Cryptic species and Miocene diversification of Palaearctic naked-toed geckos (Squamata: Gekkonidae) in the Indian dry zone

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We sampled Palaearctic naked-toed geckos from across their range in India and used two mitochondrial and two nuclear genes to reconstruct relationships within a global phylogeny. Published sequences of Peninsular Indian *Hemidactylus* allow us to contrast these two groups in dating analyses – providing insights into the history of the Indian dry zone. Palaearctic naked-toed geckos first moved onto the Indian Plate in the Oligocene, with higher-level diversification probably linked to collision of the Indian and Eurasian plates, and subsequent dispersal into-India and diversification with increasing Miocene aridity. An independent gekkonid radiation with species in the dry zone, *Hemidactylus* diversified during the same period in Peninsular India. Our results demonstrate that dry zone taxa across India may date back to at least the Miocene, with a potential historical climatic barrier between the Indus and Peninsular Indian Divisions. '*Cyrtopodion*' *aravallense* is revealed to be a complex with seven genetically and environmentally divergent lineages that began diversifying in the late Miocene, congruent with increased aridity in north-western India. This discovery of cryptic diversity in the Indian dry zone represents the first terrestrial vertebrate radiation from north-western central India and highlights how little we understand of the regions' biodiversity, emphasizing the need for systematic geographic sampling and multiline evidence to reveal true patterns of diversity. The ancestor of '*Cyrtopodion*' *aravallense* came into the nascent Indian dry zone in the Miocene and has since diversified, potentially in the absence of any sympatric scansorial rupicolous geckos. *Cyrtopodion scabrum* represents a unique case of commensalism and shows phylogeographic structure in its presumed native range. The taxonomic implications of our study include a number of undescribed species, recognition of '*Cyrtopodion*' as a distinct lineage and the non-monophyly of *Altiphylax*.

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Introduction

The biota of the Indian subcontinent is a complex assembly of ancient Gondwanan elements and more recent into-India dispersals, reflecting the unique geological and climatic history of the Indian Plate (Mani 1974a; Datta-Roy & Karanth 2009). The Indian Plate sutured with Asia in the late Eocene to early Oligocene, resulting in the uplift of the Himalayas and the eventual establishment of the monsoon in the Miocene (Ali & Aitchison 2008; Patnaik *et al.* 2012). Postcollision, though terrestrially connected to mainland Eurasia, the Indian Plate has maintained a high degree of faunal distinctiveness, recognized as the Indian

subregion (Corbet & Hill 1992). The most striking climatic feature of the Indian subregion is seasonality, with rainfall unequally distributed temporally and spatially (Patnaik *et al.* 2012). The establishment of the summer monsoon with subsequent increasing aridity and seasonality is thought to have resulted in fragmentation of once contiguous wet forests in the Middle to Late Miocene (Karanth 2003; Pound *et al.* 2012). The current-day Indian wet zone is restricted to the Western Ghats, north-east India and parts of the northern Eastern Ghats and Himalayas (Karanth 2003), spanning the most biodiverse regions in the Indian subcontinent (Mittermeier *et al.* 2005). Molecular phylogenies of diverse wet zone taxa support ancient origins of Indian wet-zone endemics, from Gondwanan relicts to dispersal in the early Miocene (Roelants *et al.* 2004; Joshi & Karanth 2011; Bansal & Karanth 2013; Li *et al.* 2013).

