We also treated distribution as a categorical variable and conducted an ML ancestral state reconstruction using the Mk1 model in Mesquite 3.51 (Maddison & Maddison 2018).

Morphological analysis

A total of 36 *Hemiphyllodactylus* specimens, including 11 topotypical *Hemiphyllodactylus aurantiacus* and the three new species, were examined in this study for morphological data. Museum abbreviations are as follows—Centre for Ecological Sciences, Bangalore (CES); the Bombay Natural History Society, Mumbai (BNHS) and the National Centre for Biological Sciences, Bangalore (NCBS/AQ/AK field series). Morphological data for the lectotype of *H. aurantiacus* were obtained from Zug (2010) and published data for other *Hemiphyllodactylus* species from Zug 2010; Grismer et al. 2013, 2014a, b, 2015, 2018a, b; Agarwal et al. 2012; Tri et al. 2014; Nguyen et al. 2014; Guo et al. 2015; Cobos et al. 2016; Yan et al. 2016; Sukprasert et al. 2018; Sung et al. 2018. Photographs were taken with an SLR camera in life and after preservation; counts and measurements were taken under a Wild M5 dissecting microscope and on the right side of the body, where appropriate. The terminology and methodology used to define characters follow Zug (2010) and Grismer et al. (2013, 2018a). The following

measurements were recorded using a Digimax digital calliper (rounded off to the nearest 0.1 mm)—snout vent length (SVL, from tip of snout to vent), tail length (TL, from vent to tip of tail), tail width (measured at widest point of tail), trunk length (TRL, from posterior margin of forelimb insertion to anterior margin of hindlimb insertion), body height (maximum body height), body width (maximum body width), forearm length (FL, from elbow to distal end of wrist), crus length (CL, from knee to heel), head length (HL, distance between posterior margin of retroarticular process of jaw and snout-tip), head width (HW, maximum width of head), head height (HH, maximum head depth at occiput), eye diameter (ED, greatest horizontal diameter of eye), nares to eye distance (EN, distance between anterior margin of eye and posterior edge of nostril), snout to eye distance (SE, distance between anterior margin of eye and tip of snout), ear to eye distance (EE, distance from anterior edge of ear opening to posterior margin of eye), ear length (maximum length of ear opening), internarial distance (distance between nares), interorbital distance (shortest distance between the left and right supraciliary scale rows).

Meristic characters recorded included internasal scales (the number of scales touching rostral between the supranasals); number of supralabials (SL) and infralabials (IL), from rostral and mental, respectively to posterior-most enlarged scale at angle of the jaw; chin scales (number of scales touching medial edge of infralabials and mental between juncture of 2nd and 3rd infralabials on the left and right); dorsal scales (ABS, the number of longitudinal dorsal scales at mid-body contained within one eye diameter); ventral scales (VS, the number of longitudinal ventral scales at mid-body contained within one eye diameter); the number of pore-bearing femoral scales; the number of pore-bearing precloacal scales; the number of poreless scales between the precloacal and femoral pores on each side; the number of subdigital lamellae wider than long on the first finger and toe; the lamellar formula, determined as the number of U-shaped, subdigital lamellae (split and single) on digital pads of digits II–V and the basal lamellar formula, the number of subdigital lamellae wider than long except U-shaped lamellae on the digital pads on digits II–V.

We carried out principal components analysis (PCA) to summarise multivariate variation on the meristic and mensural characters independently, including only adult specimens (SVL > 29 mm). We excluded pore counts as they are absent in females and TL and TW due to missing data. Shape was obtained from untransformed measurements by using residuals from regression against SVL, and SVL was subsequently dropped from the analysis. These data were then log transformed and scaled to their standard deviation before performing PCA using the prcomp function in R 3.5.1 (https://www.r-project.org/). This was to demonstrate the three divergent lineages named in this paper are separated from each other and *H. aurantiacus* in morphospace and to

confirm the placement of the lectotype of *H. aurantiacus*. Missing data for the lectotype of *H. aurantiacus* was replaced with median values for each character from the entire dataset.

Results

Phylogeny, species diversity, divergence times and biogeography

The overall topology matched previously published phylogenies (Grismer et al. 2013, 2018a), recovering a basal split separating the *harterti* and *typus* groups, and the seven clades within the *typus* group with slightly different interrelationships amongst each other (Fig. 2). Species described subsequent to the most recently published comprehensive phylogeny (Grismer et al. 2018a) include *H. hongkongensis* Sung

et al. 2018 from Hong Kong placed as a member of clade 6 (clade names follow Grismer et al. 2018a and are marked in Fig. 2); *H. khlonglanensis* Sukprasert et al. 2018 from Thailand recovered as sister to clade 4; and *H. flaviventris* Sukprasert et al. 2018 from Thailand sister to *H.* sp. nov. 9, the two sisters to the *H. aurantiacus* clade (together forming clade 5). All sampled Indian *Hemiphyllodactylus* were placed in a strongly supported *H. aurantiacus* clade, within which a deep basal split (up to 22.1% sequence divergence) separates a clade distributed across the hills of south India (south India clade) and a clade distributed in the northern Eastern Ghats (Eastern Ghats clade; Fig. 2). Applying the 5% sequence divergence cutoff, the south India clade includes seven lineages—*Hemiphyllodactylus aurantiacus, Hemiphyllodactylus kolliensis* sp. nov., *H.* sp. nov. IN 6; *Hemiphyllodactylus jnana* sp. nov. sister to *H.* sp. nov. IN 5, the two sister to *H.* sp. nov. IN 7 and *H.* sp. nov. IN 8 from the Western Ghats, uncorrected sequence divergence within the clade 5.7–15.8% (Table S2). The

Fig. 2 Maximum likelihood phylogeny of *Hemiphyllodactylus* (ND2) showing ancestral ranges at key nodes. Nodes with > 90% bootstrap support marked with solid black circles, clade names follow Grismer et al. (2013, 2015, 2017), outgroups not shown
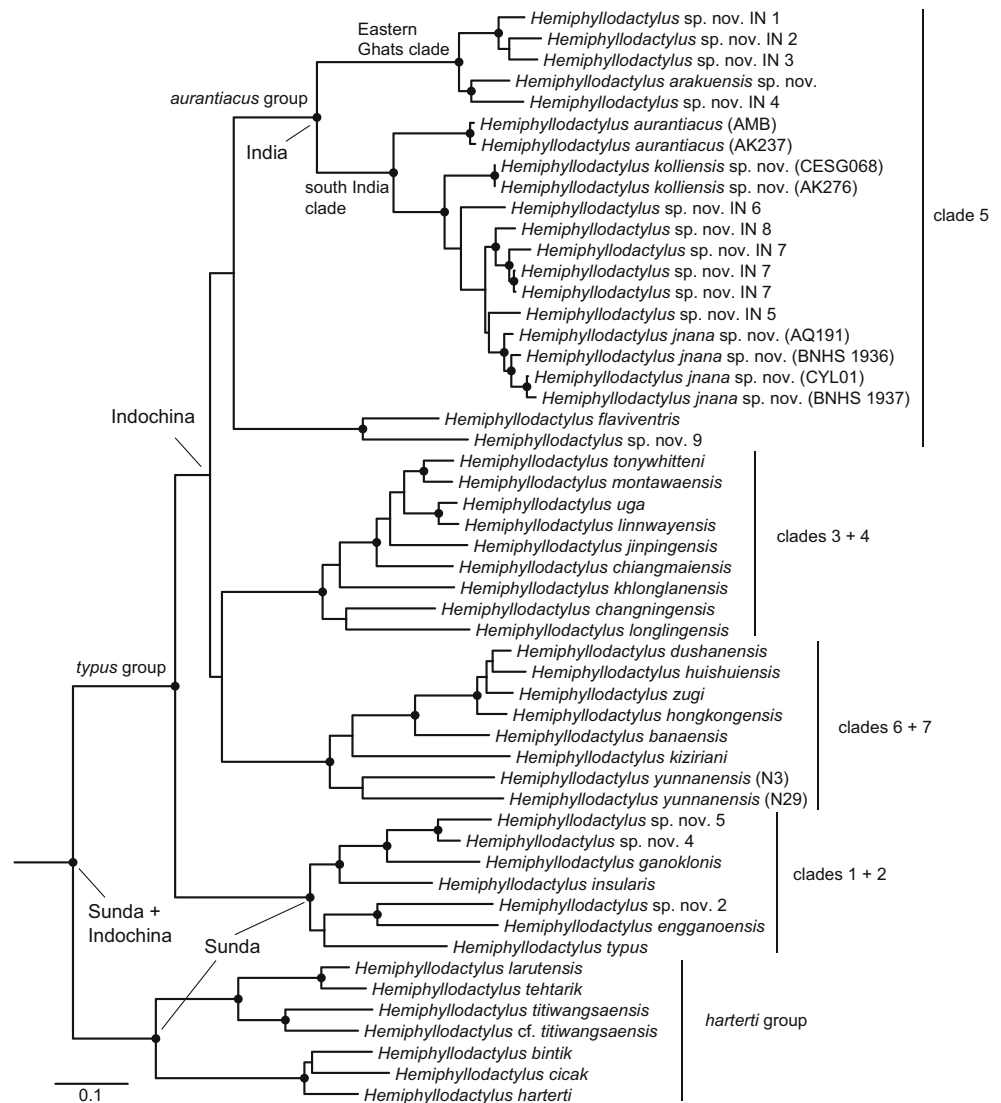
Eastern Ghats clade includes *Hemiphyllodactylus arakuensis* sp. nov. sister to *H.* sp. nov. IN 4, the two sister to an Odisha clade containing *H.* sp. nov. IN 2 from Devagiri sister to *H.* sp. nov. IN 3 from Mahendragiri, the two sister to *H.* sp. nov. IN 1 from Daringbadi; uncorrected sequence divergence 5.9–12.5% within the Eastern Ghats clade (Table S2). The elevational range of sampled lineages is between 500 m (*H.* sp. nov. IN 7 from Coimbatore) and 1400 m (*H. aurantiacus* from Yercaud).