Most of India receives an annual rainfall between 400–1600 mm, making the semi-arid or dry zone its most conspicuous feature (76% of geographic area, http://worldclim.org/). This vast area spans a number of ancient hill ranges (Valdiya 2010), but does not include any Indian biodiversity hotspots (Mittermeier *et al.* 2005) and is relatively depauperate, with few endemic vertebrates (Smith 1935, 1943; Grimmett *et al.* 1998; Menon 2003). In contrast to the relatively well-studied wet zone, the history of the Indian dry zone and its taxa remain obscure, with few dated phylogenies in the literature. The gekkonid genus *Hemidactylus*, widespread across the tropics, has an endemic Peninsular Indian radiation dating back to the Oligocene (Bansal & Karanth 2013) with a number of endemics in the dry zone including a largely dry zone terrestrial radiation (Bauer *et al.* 2008) that has not been dated. *Hemidactylus* also includes a largely Palaearctic, arid-zone radiation (Carranza & Arnold 2006) that just extends into arid western India (Bansal & Karanth 2010; Bauer *et al.* 2010a). Vagile taxa seem to have colonized the Indian dry zone recently, including examples from the Pliocene (snakes, divergence of Peninsular Indian *Echis* and Palaearctic relatives, Pook *et al.* 2009) and Pleistocene (mammals, divergence of Asian and African *Panthera*, Uphyrkina *et al.* 2001; Barnett *et al.* 2009; birds, divergence of Indian and African/Palaearctic larks, Alstrom *et al.* 2013), while more proficient dispersers such as butterflies can be widespread across the dry zone, with single species distributed from Asia to Africa (*Junonia*, Pleistocene range expansion into Asia, Kodandaramaiah & Wahlberg 2007). A time-calibrated phylogeny of *Chamaeleo*, lizards with an African origin, revealed late Miocene divergence between Africa and Arabia + Asia and a subsequent Arabia-Asia split at the Miocene-Pliocene boundary (Tolley *et al.* 2013). A Palaearctic origin is likely for many taxa in the Indian dry zone based on taxonomic affinities and distribution, but explicit

phylogenies are missing, and neither the geographic extent of these colonizations nor the time frame are known. A recently published global phylogeny of the Palaearctic naked-toed geckos (Bauer *et al.* 2013), an arid-adapted Palaearctic group with endemic species in the Indian subregion, allows us to establish the origin and timing of dispersal of this group into India.

Palaearctic naked-toed geckos are a diverse assemblage of gekkonid geckos with a largely Palaearctic distribution, found from North Africa to western China and northern and western India, which date back to the Eocene (Bauer *et al.* 2013). The broad systematics of this group were recently dealt with based on a broad sampling from across the distributional range, clarifying a number of long-standing taxonomic issues (Bauer *et al.* 2013). Within the Indian subcontinent, Palaearctic naked-toed geckos have a high diversity across hyperarid Pakistan, while India is at the south-eastern limit of the global distribution of the Palaearctic naked-toed geckos, with four genera (*Altiphylax*, *Cyrtopodion*, *Crossobamon*, *Microgecko*) known from the northern and western arid margins of the country (Fig. 1; Smith 1935; Agarwal 2009; Bauer *et al.* 2013). Two species are thought to be endemic to India – *Cyrtopodion aravallense* and *C. mansarulum*, known only from the type descriptions (Duda & Sahi 1978; Gill 1997; Uetz 2013). An earlier field survey revealed the presence of a *Cyrtopodion* from Kuno Wildlife Sanctuary, Madhya Pradesh, about 300 km south of the type locality of *C. aravallense*, in the Vindhya Range of India (I. Agarwal, unpublished data). While the species is morphologically similar to *C. aravallense*, preliminary genetic data revealed deep divergences, indicating that more than a single species might be masquerading under this nomen. This led us to believe the Indian assemblage of Palaearctic naked-toed geckos may be more diverse and geographically extensive than previously thought. We sampled gekkonids across arid and semi-arid habitats of central, north and north-west India – covering the range of potential Palaearctic naked-toed gecko habitats in India (Fig. 1). Our goals were to uncover patterns of diversity and identify the geographic extent of the Indian Palaearctic naked-toed gecko radiation and its relationships within the global phylogeny. Additionally, published sequences of the Peninsular Indian *Hemidactylus* radiation (Bauer *et al.* 2008, 2010a; Bansal & Karanth 2010) allow us to date the origins of these independently derived gekkonids that have endemics in the Indian dry zone – contributing to our understanding of the biogeographic history of the Indian dry zone.

Materials and methods
Taxon sampling, DNA data and sequence alignment
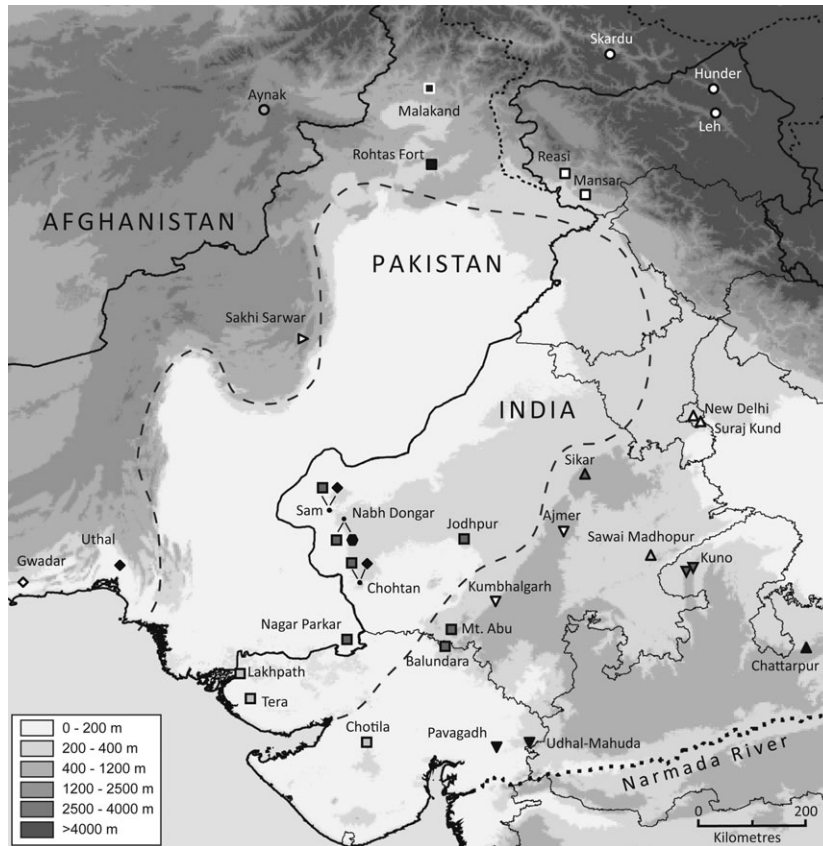We generated sequence data for 29 individuals representing ~13 species of Palaearctic naked-toed geckos from 25

Fig. 1 Map of the northern Indian subcontinent showing sampling localities of Palaearctic naked-toed geckos. Genera represented by shapes, species by fill. Circles = *Altiphylax*, white fill *A. stoliczkai*, grey fill *A. levitoni*. Diamond, solid black = *Crossobamon orientalis*, diamond, white-filled = *Agamura persica*, solid hexagon = *Microgecko persicus euphorbiacola*. Squares = *Cyrtopodion*; black fill *C. rohtasfortai*, grey fill *C. scabrum*, white fill *C. mansarulum*, light grey fill *C. kachhense*, white border and black fill *Cyrtopodion* sp. Pakistan. Triangles = '*Cyrtopodion*'; upward pointing = northern clade of '*Cyrtopodion*' *aravallense* (white fill '*Cyrtopodion*' *aravallense*, light grey fill '*Cyrtopodion*' sp. 'SWM', dark grey fill '*Cyrtopodion*' sp. 'SKR', black fill '*Cyrtopodion*' sp. 'MP'), downward pointing = southern clade of '*Cyrtopodion*' *aravallense* (white fill '*Cyrtopodion*' sp. 'CARAV', grey fill '*Cyrtopodion*' sp. 'KUNO', black fill '*Cyrtopodion*' sp. 'GUJ'), right pointing white fill = '*Cyrtopodion*' *kohsulaimanai*. Localities on the map referenced in Table S1. The dashed line represents the boundary of the Indus Division; with the Palaearctic to the west and north including the Himalayas, and the Peninsular Indian Division to the south and east of the Indus Division. Bold lines represent International borders, dotted lines disputed International borders, fine grey lines Indian state borders and the Narmada River is marked by a bold dotted line.

localities across arid and semi-arid areas of western, north-ern and central India (Table S1, Fig. 1). Type localities and other likely habitats were targeted and geckos were spotted at night by eyeshine on fieldtrips between 2008 and 2013. Tissue samples preserved in 95–100% ethanol were collected in the field from vouchered specimens and a few tissue samples were donated by other researchers (see Acknowledgements). Species identities were ascertained by the authors based on voucher specimens. Genomic DNA was extracted using Qiagen DNeasy™ tissue kits.

We generated 2793 aligned bp of sequence data including two mitochondrial genes (1050 bases of ND2 and 307 bases of CYTB) for most samples as well as two nuclear genes (1041 aligned bases of RAG1 and 395 bases of PDC)

for a subset of distinct mitochondrial lineages. These genes are widely used in squamate phylogenetics and were used by Bauer *et al.* (2013) in their phylogeny of the Palaearctic naked-toed geckos. The additional mitochondrial marker CYTB was sequenced to allow us to add some taxa sampled by Červenka *et al.* (2008) and as it amplifies easily from old samples. Primers and PCR conditions are after Červenka *et al.* (2008) and Bauer *et al.* (2013). We used published sequences of Palaearctic naked-toed geckos representing the broad lineages recovered by Bauer *et al.* (2013), *Hemidactylus* spp. including the endemic Indian terrestrial radiation, and other gekkonids and squamates as out-groups (Table S1). We used chimeric sequences of some taxa for ND2 and CYTB as the data sets of Bauer

et al. (2013) and Červenka *et al.* (2008) overlap for some species but no genes, and the only other in-group taxa with ND2 and CYTB sequences were generated by us from India (Table S1).