The divergence times we recovered had similar median ages to and broadly overlapping 95% HPDs with published estimates (Grismer et al. 2015), with the basal split within *Hemiphyllodactylus* estimated at 50 (56–44) millions of years ago (mya) (Fig. S1 for complete BEAST tree). The split between Indian *Hemiphyllodactylus* and *H.* sp. nov. 9 + *H. flaviventris* was dated to 33 (38–28) mya. The divergence between the south India clade and Eastern Ghats clade was estimated at 24 (28–20) mya, diversification within the former clade beginning at 13 (16–10) mya and within the latter at 8 (10–7) mya (Fig. 1).

The mrca of *Hemiphyllodactylus* was reconstructed as being distributed in Indochina and Sundaland (DEC, relative probability 0.80) or Sundaland (Mk1, relative probability 0.99), as was the mrca of the *typus* group (DEC, Indochina + Sundaland relative probability 0.85; Mk1, Sundaland relative probability 0.80); the mrca of clades 3–7 in Indochina (DEC & Mk1 relative probability 1.00); the mrca of clade 5 as Indochina + India (DEC, relative probability 1.00) or Indochina (Mk1, relative probability 0.95) and the Indian lineage derived through a single dispersal event from Indochina around 38–28 mya (Fig. 2).

Morphology

Sampled members of the *Hemiphyllodactylus aurantiacus* clade can be diagnosed against all other *Hemiphyllodactylus* species by the subdigital lamellar formula of 2222 on the manus (vs. > 3 lamellae below fingers two to five in all species, except

H. bintik Grismer et al. 2015 and *H. cicak* Cobos et al. 2016 that have > 3 subdigital lamellae only below fingers three and four). The first two principal components of the shape data (MoPC1–MoPC2) explained a cumulative 76% of variation in the original data, with MoPC1 accounting for 66% variation and MoPC2 an additional 10% variation, with low factor loadings across a number of characters in each principal component. The first two principal components of the shape data (MePC1–MePC2) explained a cumulative 61% of variation in the original data, with MePC1 accounting for 43% variation and MePC2 an additional 18% variation, with dorsal, ventral and snout scales loading most strongly on MePC1 and chin scales and 4th toe lamellae on MePC2. Most of the variation in MoPC1–PC2 is not discriminatory, while MePC1–PC2 provide slightly more separation but are unable to separate *Hemiphyllodactylus aurantiacus* and the three new species completely (Fig. 3). We provide an expanded diagnosis for *Hemiphyllodactylus aurantiacus* and describe three genetically and morphologically divergent lineages from Bangalore, the Kolli Hills and Araku as new species below.

Systematics

Hemiphyllodactylus aurantiacus

Hemidactylus aurantiacus (Beddome 1870, p. 33)
Shevaroy slender gecko
(Figure S2)

Lectotype

Adult male (BMNH 74.4.29.1333), from 'Shevaroys, under stones about Yercaud and elsewhere at an elevation of 4000 feet'.

Fig. 3 Plot of first two principal components (PC1–2) for morphometric (Mo) and meristic (Me) data showing the position in morphospace of *Hemiphyllodactylus aurantiacus*, *H. arakuensis* sp. nov., *H. jnana* sp. nov. and *H. kolliensis* sp. nov. The holotype of *H. aurantiacus* is marked by an asterisk (*)
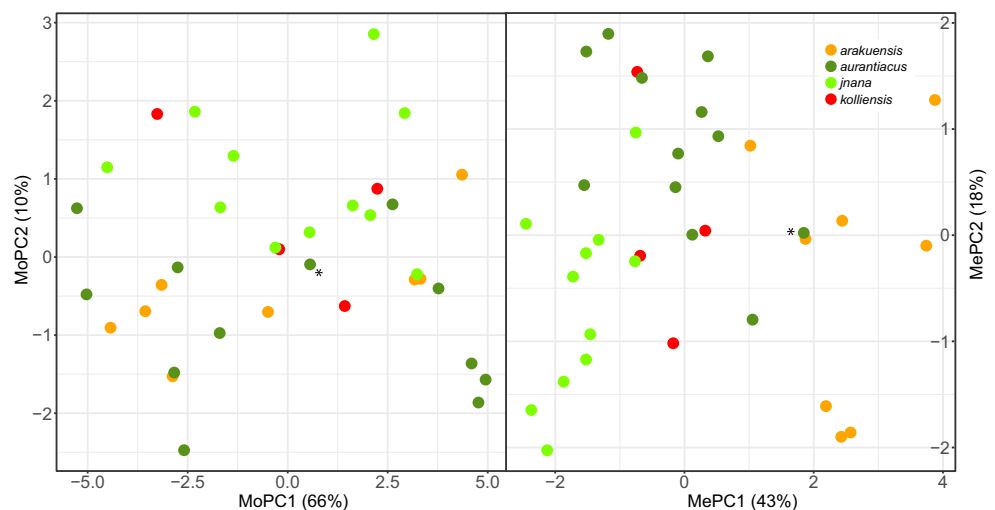
Paralectotypes

BMNH 74.429.1332, 1334–1337, ZMB 10233 (one adult male, three females and four juveniles), same collection locality as lectotype.

Referred material

Adult males (AK 240–241, AK 244–247) and adult females (AK 237–239 AK 242–243) from near Grange resort, Yercaud, (11.775° N 78.219° E; ca. 1390 masl.), Salem district, Tamil Nadu state, India, collected by A. Khandekar, I. Agarwal and N. Gaitonde on 12 September 2018.

Diagnosis

Hemiphyllodactylus aurantiacus can be distinguished from other members of the genus by a combination of maximum SVL of 40.9 mm; 9–12 chin scales, postmentals not enlarged, 9–13 SL, 10–13 IL, 13–16 dorsal scales and 9–12 ventral scales at mid-body contained within one longitudinal eye diameter; 3–5 subdigital lamellae on the first finger and toe; lamellar formula of manus 2222; lamellar formula of pes 2333; males with six or seven precloacal scales separated by 8–11 unpored scales from a series of six or seven pore-bearing femoral scales on each thigh; no plate-like enlarged subcaudals; dark postorbital stripe and longitudinal markings on nape extending to or beyond forelimb insertions; dorsal pattern of irregular dark bands or strong reticulations, fine light paravertebral spots present; postsacral marking with light-coloured anteriorly projecting arms, belly stippled with black.

Note

Zug (2010) designated a lectotype and provided a redescription of the type series, while Bauer & Das (1999) provided a diagnosis based on topotypic material. We provide a summary of the characters in *H. aurantiacus* based on our material from the type locality and published data on the lectotype in Table 1 and data for individual specimens in Table 2.