Purification and sequencing of PCR products were carried out at Amnion Biotech Pvt. Ltd. (Bangalore, India). Complementary strands were sequenced in most cases to ensure sequence accuracy. Sequence alignment was carried out using ClustalW (Thompson *et al.* 1994) incorporated in MEGA 5.2 (Tamura *et al.* 2011) and finally edited by eye. As these are protein coding genes, translated amino acid alignments were examined for premature stop codons to rule out the sequencing of pseudogenes.

Phylogenetic analyses

Phylogenetic relationships were reconstructed using likelihood (ML) and Bayesian inference (BI). We analysed the data in two subsets – ND2 + RAG1 + PDC (=combined) with a broad sampling of Palaearctic naked-toed geckos (equivalent to the data set of Bauer *et al.* 2013), and ND2 + CYTB (=mtDNA) to add taxa sampled by Červenka *et al.* (2008). Analyses had genes partitioned by codon position and the model of sequence evolution selected from three substitution schemes (=24 models) using BIC in JModelTest (Darriba *et al.* 2012). Partitioned ML analyses were conducted using raxmlGUI v1.3 (Silvestro & Michalak 2012) that implements RAxML HPC 7.4.2 (Stamatakis 2006). As RAxML executes a single model across partitions, we used GTR + G + I and assessed support with 1000 rapid bootstraps. Partitioned Bayesian analyses were carried out in MrBayes 3.2.1 (Ronquist *et al.* 2012) using default priors and GTR + G + I (mitochondrial data) and HKY + G/HKY + G + I (PDC, RAG1) with 5 000 000 generations, sampling every 500 generations with the first 25% discarded as burn-in, using the standard deviation of split frequencies as a convergence diagnostic (<0.01). We use genetic distance or % divergence to indicate uncorrected p distance.

Divergence dating

We included published sequences of *Hemidactylus* spp. from the Peninsular Indian radiation including two sister clades with numerous species in the dry zone – the *H. flaviviridis* group and the *H. brookii* group (Bansal & Karanth 2010) which includes the terrestrial clade (Bauer *et al.* 2008); representing an independently derived gekkonid radiation with species in the dry zone (Table S1). The third clade within Peninsular Indian *Hemidactylus*, the *H. prashadi* group (Bansal & Karanth 2010) has species restricted largely to the wet zone (Smith 1935; Bansal & Karanth 2010) and was represented by *H. depressus* (from Sri Lanka). Divergence dates were estimated in BEAST v1.7.5 (Drummond *et al.*

2012) using the combined ND2 + RAG1 + PDC data set and an ultrametric starting tree estimated in PathD8 (Britton *et al.* 2007) with Yule speciation tree priors and a separate relaxed uncorrelated lognormal clock model for each gene. We partitioned the data set by gene and used simpler models of sequence evolution than the best-fit models (ND2: GTR + G + I; nuclear: HKY + G) due to issues with stationarity (lack of convergence after > 100 million generations). We evaluated seven alternate approaches to divergence date estimation including four fossil-calibrated analyses, two published mitochondrial rates and a secondary calibration. For all fossil-calibrated analyses, we used three priors that have been previously used (Heinicke *et al.* 2011, 2012; Bauer *et al.* 2013) to date gekkotan phylogenies: *Sphaerodactylus roosevelti* vs. *S. torrei* (divergence of *cinereus* group from other *Sphaerodactylus*, exponential prior, mean 3, offset 15), *Lialis* vs. *Pygopus* (diversification of crown pygopods, exponential prior, mean 10, offset 20), *Woodworthia* vs. *Oedura* (divergence between New Zealand and Australian diplodactylids, exponential prior, mean 17, offset 16); and one prior using a geological calibration, the divergence of *Phelsuma inexpectata* and *P. rosagularis* (uniform prior, 0.05–8). *Cretaceogekko*, an amber-preserved gekkotan from Myanmar dated to 97–110 million years ago (mya) is an important fossil, representing the oldest known gekkotan (Arnold & Poinar 2008; Daza *et al.* 2014). *Cretaceogekko* has been used to calibrate the gekkonid/phyllodactylid split on biogeographic grounds (Heinicke *et al.* 2011, 2012; Bauer *et al.* 2013), but a recent re-evaluation of fossil geckos recovers *Cretaceogekko* as an unresolved polytomy at the base of the gekkotan tree (Daza *et al.* 2014). We prefer to use it as a hard minimum for the Gekkota (Pepper *et al.* 2011) and assigned a broad exponential prior distribution to account for uncertainty in its phylogenetic position (mean 20, offset 97). We evaluated two alternate root calibrations. The first is a commonly used root calibration in gekkotan divergence dating (Heinicke *et al.* 2011, 2012; Wood *et al.* 2012; Bauer *et al.* 2013), the estimated time of divergence of gekkotans from squamates ~200 mya (Vidal & Hedges 2005). We tested this root calibration for a squamate-only data set (uniform prior, 175–225) and the bird–lizard divergence (Benton & Donoghue 2007) as an alternate root calibration for a data set including birds (exponential prior, mean 13, offset 260; 95% HPD includes the soft upper bound of 300; Table S1). Additionally, we ran analyses using *Cretaceogekko* to calibrate the gekkonid/phyllodactylid split (exponential prior, mean 20, offset 97) to compare our estimates with Bauer *et al.* (2013); as well as with only nuclear data using the bird root calibration and *Cretaceogekko* as a basal gekkotan. We also ran analyses using a secondary calibrations for Palaearctic naked-toed geckos from Bauer *et al.* (2013) and

two published lizard mtDNA substitution rates (0.57% per million years, Macey *et al.* 1999; 2.05%, Brown *et al.* 2008). We ran final analyses for 100 million generations each, sampling every 5000 generations, with the first 25% discarded as burn-in. Stationarity was assessed in Tracer 1.5 and trees summarized using TreeAnnotator 1.5.3 (Rambaut & Drummond 2007).

Ancestral area reconstructions

Ancestral areas were reconstructed with default settings using S-DIVA (Yu *et al.* 2010) and Bayesian Binary MCMC (BBM; Ali *et al.* 2012) in RASP (Yu *et al.* 2012) using a data set including only the Palaearctic naked-toed geckos, *Cyrtodactylus* and *Hemidactylus*, with *Microgecko* used to root the tree. MrBayes was used to generate input tree files for reconstructions. Three broad areas were designated for reconstructions (modified from Corbet & Hill 1992): the Palaearctic, defined here as all areas north and west of the mountains of Pakistan and north of the Himalayas; and within the Indian Subregion, the Indus Division (including the lowlands of Pakistan <800 m elevation, and western margin of India <400 mm rainfall), and the Peninsular Indian Division, which includes all areas to the south and east of the Indus Division (Fig. 1). The Indus Division includes largely hyperarid desert areas and the Peninsular Indian Division corresponds to the Indian dry zone. Similar to the pattern seen for mammals (Corbet & Hill 1992), the Palaearctic and Indus Divisions share gekkonid genera and species, with a sharper divide between the Indus and Peninsular Indian Division (Smith 1935; Minton 1966; Uetz 2013). We chose these broad areas to try and identify the direction and sequence of dispersal within the Palaearctic naked-toed geckos and Indian *Hemidactylus*. Taxa outside these regions or outside of Palaearctic naked-toed geckos and *Hemidactylus* were assigned out-group distributions and we coded *H. flaviviridis* as being distributed in the Peninsular Indian Division as this commensal is likely to have originated in peninsular India (Bansal & Karanth 2010).