Table 1 Major diagnostic characters across all Indian *Hemiphyllodactylus* species. Mean given in parentheses

Species	H. aurantiacus	H. arakuensis sp. nov.	H. jnana sp. nov.	H. kolliensis sp. nov.
Maximum SVL	41	39	41	39
Chin scales	9–12	8–11	10–12	10–12
Supralabials	9–12	9–12	10–12	9–11
Infralabials	10–13	9–12	9–13	10–11
Internasals	3–4	2–3	3–5	3–4
Dorsal scales	13–16 (14.8)	13–16 (15)	16–20 (18.3)	16
Ventral scales	9–13 (11.1)	7–9 (7.9)	11–15 (13.5)	10–13 (11.3)
Lamellae under first finger	3–5	4 or 5	4 or 5	3 or 4
Lamellae under first toe	4 or 5	5 or 6	4 or 5	4 or 5
Lamellar formula of manus	2222	2222	2222	2222
Lamellar formula of pes	2233, 2333 or 3333	2333 or 3333	2222	2222
Precloacal pores	6–7	8–9	9–10	9
Scales between precloacal and femoral pores	9–11	11–14	10–12	5
Femoral pores	6–8	2–3	6–7	8
TRL/SVL	0.47–0.51	0.48–0.56	0.50–0.55	0.51–0.55
HL/SVL	0.20–0.22	0.20–0.23	0.19–0.24	0.19–0.21
HW/HL	0.80–0.97	0.75–0.86	0.68–0.85	0.78–0.86
Dark postorbital stripe	Y	Y	Y	Y
Light paravertebral spots on trunk	Y	N	Y	Y
Dark dorsal transverse bands/blotches	Reticulations, sometimes forming irregular bands	Regular or irregular bands	Fine paravertebral reticulations	Paravertebral reticulations
Extent of longitudinal markings on nape	Usually beyond forelimb insertion	Up to forelimb insertion	Up to forelimb insertion	Up to forelimb insertion
Postsacral marking with light-coloured anteriorly projecting arms	Y	Indistinct	Y	Y

Table 2 Data for *Hemiphyllodactylus aurantiacus*. Asterisk (*) indicates broken tail or measurement/count could not be taken, data for lectotype from Zug (2010)

| | *Hemiphyllodactylus aurantiacus* | | | | | | | | | | | |
| | Lectotype | Referred material | | | | | | | | | | |
Specimen no.	BMNH 74.4.29.1333	AK 240	AK 241	AK 244	AK 245	AK 246	AK 247	AK 237	AK 238	AK 239	AK 242	AK 243
Sex	M	M	M	M	M	M	M	F	F	F	F	F
Snout to vent length	34.5	29.2	29.3	32.9	37.9	32.6	32.2	40.9	33	41	40.1	39.1
Tail length	*	19.5	19.33	25.4	31.2	20.8	19	11*	2.5*	24.1	24.2	29.9
Tail width	*	2.2	2.5	2.6	3	3	2.3	3.6	3.3	3.4	3.7	2.8
Trunk length	17.5	14.1	14	15.7	18.7	16.6	15.5	21.1	16.8	19.2	20.7	18.8
Body height	*	2.5	2.5	2.8	3.6	2.7	3.1	4.8	3.76	5.3	5.7	5.1
Body width	*	6	5.66	5.7	7.1	5.6	5.6	8.1	5.6	7.9	7.4	7.5
Head length	7.8	6.5	6.1	6.9	7.8	6.9	6.8	8.1	6.8	8.2	8.1	8
Head width	5.6	5.3	5.9	5.6	7.1	5.7	5.9	7	5.7	6.9	6.5	6.5
Head height	*	3.2	3.2	3.2	3.7	3.6	3.6	4.5	3.4	4	4.7	3.9
Forearm length	*	2.8	2.9	3.3	3.7	3.2	3.2	4.1	3	4	4.1	3.8
Crus length	*	3.5	3.3	3.8	4.4	3.8	3.4	4.6	3.9	4.5	4.7	4.3
Eye diameter	2.0	1.7	1.6	1.7	1.9	1.6	1.6	2	1.8	1.9	1.9	1.9
Nostril to eye distance	2.8	2.1	2.2	2.4	2.7	2.4	2.4	2.8	2.5	2.8	2.8	3
Snout to eye distance	3.7	2.9	3.1	3.2	3.6	2.9	3	3.8	3.2	3.8	3.7	3.9
Eye to ear distance	*	2.6	2.5	3	3.3	2.9	3.1	3.3	3	3.4	3.3	3.2
Ear length	*	0.5	0.3	0.5	0.4	0.4	0.6	0.7	0.6	0.7	0.7	0.5
Internarial distance	*	0.9	1	0.9	1.1	1	1.1	1.1	0.9	1.2	1.2	1.3
Interorbital distance	*	1.8	1.7	1.6	2.4	2	1.6	2	2.1	2.2	2	2
Supralabials (L/R)	13	11/9	12/12	11/10	10/9	12/10	12/11	10/10	11/10	11/11	10/10	10/11
Infralabials (L/R)	11	11/11	12/11	10/12	12/10	13/10	12/12	10/11	12/10	11/11	11/12	12/11
Internasals	*	3	4	3	3	4	4	3	3	4	3	4
Chin scales	*	10	9	10	10	10	12	10	10	10	12	10
Dorsal scales	16	16	16	16	14	16	15	13	16	13	14	14
Ventral scales	12	9	13	12	11	12	12	11	12	9	10	11
Femoral pores (L/R)	7/8	6/6	7/7	7/8	7/7	8/7	7/6	0	6/6	0	0	0
Precloacal pores	7	6	7	7	6	7	7	0	7	0	0	0
Scales between femoral and precloacal pores (L/R)	*	10/10	9/9	10/10	8/6*	10/10	10/10	0	11/9	0	0	0
Lamellae under first finger	*	4/4	4/4	4/4	4/4	4/3	4/4	4/5	4/4	4/4	5/4	4/4
Lamellae under first toe	*	4/4	4/4	5/5	5/5	4/3	4/4	5/5	4/4	4/4	5/5	5/5
Lamellar formula of manus	2222	2222	2222	2222	2222	2222	2222	2222	2222	2222	2222	2232
Lamellar formula of pes	2333	2333	2333	2333	2333	2333	2333	2333	2333	2233	2233	3333
Basal lamellar formula of manus	*	3554	3554	3464	3455	3354	3454	4465	3554	3465	4564	3555
Basal lamellar formula of pes	*	3554	4454	3464	3455	4454	3453	3564	3554	3575	3575	3554

Distribution

Hemiphyllodactylus aurantiacus is known only from the vicinity of Yercaud, Salem District, Tamil Nadu.

Natural history

Hemiphyllodactylus aurantiacus was described from an elevation of ~ 1200 m (Beddome 1870) and other localities are also in and around Yercaud (~ 1200–1600 m) (Beddome 1870; Bauer & Das 1999; Ganesh & Arumugam 2015). We encountered the species after dark along low stone walls in Grange Resort, Yercaud (~ 1390 m) in high abundance, with over 25 specimens encountered in about an hour of search. The vegetation in the Shevaroys varies from scrub at the foothills, transitioning to deciduous forests at middle elevations with evergreen forests on parts of the plateau (Jayakumar et al. 2009).

Hemiphyllodactylus jnana sp. nov.

Bangalore slender gecko
(Figures S3–5)

Holotype

Adult male (AQ 191) collected 26 October 2015 by Rajesh Sanap and Zeeshan Mirza from the National Centre for Biological Sciences campus, Bangalore, Bangalore Urban District, Karnataka, India (13.072° N, 77.581° E, 930 m).

Paratypes

Adult males (AQ 186, AQ 187) and adult females (AQ 188–190, AQ 192–195) have same collection data as holotype; adult female (CESL 014) collected on 10 April 2010 by Saunak Pal and Mrugank Prabhu, from Indian Institute of Science, Bangalore, Bangalore Urban District, Karnataka (13.019° N, 77.567° E, 950 m); adult female (G 470) collected on 30 November 2014 by Aparna Lajmi and Tarun Khichi from near Kolar, Kolar District, Karnataka (13.134° N, 78.09° E, 1020 m) and adult female (CYL 01) collected on 5 December 2016 by R Krishna Chaitanya from Yelagiri, Vellore District, Tamil Nadu (12.576° N, 78.654° E, 960 m).

Referred material

Adult male (BNHS 1936) collected on 17 September 2008 by Jahnavi Joshi from Indian Institute of Science, Bangalore, Bangalore Urban District, Karnataka (13.019° N, 77.567° E, 950 m) and adult male (BNHS 1937) collected on 14 December 2008 by Varun Torsekar, Henrik Krehenwinkel and Ishan Agarwal from Aiyur, Hosur District, Tamil Nadu (12.415° N, 77.841° E, 980 m).

Diagnosis

Hemiphyllodactylus jnana sp. nov. can be distinguished from other members of the genus by a combination of maximum SVL of 39.6 mm; 10–12 chin scales; postmentals not enlarged; 10–12 SL; 9–13 IL; 16–20 dorsal scales and 11–15 ventral scales at mid-body contained within one longitudinal eye diameter; four or five subdigital lamellae on the first finger and toe; lamellar formula of manus and pes 2222; males with nine or ten pored precloacal scales separated by 10–12 unpored scales from a series of six or seven pore-bearing femoral scales on each thigh; no plate-like subcaudals; fine, broken, dark postorbital stripe just extending onto trunk and sometimes extending to tail base; longitudinal markings on nape usually not extending beyond forelimb insertion; dorsal colour pattern of indistinct darker reticulations or longitudinal paravertebral markings, light paravertebral spots present; postsacral marking without distinct light-coloured anteriorly projecting arms and belly stippled with black.

Etymology

The specific epithet, *jnana* (jñāna or nyaa-na), is the Kannada word for knowledge, derived from the same root in Pali/Sanskrit and is used as a noun in apposition. The name is given in honour of two scientific institutions in Bangalore, the Indian Institute of Science (IISc) and the National Centre for Biological Sciences (NCBS), within the grounds of which the species was first found. The Centre for Ecological Sciences (CES) at IISc and NCBS are at the centre of research in ecology and evolution in India, and the authors have all either worked or studied at these institutions.