Environmental and ecological data

Preliminary molecular data suggested numerous cryptic lineages within the *C. aravallense* complex and we used climatic data (Worldclim database; Hijmans *et al.* 2005) to establish whether genetically divergent lineages are also environmentally distinct. We included maximum temperature of warmest month (BIO5) and annual precipitation (BIO12), and also tested additional variables (BIO1, BIO3, BIO6, BIO15) in multivariate space using a PCA to reduce the number of variables (not shown). Hawth's Tools (Beyer 2004) in ArcGIS 9.3 (ESRI, Inc., Redland, CA, USA) was used to generate 1000 random points from within an arbitrary 50 km buffered MCP around all *C. aravallense* sampling localities and the corresponding environmental information was extracted in DIVA-GIS (version 7.5, http://www.diva-gis.org). This was carried out to visualize the environmental space that the geographic range of this complex represents. We plotted these background points and sampling localities of *C. aravallense* lineages to visualize environmental niches. *Cyrtodactylus*, *Hemidactylus* and the Palaearctic naked-toed geckos have largely complementary global distributions, overlapping only in the northern Indian subcontinent (Bauer *et al.* 2013; Uetz 2013). The role of competition in historical diversification of the Gekkonidae has been previously suggested (Heinicke *et al.* 2011), and we collected data on sympatric geckos to understand patterns of overlap with other Indian genera, mainly *Hemidactylus*, and potentially *Cyrtodactylus*.

Results

Phylogenetic relationships of Palaearctic naked-toed geckos

ML and Bayesian analyses of the combined, mtDNA-only and nuclear-only data sets had comparable topologies, with similar membership within well-sampled clades (Figs 2 and 3). Results of the combined analyses are presented below, along with additions/conflicts from the mitochondrial tree. We recovered the same overall relationships as Gamble *et al.* (2012) and Bauer *et al.* (2013), with a well-supported *Hemidactylus* + *Cyrtodactylus* + Palaearctic naked-toed gecko clade, with *Alsophylax pipiens* and *Microgecko persicus euphorbiacola* outside the main Palaearctic naked-toed radiation as poorly supported sisters in a basal polytomy within the Gekkonidae (Fig. 2). Both *Hemidactylus* and *Cyrtodactylus* are well-supported sister groups, together sister to the Palaearctic naked-toed geckos. The Peninsular Indian radiation of *Hemidactylus* is well supported, as are the *H. flaviviridis* and terrestrial *Hemidactylus* clades.