Description of holotype

Adult male fixed in a slightly sigmoid shape, small vertical incision on thorax (2.4 mm) for tissue collection. SVL 33.7 mm. Head short (HL/SVL 0.20), slightly elongate (HW/HL 0.80), slightly depressed (HH/HL 0.52) and distinct from neck. Prefrontal region flat; canthus rostralis rounded, snout rounded in dorsal profile. Snout short (SE/HL 0.46), slightly longer than eye diameter (ED/SE 0.59); scales on snout, canthus rostralis, prefrontal, inter-orbital and occipital region homogenous, granular; scales on the snout and canthus rostralis much larger and pronounced than those on occipital, prefrontal and inter-orbital regions, two or three rows bordering supralabials flat and slightly elongate. Eye small (ED/HL 0.27); pupil vertical with crenulated margins; supraciliaries small, slightly mucronate, gradually increasing in size towards front of the orbit, those at the anterior end of orbit larger. Ear opening sub-circular (greatest diameter 0.5 mm); eye diameter three-fourth eye to ear distance (ED/EE 0.76). Rostral undivided, wider than deep (length/width 0.50); single large

supranasal on each side, separated by a slightly smaller single scale; single large postnasal, subequal in size to supranasals on each side; rostral in contact with nostril, supralabial I, supranasals and small scale separating supranasals; nostrils small, oval; external nares surrounded by rostral, supralabial I, single postnasal, scale between postnasal and supranasal (slightly separated but no intervening scales). Mental triangular, bordered laterally by infralabial 1 on either side and posteriorly by three chin scales; twelve scales along internal edge of infralabials and mental between juncture of 2nd and 3rd infralabials on either side. Labials gradually decrease in size posteriorly, supralabial I and infralabial I largest; supralabials (to midorbital position) 8 (right)—8 (left) on both sides; supralabials (to angle of jaw) 11 (right)—11 (left); infralabials (to angle of jaw) 10 (right)—11 (left).

Body moderately elongate (TRL/SVL 0.50), ventrolateral folds indistinct. Scales on dorsum of head and neck granular, smaller than those on the snout and prefrontal region; scales on body dorsum larger, flat and rounded and 20 scales contained within one eye diameter at mid-body. Ventral scales much larger than dorsals, smooth, imbricate and sub-circular, gradually increasing in size and becoming strongly imbricate and pointed posteriorly, except five or six rows above cloaca that are much smaller; 14 scales contained within one eye diameter at mid-body. Gular scales granular, smaller than ventrals and similar in size to dorsals, slightly larger, flat and juxtaposed on anterior aspect. Scales on palm and sole flat and rounded; scales on dorsal and ventral aspect of limbs flat and subimbricate, those on anterolateral aspect of thigh largest. Fore and hind limbs stout, forearm short (FL/SVL 0.09) and tibia short (CL/SVL 0.11). Digits with well-developed lamellar pad; first digit on manus and pes vestigial, slender partially sheathed claw visible under first toe; digits II–V well developed, with free terminal phalange arising from within lamellar pad, ending in an unsheathed, recurved claw; lamellar pads of digits II–V with basal series of undivided, transverse lamellae, and apical series of large U-shaped lamellae, which are divided/deeply notched, with a single wedge-shaped terminal lamella; four transversely expanded lamellae on digit I of manus, proximal lamellar formula 2222 (right, left), basal lamellar formula 3554 (right, left); five transversely expanded lamellae on digit I of pes, proximal lamellar formula 2222 (right, left) and basal 4355 (right, left).

Tail original except for one-fifth which is regenerated, not segmented; tail slightly shorter than snout vent length (TL/SVL 0.85); scales on tail flat, subimbricate, smooth and rounded; scales on dorsal aspect of tail larger than those on body dorsum, gradually increasing in size ventrally. Two enlarged, subequal postcloacal spurs on both sides. Nine pored precloacal scales in an angular series flanked by seven pore-bearing femoral scales on each side, both series separated by a diastema of 12 (right) and 10 (left) poreless scales.

Colouration in life (based on BNHS 1936; Fig. S3)

Ground colour of dorsum, head and limbs brown. Indistinct dark pre-orbital stripe, two broken, fine, dark post-orbital stripes that extend to tail base, more broken from mid-body to tail base; a pair of indistinct paravertebral stripes on nape terminating between forelimb insertions. Dorsum with light paravertebral spots and indistinct dark longitudinal markings, head dirty brown without distinct markings. Limbs with indistinct fine dark reticulations. Postsacral marking light brown to cream, chevron shaped, flanked anteriorly by narrow black chevron that divides lighter marking; light-coloured anteriorly projecting arms indistinct. Original tail light brown with irregular crossbars formed by dark scales flanked by a few light scales, orange ventrally. Ventral surfaces off-white, with some dark scales and fine dark spots on lighter scales.

Colouration in preservative (based on holotype NCBS AQ191; Fig. S4)

Ground colour of dorsum, head and limbs pale brown. Indistinct dark pre-orbital stripe, two distinct dark post-orbital stripes that terminate posterior to forelimb insertion, being replaced by indistinct dark reticulations enclosing white spots along the dorsolateral aspect of body, a pair of indistinct paravertebral stripes on nape. Head mottled with few darker markings. Limbs with indistinct reticulations. Postsacral marking pale buff, consisting of a crossbar divided anteriorly by black chevron; no anteriorly projecting arms. Original tail brown with ~ 5 pairs of indistinct black crossbars posterior to postsacral marking, pale buff ventrally, regenerated portion spotted. Ventral surfaces off-white, stippled with fine dark spots on lighter scales and with few darker scales.

Variation (Fig. S5)

Dorsal colour pattern varies from almost uniform (AQ 193–194) to strong reticulations with numerous lighter spots (AQ 187); 10–12 black markings on original tail, regenerated tail mottled brown; amount of stippling on the ventrum variable. Female paratypes without pores, with prominently swollen white endolymphatic sacs, most prominent in AQ 188–190, AQ 192–194. Variation in important scalation and measurements is given in Table 3.

Distribution

Hemiphyllodactylus jnana sp. nov. is known from Bangalore, Bangalore Urban District and Kolar, Kolar District in Karnataka, and Aiyur, Hosur District and Yelagiri, Vellore District in Tamil Nadu. These naturally occurring populations were previously misidentified as *H. aurantiacus* and their

Table 3 Type series of *Hemiphyllodactylus jnana* sp. nov. Asterisk (*) indicates broken tail or measurement/count could not be taken

Hemiphyllodactylus jnana sp. nov.

	Holotype	Paratypes									
Specimen no.	AQ 191	AQ 186	AQ 187	AQ 188	AQ 189	AQ 190	AQ 192	AQ 193	AQ 194	AQ 195	CYL 01
Sex	M	M	M	F	F	F	F	F	F	F	F
Snout to vent length	33.7	33.7	30.4	39.6	38.1	37	38.2	34.9	38.3	31.5	38.4
Tail length	28.8	24.5	10.7*	26.7	38.3	23.8	25.4	25.0	3.2*	4.4*	34
Tail width	2.9	2.7	2.5	3.1	3.2	3.2	2.8	2.6	2.7	2.4	2.6
Trunk length	15.2	18.1	15.3	20.8	19.6	19.2	19.5	18.8	19.7	16.7	21.3
Body height	2.6	3.3	2.4	3.8	2.8	3.8	2.8	3.6	3	3.6	3.2
Body width	5.7	6.3	5.3	8.5	6.8	7	6.4	6.2	7.3	5.7	7.2
Head length	6.9	7.3	7	7.5	7.7	7.8	7.8	7.3	7.8	7.6	7.7
Head width	5.5	5.7	5.6	6.2	6.3	6.2	6.6	5.6	6.2	5.2	5.8
Head height	3.6	3.2	2.7	3.7	3.6	3.9	3.9	3.5	3.9	3.3	3.6
Forearm length	3.3	3.4	3	3.9	3.7	3.3	3.8	3.5	3.6	2.9	3
Crus length	4.0	3.8	3.5	4.9	4.4	4.0	4.2	3.8	4.1	3.8	4.1
Eye diameter	1.9	1.8	1.7	1.9	1.8	2.0	2.0	1.8	2.0	1.7	2.0
Nostril to eye distance	2.9	2.5	2.2	2.8	2.5	2.7	3.0	2.5	2.9	2.4	2.4
Snout to eye distance	3.2	3.1	2.9	3.5	3.5	3.5	3.7	3.3	3.5	3.5	3.3
Eye to ear distance	2.5	2.7	2.5	2.9	3.1	2.9	3.2	2.9	2.9	2.6	3.1
Ear length	0.5	0.4	0.4	0.4	0.5	0.6	0.7	0.5	0.3	0.3	0.4
Internarial distance	1.0	1.0	1.1	1.1	1.2	1.2	1.3	1.1	1.2	1.0	1.2
Interorbital distance	2	2.3	2	2.6	2.5	2.5	2.4	2.2	2.7	2.2	1.8
Supralabials (L/R)	11/11	11/11	11/11	12/11	11/12	10/11	11/11	10/11	10/11	12/11	11/11
Infralabials (L/R)	11/10	10/10	11/11	11/11	11/11	9/11	11/12	11/11	11/10	12/11	10/9
Internasals	4	4	4	4	4	3	5	4	5	4	3
Chin scales	6/6	5/5	6/5	6/6	6/5	5/5	5/6	5/5	5/5	5/5	5/6
Dorsal scales	20	18	19	17	18	16	20	20	19	18	17
Ventral scales	14	13	15	12	14	14	14	13	14	14	13
Femoral pores (L/R)	7/7	7/7	6/6	0	0	0	0	0	0	0	0
Precloacal pores	9	9	10	0	0	0	0	0	0	0	0
Scales between femoral and precloacal pores (L/R)	10/12	12/12	10/11	0	0	0	0	0	0	0	0
Lamellae under first finger	4/4	4/4	4/4	4/4	4/4	4/4	4/4	4/4	4/4	4/4	4/4
Lamellae under first toe	5/5	4/4	5/4	4/4	5/4	4/4	5/4	5/5	4/4	5/5	4/4
Lamellar formula of manus	2222	2222	2222	2222	2222	2222	2222	2222	2222	2222	2222
Lamellar formula of pes	2222	2222	2222	2222	2222	2222	2222	2222	2222	2222	2222
Basal lamellar formula of manus	3554	3455	3453	4565	4555	3554	4564	*465	3555	3465	4454
Basal lamellar formula of pes	4355	3545	3554	3554	4554	4554	4565	3555	3545	4455	4454