The Palaearctic naked-toed gecko clade receives high support, and though basal relationships are poorly supported a number of clades are resolved. Clades A (*Altiphylax*) and B (*Mediodactylus*, *Pseudoceramodactylus* + *Tropiocolotes* + *Stenodactylus*) are similar to those recovered by Bauer *et al.* (2013), except that *Altiphylax* is not monophyletic, with *A. levitoni* poorly supported as sister to *Mediodactylus* and *Pseudoceramodactylus* + *Tropiocolotes* + *Stenodactylus* in combined analyses (Fig. 2) and part of an unresolved basal polytomy in the mtDNA tree (Fig. S1). The remaining Palaearctic naked-toed geckos lie in a well-supported clade with the same recovered membership as Bauer *et al.* (2013), plus the additional Indian and Iranian species (Clades C–F, Fig. 2). Relationships within this group are poorly resolved, though five well-supported subclades were recovered in both analyses: C, 'Cyrtopodion'; D, *Agamura* + *Bunopus* + *Crossobamon*; E, *Tenuidactylus*; and F, *Cyrtopodion*.
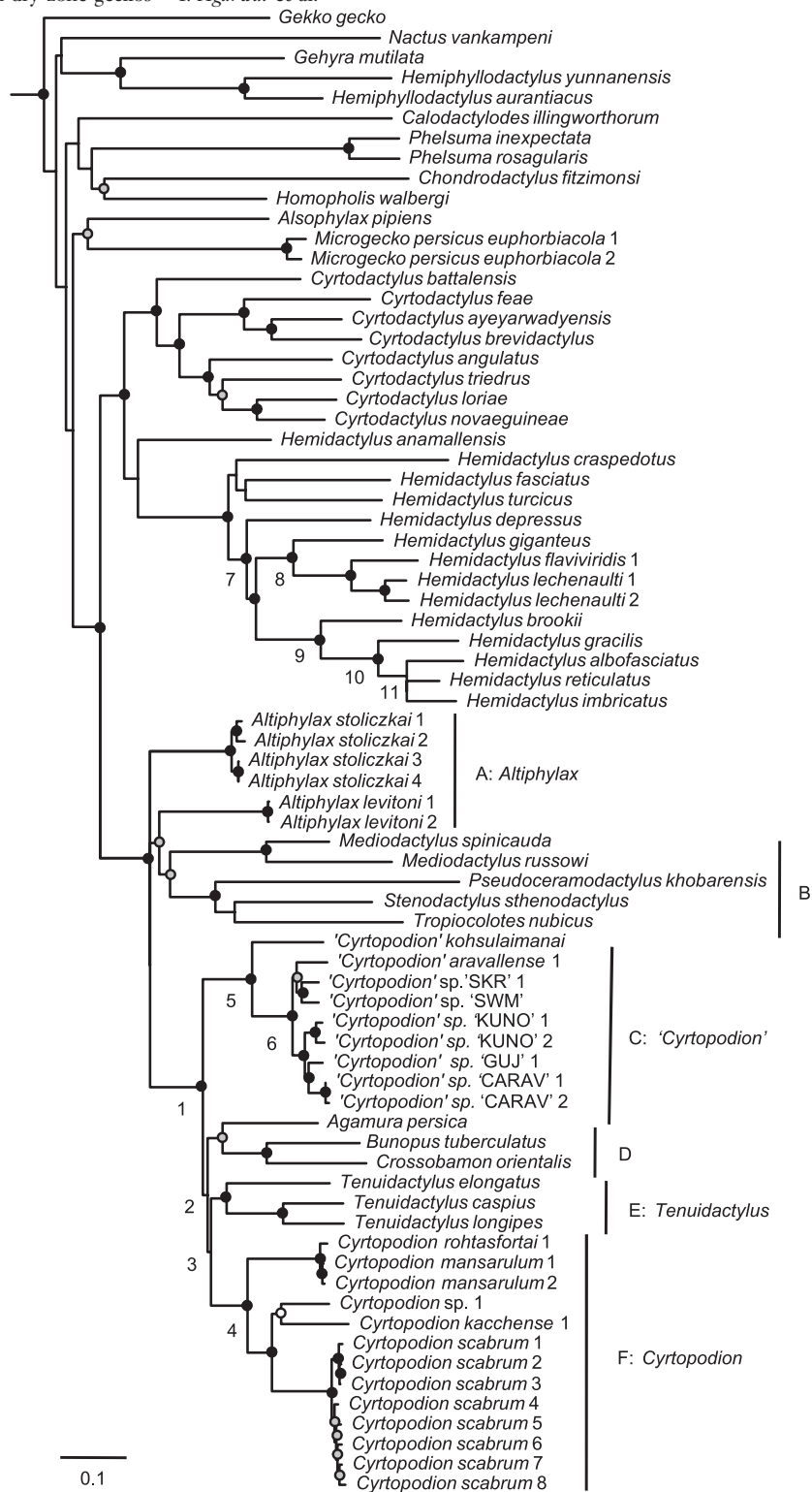
Fig. 2 Maximum-likelihood phylogeny of Palaearctic naked-toed geckos (combined data: ND2, RAG1, PDC). Non-gekkonid out-groups not shown. Nodes with high support are indicated by black-filled circles (ML bootstrap ≥ 75, Bayesian PP ≥ 0.95), nodes with support only from ML analyses by white-filled circles (ML bootstrap ≥ 75, Bayesian PP<0.95), and nodes with moderate support only from Bayesian analyses by grey-filled circles (Bayesian PP ≥ 0.90, ML bootstrap <75). Major clades are marked by a letter; nodes of interest in dating analyses are marked by a bold number (Fig. 3, Table 1).
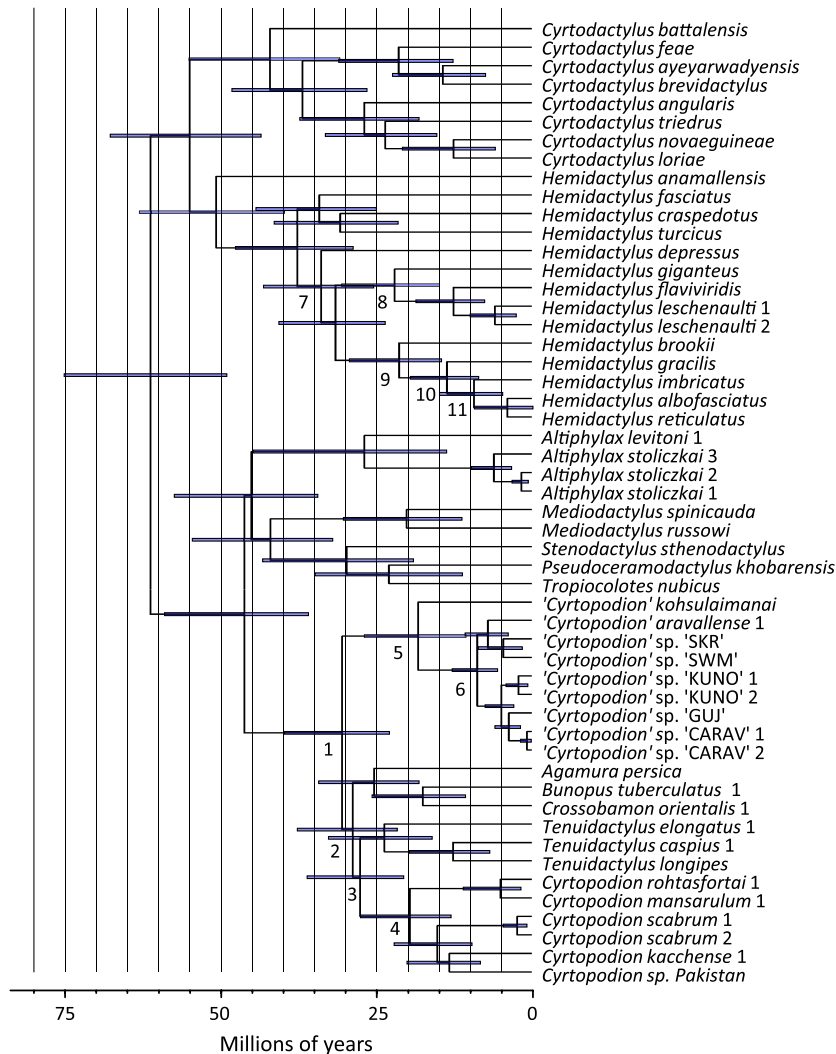
Fig. 3 Bayesian timetree of the Palaearctic naked-toed geckos, *Cyrtodactylus* and *Hemidactylus* (combined data: ND2, RAG1, PDC). Nodes of interest are marked by a bold number (referenced in Fig. 2, Table 1). Bars at nodes represent 95% HPD, out-group taxa not shown (see Fig. S2 for complete chronogram).