disjunct distribution in urban areas around Bangalore led to the speculation that these were accidentally introduced by humans (Daniels 1994; Bauer & Das 1999; Zug 2010). The species is still seen in Bangalore City, and an uncollected adult male was observed on McPherson Road, Cooke Town on 22 February 2019.

Natural history

Hemiphyllodactylus jnana sp. nov. has been recorded from scattered localities on the southern edge of the Mysore Plateau at elevations between 930 and 1020 m, across a range of habitats that include a mixture of scrub and degraded deciduous forest, besides plantations and other human modified habitats (also see Giri et al. 2009; Agarwal 2016). The species has been encountered from an hour after dark to ~ 6 h after sunset, mainly on trees and walls in and around human habitation as well as on the ground. The species has been seen during the day beneath tree bark and in crevices in trees at the type locality (Rajesh Sanap, *pers obs*), besides in leaf litter and twice on a shaded road. The new species is common at its type locality, in

the NCBS lawns and adjacent GKVK campus which include mainly exotic tree species, and we have encountered 10–12 individuals in about two man hours of search.

Comparisons

Hemiphyllodactylus jnana sp. nov. can be distinguished from *H. aurantiacus* by the presence of two lamellae under toes four and five (vs. three lamellae under toes four and five), more precloacal pores in males (mean 9.3, range nine or 10 vs. 6.7, six or seven) and more dorsal scales (mean 18.3, range 16–20 vs. 14.8, 13–16) and ventral scales (mean 13.5, range 11–15 vs. 11.1, 9–13). *Hemiphyllodactylus jnana* sp. nov. is compared against *H. kolliensis* sp. nov. and *H. arakuensis* sp. nov. after their descriptions. Major diagnostic characters across all Indian *Hemiphyllodactylus* species are scored in Table 1.

Hemiphyllodactylus kolliensis sp. nov.

Kolli slender gecko
(Figures S6–8)

Holotype

Adult male (CES G138) collected on 23 March 2011 by Aniruddha Datta-Roy and Ishan Agarwal from near Selur Nadu, Kolli Hills (known locally as Kollimalai), Namakkal District, Tamil Nadu, India (11.219° N, 78.354° E, 1170 m).

Paratypes

Adult females (AK 276–278) have same collection data as holotype except, collected on 20 April 2011, AK 277 from near Semmedu (11.268° N, 78.321° E, 1180 m) and AK 278 from near Thinnanurnadu (11.242° N 78.330° E, 1100 m).

Diagnosis

Hemiphyllodactylus kolliensis sp. nov. can be distinguished from other members of the genus by a combination of maximum SVL of 39.3 mm; 10–12 chin scales; postmentals not enlarged; 9–11 SL; 10 or 11 IL; 16 dorsal scales and 10–13 ventral scales at mid-body contained within one longitudinal eye diameter; three or four subdigital lamellae on the first finger and four or five on toes; lamellar formula of manus and pes 2222; males with 10 pored precloacal scales separated by 5 unpored scales from a series of 8 pore-bearing femoral scales on each thigh; no plate-like subcaudals; dark postorbital stripe just extending onto trunk; longitudinal markings on nape extending beyond forelimb insertion; dorsal pattern of few scattered light spots and indistinct reticulations or dark paravertebral reticulations enclosing light paravertebral spots; postsacral marking with light-coloured anteriorly projecting arms and belly stippled with black.

Etymology

The specific epithet is a toponym for the type locality of the species, the Kolli Hills (known locally as Kollimalai).

Description of holotype

Adult male fixed with the head bent towards the left, tail missing. SVL 32.7 mm. Head short (HL/SVL 0.21), slightly elongate (HW/HL 0.78), slightly depressed (HH/HL 0.47) and distinct from neck. Prefrontal region flat; canthus rostralis rounded, snout rounded in dorsal profile. Snout short (SE/HL 0.45), slightly longer than eye diameter (ED/SE 0.54); scales on snout, canthus rostralis, prefrontal, inter-orbital and occipital region homogenous, granular; scales on the snout and canthus rostralis much larger than those on occipital, prefrontal and inter-orbital regions, two or three rows bordering supralabials flat and slightly elongate. Eye small (ED/HL 0.25); pupil vertical with crenulated margins; supraciliaries small, slightly mucronate, gradually increasing in size towards front of the orbit, those at the anterior end of orbit larger. Ear opening sub-circular (greatest diameter 0.3 mm); eye diameter ~ two-thirds eye to ear distance (ED/EE 0.68). Rostral undivided, wider than deep (length/width 0.42); a single large supranasal on each side, separated by three slightly smaller scales; single large postnasal, slightly smaller than supranasals; rostral in contact with nostril, supralabial I, supranasals and three small scales separating supranasals; nostrils small, oval; external nares surrounded by rostral, supralabial I, single postnasal, scale between postnasal and supranasal. Mental triangular, bordered laterally by infralabial I on either side and posteriorly by three chin scales; twelve scales along internal edge of infralabials and mental between juncture of 2nd and 3rd infralabials on either side. Labials gradually decrease in size posteriorly, supralabial I and infralabial I largest; supralabials (to midorbital position) 7 (right)—8 (left); supralabials (to angle of jaw) 10 (right)—9 (left); infralabials (to angle of jaw) 11 (right)—10 (left).

Body moderately elongate (TRL/SVL 0.51), ventrolateral folds indistinct. Scales on dorsum of head and neck granular, smaller than those on the snout and prefrontal region; scales on body dorsum larger, flat and rounded; 16 scales contained within one eye diameter at mid-body. Ventral scales much larger than dorsals, smooth, imbricate and sub-circular in outline, gradually increasing in size and becoming strongly imbricate and pointed posteriorly, except 4–5 rows above cloaca that are much smaller; 11 scales contained within one eye diameter at mid-body. Gular scales granular, smaller than ventrals and similar in size to dorsals, slightly larger, flat and juxtaposed on anterior aspect. Scales on palm and sole flat and rounded; scales on dorsal and ventral aspect of limbs flat and subimbricate, those on anterolateral aspect of thigh largest. Fore and hind limbs stout; forearm short (FL/SVL ratio 0.

09); tibia short (CL/SVL ratio 0.11). Digits with well-developed lamellar pad; first digit on manus and pes vestigial, slender partially sheathed claw visible under first toe; digits II–V well developed, with free terminal phalange arising from within lamellar pad, ending in an unsheathed, recurved claw; lamellar pads of digits II–V with basal series of undivided, transverse lamellae and apical series of large U-shaped lamellae, which are divided/deeply notched, with a single wedge-shaped terminal lamella; four transversely expanded lamellae on digit I of manus, proximal lamellar formula 2222 (right, left), basal lamellar formula 3453 (right, left); five(right) and four (left) transversely expanded lamellae on digit I of pes, proximal lamellar formula 2222 (right, left) and basal 3565 (right, left).

Tail original, two-thirds missing, rounded, not forming caudal segments; scales on dorsal aspect of tail larger than those on body dorsum, gradually increasing in size ventrally. Two enlarged, subequal postcloacal spurs on the left and three on the right. Ten precloacal scales with pores in an angular series flanked by eight femoral pore-bearing scales on each side, both series separated by a diastema of five poreless scales.

Colouration in life (Fig. S6)

Ground colour dark coffee, faintly suffused with dark rust orange, more prominently on the head. Faint orange stripe on each side running from snout through eye, along dorsolateral margin of body and coming together at tail base; a pair of indistinct paravertebral stripes on nape extending to forebody. Limbs and body with small orange spots, most formed by 2–4 orange scales. Postsacral marking saffron, with saffron anteriorly projecting arms, dark medial spot and two broad markings covering tail dorsum. Original tail with alternating orange and dark colouration dorsally, dark markings laterally and orange white ventrally, regenerated portion uniformly mottled brown black. Throat strongly stippled with dark spots and belly with numerous dark scales, underside of limbs and precloacal region strongly pigmented.

Colouration in preservative (Fig. S7)

Ground colour brown. Dull light stripe on each side running from snout and through eye, until beyond forelimb insertions, dark, indistinct pre-orbital and two postorbital streaks, a pair of indistinct paravertebral stripes on nape. Limbs with small light spots. Postsacral marking off-white, with prominent light-coloured anteriorly projecting arms and dark medial spot. Throat strongly stippled with dark spots and belly with numerous dark scales, underside of limbs and precloacal region strongly pigmented.

Variation (Fig. S8)

The three female paratypes lack precloacal or femoral pores but are otherwise similar to the holotype in scalation and measurements (Table 4). Paratypes lighter in ground colouration and with more prominent dark dorsal markings than holotype, nuchal stripes extending past forelimb insertions, indistinct dark reticulations enclosing lighter spots on flanks, amount of stippling on ventrum variable.

Distribution

Hemiphyllodactylus kolliensis sp. nov. is known from three localities within 10 km of each other in the Kolli Hills, Namakkal District, Tamil Nadu, India.

Natural history

The Kolli Hills are an isolated massif about 40–60 km south of the Shevaroys in southern peninsular India, which rise steeply from a base elevation of ∼300 to ∼1400 m, forming an undulating plateau above ∼1000 m. The vegetation varies from scrub at the foothills, transitioning to deciduous forests at middle elevations with evergreen forests on parts of the plateau (Jayakumar et al. 2009). *Hemiphyllodactylus kolliensis* sp. nov. has been collected between 1930 and 2230 h at elevations of 1100–1180 m. The holotype was collected on the low wall of a small culvert, one paratype was on the ground near a stone wall, one was in leaf litter and another about 5 cm off the ground on a small shrub. The three paratypes were collected on a single night. All the habitats we collected this species from are human modified, a mix of coffee plantations, farmlands and small towns and villages interspersed with small patches of degraded evergreen and moist deciduous forests. We did not see any *Hemiphyllodactylus* on the walls of the resort at which we stayed in ∼6 h of searching across 5–6 nights though there were numerous *Cnemaspis* sp. both during the day and night.

Comparisons

Hemiphyllodactylus kolliensis sp. nov. can be distinguished from *Hemiphyllodactylus aurantiacus* by the presence of 2 lamellae under toes four and five (vs. 3 lamellae under toes four and five), greater number of pore-bearing precloacal scales in males (9 vs. 6–7) and fewer unpored scales separating the pore-bearing precloacal and femoral scales on each side (5 vs. 9–11) and a slightly more elongate trunk (TRL/SVL 0.51–0.55 vs. 0.47–0.51). *Hemiphyllodactylus kolliensis* sp. nov. differs from *Hemiphyllodactylus jnana* sp. nov. in having more pore-bearing femoral scales in males (8 vs. 6–7) and fewer unpored scales separating the pore-bearing precloacal and femoral scales on

Table 4 Type series of *Hemiphyllodactylus kolliensis* sp. nov. Asterisk (*) indicates broken tail

	Holotype	Paratypes		
Specimen no.	CES G138	AK 276	AK 277	AK 278
Sex	M	F	F	F
Snout to vent length	32.7	37.3	39.3	38.3
Tail length	4.6*	11	16.9*	32.4
Tail width	2.6	2.7	2.8	2.7
Trunk length	16.8	19.6	21.7	19.8
Body height	2.7	2.8	4.5	4.7
Body width	6.6	6.4	7.3	7.4
Head length	6.8	7.4	7.6	7.6
Head width	5.3	6.0	6.1	6.6
Head height	3.2	3.7	3.7	4
Forearm length	3.1	3.3	3.3	3.4
Crus length	3.7	4.1	4.1	4.2
Eye diameter	1.7	1.8	2.0	2.0
Nostril to eye distance	2.4	2.4	2.5	2.7
Snout to eye distance	3.1	3.2	3.3	3.5
Eye to ear distance	2.5	2.9	3.1	2.9
Ear length	0.3	0.5	0.5	0.4
Internarial distance	1.0	1.1	1.1	1.1
Interorbital distance	2.0	2.1	1.8	2.2
Supralabials (L/R)	9/10	10/10	10/10	11/10
Infralabials (L/R)	10/11	10/10	10/11	11/11
Internasals	3	3	4	3
Chin scales	6/6	5/5	5/5	5/5
Dorsal scales	16	16	16	16
Ventral scales	11	10	13	11
Femoral pores (L/R)	8/8	0	0	0
Precloacal pores	9	0	0	0
Scales between femoral and precloacal pores (L/R)	5/5	0	0	0
Lamellae under first finger	4/4	3/3	4/3	4/4
Lamellae under first toe	4/5	4/4	5/4	5/4
Lamellar formula of manus	2222	2222	2222	2222
Lamellar formula of pes	2222	2222	2222	2222
Basal lamellar formula of manus	3453	2353	3554	3453
Basal lamellar formula of pes	3565	3545	4555	3555

each side (5 vs. 10–12), fewer dorsals (16 vs. mean 18.3, range 16–20) and fewer ventrals (mean 13.5, range 11–15 vs. 11.3, 10–13). *Hemiphyllodactylus kolliensis* sp. nov. is compared against *Hemiphyllodactylus arakuensis* sp. nov. after its description. Major diagnostic characters across all Indian *Hemiphyllodactylus* species are recorded in Table 1.

Hemiphyllodactylus arakuensis sp. nov.

Araku slender gecko
(Figures S9–11)

Holotype

Adult male (G 446) collected on 2 March 2014 by Aparna Lajmi, V. Deepak and Aniruddha Datta-Roy from Forest Rest House, Araku, Visakhapatnam District, Andhra Pradesh, India (18.326° N, 82.877° E, 940 m).

Paratypes

Five adult females (G 442–G 444, G 448–449), two adult males (G 445, G 447), have same collection data as holotype.

Referred material

Adult male (BNHS 2275) collected on 18 September 2014 by Aniruddha Datta-Roy, Tarun Khichi and Ishan Agarwal from near Araku (18.255° N, 82.991° E, 1170 m).

Diagnosis

Hemiphyllodactylus arakuensis sp. nov. can be distinguished from other members of the genus by a combination of maximum SVL of 39.0 mm; 8–11 chin scales; postmentals not enlarged; 9–12 SL; 9–12 IL; 13–16 dorsal scales and 7–9 ventral scales at mid-body contained within one longitudinal eye diameter; four or five subdigital lamellae on the first finger and five (rarely six) on toes; lamellar formula of manus 2222; lamellar formula of pes 2333/3333; males with eight or nine precloacal scales separated by 11–14 unpored scales from a series of two or three pore-bearing femoral scales on each thigh; no plate-like enlarged subcaudals; dark postorbital stripe and longitudinal markings on nape extending to forelimb insertions; dorsal pattern of 7–9 irregular dark bands or strong reticulations, light paravertebral spots very fine if present; postsacral marking with light-coloured anteriorly projecting arms and belly stippled with black.

Etymology

The specific epithet is a toponym for the type locality of the species, Araku.

Description of holotype

Adult male fixed with tail-tip bent towards the left and everted hemipenes. SVL 30.1 mm. Head short (HL/SVL 0.23), slightly elongate (HW/HL 0.77), slightly depressed (HH/HL 0.49) and distinct from neck. Prefrontal region flat; canthus rostralis rounded, snout rounded in dorsal profile. Snout short (SE/HL 0.45), slightly longer than eye diameter (ED/SE 0.52); scales on snout, canthus rostralis, prefrontal, inter-orbital and occipital region homogenous, granular; scales on the snout and canthus rostralis much larger than those on prefrontal, occipital and inter-orbital regions, two or three rows bordering supralabials flat and slightly elongate. Eye small (ED/HL ratio 0.23); pupil vertical with crenulated margins; supraciliaries small, slightly mucronate, gradually increasing in size towards front of the orbit, those at the anterior end of orbit larger. Ear opening sub-circular (greatest diameter 0.6 mm); diameter of eye greater than half eye to ear distance (ED/EE 0.57). Rostral undivided, wider than deep (length/width 0.54), a single large supranasal on each side, separated by two slightly smaller scales; single large postnasal on each side, slightly smaller in size than supranasals; rostral in contact with nostril, supralabial I, supranasals and two small scales separating supranasals; nostrils small, oval; external nares surrounded by rostral, supralabial I, single postnasal, scale between postnasal and supranasal. Mental triangular, bordered laterally by infralabial I on either side and posteriorly by two slightly larger chin scales; ten scales touching internal edge of infralabials and mental between juncture of 2nd and 3rd infralabials on either side. Labials gradually decrease in size posteriorly towards angle of jaw, supralabial I and infralabial I largest; supralabials (to midorbital position) 7 (right)—7 (left); supralabials (to angle of jaw) 10 (right)—10 (left); infralabials (to angle of jaw) 10 (right)—9 (left).

Body moderately elongate (TRL/SVL ratio 0.49), ventrolateral folds indistinct. Dorsal scales of head and neck granular, smaller than those on snout and prefrontal region, those on the body dorsum slightly larger than the rest, flat and rounded; 15 scales contained within one eye diameter at mid-body. Ventral scales much larger than dorsals, smooth, imbricate and sub-circular, gradually increasing in size and becoming strongly imbricate and pointed posteriorly, except five or six rows above cloaca that are much smaller; eight scales contained within one eye diameter at mid-body. Gular scales granular, smaller than ventrals and similar in size to dorsals, slightly larger, flat and juxtaposed on anterior aspect. Scales on palm and sole flat and rounded; scales on dorsal and ventral aspect of limbs flat and subimbricate, those on anterolateral aspect of thigh largest. Fore and hind limbs stout; forearm short (FL/SVL ratio 0.10); tibia short (CL/SVL ratio 0.12). Digits with well-developed lamellar pad; first digit on manus and pes vestigial, slender partially sheathed claw visible under first toe; digits II–V well developed, with free terminal phalange arising from within lamellar pad, ending in an unsheathed, recurved claw; lamellar pads of digits II–V with basal series of undivided, transverse lamellae and apical series of large U-shaped lamellae, which are divided/deeply notched, with a single wedge-shaped terminal lamella; four transversely expanded lamellae on digit I of manus, proximal lamellar formula 2222 (right, left), basal lamellar formula 3564 (right, left); five transversely expanded lamellae on digit I of pes, proximal lamellar formula 2333 (right, left) and basal 4552 (right, left).

Tail original, rounded, no segments; tail slightly longer than snout vent length (TL/SVL ratio 1.17); scales on tail flat, subimbricate, smooth and rounded; scales on dorsal aspect of tail larger than those on body dorsum, gradually increasing in size ventrally. Two enlarged, subequal postcloacal spurs on the left and three on right. Nine precloacal scales bearing pores in an angular series flanked by three (right) and two (left) pore-bearing femoral scales, both series separated by a diastema of 13 (right)—14 (left) poreless scales.

Colouration in life (Fig. S9)

Ground colour of dorsum, head and limbs coffee. Indistinct dark pre-orbital stripe, two distinct dark post-orbital stripes that terminate at forelimb insertions. Dorsum with 9 narrow black crossbars with a fine posterior margin of light scales, head mottled with darker markings. Limbs with indistinct crossbars, reticulations and small orange spots. Postsacral marking saffron, chevron shaped, flanked anteriorly by black chevron that just divides saffron marking, no anteriorly projecting arms. Original tail orange with ~ 10 pairs of indistinct black crossbars posterior to postsacral marking, bright orange ventrally. Ventral surfaces off-white, stippled with fine dark spots on lighter scales.

Colouration in preservative (Fig. S10)

Ground colour of dorsum, head and limbs brown. Indistinct dark pre-orbital stripe, two distinct dark post-orbital stripes that terminate posterior to forelimb insertion. Dorsum with 9 narrow black crossbars, head mottled with darker markings. Limbs with indistinct crossbars and reticulations and small pale orange spots. Postsacral marking pale buff, chevron shaped, flanked anteriorly by black chevron; no anteriorly projecting arms. Original tail off-white with ~ 10 pairs of indistinct black crossbars posterior to postsacral marking, pale buff ventrally. Ventral surfaces off-white, stippled with fine dark spots on lighter scales.

Variation (Fig. S11)

Dorsal pattern varies from more or less well-formed crossbars to strong reticulations, regenerated tail with few black spots. There is little variation in scale counts, the number of infralabials and supralabials varies from nine (G 443) to 12 (G 445); precloacal pores are absent in females and the number in males varies between eight and nine (Table 5).

Distribution

Hemiphyllodactylus arakuensis sp. nov. is only known from in and around its type locality Araku, Visakhapatnam District, Andhra Pradesh.

Natural history

Araku is a small town at ~ 940-m elevation in the Mahendragiri Hill Range, just 80 km from the east coast in Visakhapatnam District, Andhra Pradesh. The elevation ranges from < 100 m at the foothills to > 1500 m, with mainly deciduous forests and some evergreen species at higher elevations. *Hemiphyllodactylus arakuensis* sp. nov. has been collected from two localities at 940 m and 1170 m around Araku.

The collection locality in Araku was the compound of the Forest Department Rest House, with mainly non-native vegetation including many large *Eucalyptus* trees, while the other locality was near a small riparian patch of forest in a coffee plantation (also see Agarwal et al. 2012; Datta-Roy et al. 2013). Geckos were spotted after dark on the base of trees (< 1 m high), rocks and walls and a few were on the ground. This species was locally abundant at its type locality with ~ 10 specimens found by IA in 1 h of searching after dark.

Comparisons

Hemiphyllodactylus arakuensis sp. nov. can be distinguished from Indian congeners by males having two or three pore-bearing femoral scales on each thigh (vs. 6–8 in *Hemiphyllodactylus aurantiacus*, six or seven in *H. jnana* and 8 in *H. kolliensis*), 7–9 ventral scales at mid-body contained within one longitudinal eye diameter (9–13 in *H. aurantiacus*, 11–15 in *H. jnana* and 10–13 in *H. kolliensis*) and lamellar formula of toes 2333 or 3333 (vs. 2222 in *H. jnana* and *H. kolliensis*). Major diagnostic characters across all Indian *Hemiphyllodactylus* species are scored in Table 1.

Discussion

Species diversity

The discovery of three new species and as many as eight additional unnamed deeply divergent *Hemiphyllodactylus* lineages from south India and the Eastern Ghats (descriptions of additional species in prep) adds to the list of Indian endemic radiations (Karanth 2015), highlighting the deep diversity of peninsular India and how poorly this is known. The landscapes within which *Hemiphyllodactylus* are distributed are emerging as centres of reptile endemism—the type locality for three geckos are in the vicinity of Bangalore, *Hemidactylus graniticolus* Agarwal et al., 2011, *Cyrtodactylus* (*Geckoella*) *srilekhae* Agarwal, 2016 and *Cnemaspis mysoriensis* (Jerdon, 1853; Agarwal et al. 2013) (see Giri et al. 2009), the latter two restricted to nearly the same region as *Hemiphyllodactylus jnana* sp. nov. The Kolli Hills has a few undescribed *Cnemaspis* Strauch, a *Cyrtodactylus* Gray and a *Hemidactylus* Oken (Agarwal, Khandekar and Giri, in prep) besides an endemic uropeltid snake *Rhinophis goweri* Aengals and Ganesh, 2013; Addo-Bediako et al. 2003, and Yercaud is the type locality for *Cnemaspis yercaudensis* Das and Bauer, 2000; Agarwal et al. 2015, an endemic uropeltid snake *Uropeltis shorttii* (Beddome, 1863; Aengals 2013) (Ganesh et al. 2014) and has a number of undescribed *Cnemaspis* and a *Cyrtodactylus* (Agarwal unpubl. data; Ganesh and

Table 5 Type series of *Hemiphyllodactylus arakuensis* sp. nov. Asterisk (*) indicates broken tail or measurement could not be taken

Hemiphyllodactylus arakuensis sp. nov.

	Holotype	Paratypes						
Specimen no.	CES G446	CES G442	CES G443	CES G444	CES G445	CES G447	CES G448	CES G449
Sex	M	F	F	F	M	M	F	F
Snout to vent length	30.1	38.3	39	36.4	30.7	29.4	31.7	35.3
Tail length	35.3	21.3	24.3	23.6	30.5	2.7*	30	11*
Tail width	2.9	2.6	3.0	3.3	2.4	2.7	2.3	3.0
Trunk length	15.0	21.3	21.2	18.1	14.8	15.3	16.6	17.8
Body height	3.7	4.6	4.6	5.0	2.6	2.4	2.7	3.3
Body width	5.9	7.9	7.4	8.5	6.3	5.8	6.1	6.8
Head length	6.9	8.0	8.1	8	6.4	6.9	6.7	7.1
Head width	5.3	6.1	6.4	6.6	5.5	5.2	5.4	5.4
Head height	3.4	3.8	3.6	3.8	3.2	3.1	3.4	3.3
Forearm length	3.1	3.9	3.4	3.7	3.2	2.8	3.0	3.5
Crus length	3.8	4.5	4.6	4.9	3.5	3.7	3.8	4.1
Eye diameter	1.6	1.9	1.9	1.9	1.5	1.7	1.6	1.8
Nostril to eye distance	2.3	2.6	2.8	2.7	2.2	2.3	2.2	2.5
Snout to eye distance	3.1	3.6	3.7	3.7	3.0	3.0	3.1	3.2
Eye to ear distance	2.8	3.0	3.2	3.1	2.8	3.0	3.0	3.2
Ear length	0.6	0.6	0.5	0.5	0.4	0.5	0.4	0.5
Internarial distance	1.0	1.3	1.3	1.5	1.0	1.1	1.0	1.1
Interorbital distance	1.8	2.1	1.9	2.7	1.6	1.8	1.9	1.9
Supralabials (L/R)	10/10	10/9	9/9	10/10	12/10	10/9	10/10	11/10
Infralabials (L/R)	9/10	10/10	9/9	8/10	12/11	9/9	11/9	10/10
Internasals	2	3	3	2	3	3	2	3
Chin scales	5/5	5/5	6/5	5/5	5/5	5/5	5/3	5/5
Dorsal scales	15	15	15	13	15	16	15	16
Ventral scales	8	7	8	8	8	9	7	8
Femoral pores (L/R)	2/3	0	0	0	2/3	2/2	0	0
Precloacal pores	9	0	0	0	9	8	0	0
Scales between femoral and precloacal pores (L/R)	14/13	0	0	0	13/13	11/12	0	0
Lamellae under first finger	4/4	4/4	5/5	5/5	4/4	5/5	5/5	5/5
Lamellae under first toe	5/5	5/5	5/5	5/5	5/5	5/5	5/5	6/6
Lamellar formula of manus	2222	2222	2222	2222	2222	2223	2222	2222
Lamellar formula of pes	2333	2333	2333	2333	2333	3333	2333	2333
Basal lamellar formula of manus	3564	4554	4563	4565	3464	3454	3454	4564
Basal lamellar formula of pes	4552	4464	4565	4565	4444	3445	3454	5555

Arumugam 2016). In the Eastern Ghats, Araku is close to the type locality of the caecilian *Gegeneophis orientalis* Agarwal et al. 2013, the gecko *Cyrtodactylus* (*Geckoella*) *nebulosus* (Beddome, 1870) and the skink *Sepsophis punctatus* Beddome, 1870 (Datta-Roy et al. 2013), while the geckos *Cyrtodactylus* (*Geckoella*) *jeyporensis* (Beddome, 1878; Aengals et al. 2013) (Agarwal et al. 2013; Agarwal et al. 2012) and *Hemidactylus sushilduttai* Giri et al., 2017; Agarwal et al. 2017 are also distributed in the region, all endemic to the Mahendragiris. Collection-based biodiversity inventory is essential for a baseline understanding of diversity and distributions across peninsular India. Photo-based surveys without collections are not always useful, as an example consider that Ganesh and Arumugam (2016) conceived of *Hemiphyllodactylus aurantiacus* as a single widely distributed taxon across the southern Eastern Ghats, but their observations are likely to include at least four species. Our taxonomic revision of this species complex from peninsular India is in line with recent work on this genus from Myanmar (Grismer et al. 2018b), southern China (Sung et al. 2018), across the Siam peninsula (Sukprasert et al. 2018) and through Malaysia and Sundaland (e.g. Grismer et al. 2013, 2014a, 2015).

Biogeography of peninsular India

Peninsular India was ancestrally forested and has gradually become more arid and open since at least the Oligocene (e.g. Morley 2000, 2007; Molnar & Rajagopalan 2012; Licht et al. 2014), and the dry zone and open landscapes have dominated since the middle-late Miocene (Pound et al. 2012; Agarwal and Ramakrishnan 2017). The role of isolated high-elevation habitats in shaping diversification within peninsular Indian forest taxa has previously only been discussed in the context of the Western Ghats, for frogs and birds (Vijayakumar et al. 2016; Robin et al. 2010, 2015, 2017). The discovery of these paleoendemic species in montane forest habitats across peninsular India confirms their status as relict habitats, islands of unique biodiversity that have persisted for millions of years (Daniels and Vencatesan 1998). The four named species and additional eight unnamed lineages of Indian *Hemiphyllodactylus* are distributed at elevations of 600–1400 m, with deep genetic divergences between montane lineages that are only 50–100 km apart, separated by much hotter and drier low elevation habitats. *Hemiphyllodactylus jnana* sp. nov. has shallow genetic divergence (1.0–2.7%) between localities 80–120 km apart; all on the southern edge of the Mysore Plateau that has an extensive area above 900 m, mirroring the pattern seen in *Cyrtodactylus srilekhae* (Agarwal, 2016). The only other lineage with multiple localities is *Hemiphyllodactylus* sp. nov. IN 7, with 2.3% sequence divergence between two localities that are just 35 km apart, at 500 m and 1230 m. These patterns and the deep divergence between montane localities suggest conservatism in thermal tolerance is likely to emerge as a major driver of diversification in this sky island system (Wiens and Graham 2005). The phylogenetic data presented here, the restricted, montane distribution of other species in the genus (Grismer et al. 2018a, b) and the existence of some sympatric species (Grismer et al. 2015) suggests there are many *Hemiphyllodactylus* species to be discovered across other high elevations in south India and the northern Eastern Ghats. Many gekkonids from Southeast Asia are known only from karst forest habitats (e.g. Grismer et al. 2018a, b, c, d and references therein), and it may be that the high diversity and endemicity of nocturnal geckos in rocky, montane forest habitats in India is due to shared characteristics with karst forest habitats—rocky substrates with varied microhabitats under a forest canopy, providing protection from the heat of the day and multiple niches for locomotion at night, habitat heterogeneity with elevation, and isolation from other similar habitats and microhabitats (Grismer et al. 2018a).

The estimated time of divergence between the south India clade and Eastern Ghats clade is almost identical to that between the *Cyrtodactylus* (*Geckoella*) *collegalensis* (Beddome,

1870) and *C. nebulosus* complexes (Fig. S1). Based on the distribution of the south India and Eastern Ghats *Hemiphyllodactylus* clades and the *Cyrtodactylus* (*Geckoella*) *collegalensis* and *C. nebulosus* complexes (Agarwal et al. 2015); the discontinuous Eastern Ghats mountain range encompasses two distinct biogeographic entities: the southern and northern Eastern Ghats. The southern Eastern Ghats have affinities with other hill ranges in the south including the Western Ghats, BR and MM Hills and other scattered mountains and are characterised by members of the *Cyrtodactylus collegalensis* complex, *Cnemaspis* species and members of the south India *Hemiphyllodactylus* clade. The northern Eastern Ghats has a distinct assemblage of geckos, including members of the *Cyrtodactylus nebulosus* complex and the Eastern Ghats *Hemiphyllodactylus* clade, and the absence of *Cnemaspis* (Agarwal unpubl. data). All the hill ranges south of the Jawadhi Hills have been treated as a part of the Western Ghats based on the distribution and endemicity of land snails (Raheem et al. 2014; Ali et al. 2008; Fig. 1). The only biogeographic range analysis across peninsular India, using bird subspecies data, also suggests a split between south India and regions north of the Godavari (Ramachandran et al. 2017; Bauer et al. 1999). The boundary between the northern Eastern Ghats and the hills of south India may be formed by either the Pennar or Krishna-Godavari Basins (Ramachandran et al. 2017), pending data from the northern Nallamala. We have seen *Cyrtodactylus* (*Geckoella*) cf. *collegalensis* and *Cnemaspis* sp. 20 km south of the Pennar River, and *Cyrtodactylus* (*Geckoella*) cf. *nebulosus* about 10 km north of the Krishna River (Agarwal unpubl. data), with no data from the intervening region.

Indian *Hemiphyllodactylus* and *Cyrtodactylus* (*Geckoella*) both have a Southeast Asian origin (Wood Jr et al. 2012; Agarwal and Karanth 2015; Grismer et al. 2015) and have retained a preference for forest habitats. The mrca of *Cyrtodactylus* (*Geckoella*) probably dispersed to peninsular India via transoceanic dispersal across the Bay of Bengal from somewhere in Sundaland (Wood Jr et al. 2012; Agarwal and Karanth 2015). The scale of our biogeographic analysis cannot ascertain where in Indochina the mrca of Indian *Hemiphyllodactylus* originated from, though the timing is well after the suturing of the Indian plate and Asia (Ali and Aitchison 2008). This is indicative of geodispersal, though transoceanic dispersal cannot be ruled out due to the strong geographic disjunction in the distribution of *Hemiphyllodactylus* between peninsular India and eastern Myanmar. Mirroring the patterns seen in *Cyrtodactylus* (*Geckoella*), most species diversification within Indian *Hemiphyllodactylus* is from the late Miocene on, a time of increased aridification in peninsular India (Agarwal and Karanth 2015), also coincident with diversification in *Hemiphyllodactylus* across the rest of its range (Grismer et al. 2015).

Compliance with ethical standards

Ethical approval No live animals were used in experiments, and specimens were collected with permits from the Andhra Pradesh and Tamil Nadu forest Departments, besides from private land and other non-forest areas. Specimens collected for this study were euthanized with halothane, tissue vouchers stored in ethanol and whole specimens fixed with formalin. This study was approved by the National Centre for Biological Sciences, Bangalore (NCBS) animal ethics committee.

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