'*Cyrtopodion*' includes '*Cyrtopodion*' *kohsulaimana*i sister to the '*Cyrtopodion*' *aravallense* group. '*Cyrtopodion*' *aravallense* is revealed to be a species complex with deep divergences separating six lineages in the combined data set (Fig. 2) with an unsampled seventh lineage in the mtDNA analysis (Fig. S1). Within the '*Cyrtopodion*' *aravallense* complex are two broad groups, a poorly supported northern clade and a southern clade that receives high support. The northern clade includes '*Cyrtopodion*' *aravallense* from Delhi as the weakly supported sister to '*Cyrtopodion*' sp. 'SWM' and '*Cyrtopodion*' sp. 'SKR' with '*Cyrtopodion*' sp. 'MP' added in mtDNA analyses as the sister to '*Cyrtopodion*' sp. 'SKR' (Fig. S1). The southern clade has '*Cyrtopodion*' sp. 'KUNO' sister to *Cyrtopodion*' sp. 'GUJ' 1 and *Cyrtopodion*' sp. 'CARAV' 1. All

lineages with more than a single specimen within the '*Cyrto-podion*' *aravallense* complex are monophyletic, with uncorrected genetic distances between candidate lineages for the mitochondrial markers from 8% to 16% and within candidate lineages to 5% (Table S2). Only the southern clade receives high support in single gene and mtDNA analyses. Clades D and E are identical to the phylogeny of Bauer *et al.* (2013) in combined analyses, though in mtDNA analyses *Crossobamon* is nested within *Bunopus*, the entire complex forming two broad clades corresponding to NW + NE Iran, and Central Iran east to India. *Cyrtopodion sensu stricto* includes *Cyrtopodion scabrum* sister to *C. kachhense* and *Cyrtopodion* sp. Pakistan, in turn sister to *C. rohtasfortai* + *C. mansarulum* (Fig. 2). The mtDNA analysis has the additional

Iranian species *C. sistanensis* sister to *C. kachhense* and *Cyrtopodion* sp. Iran sister to *C. rohtasfortai* + *C. mansarulum* (Fig. S1), though in ML analyses *C. rohtasfortai* + *C. mansarulum* was sister to *C. scabrum*. Genetic distances suggest *C. mansarulum* may be conspecific with *C. rohtasfortai* (uncorrected ND2 divergence <3%). Two clades are retrieved within *C. scabrum* in combined analyses, the first including animals from Egypt and Sam, Rajasthan (Fig. 2; sequence from Iran added in mtDNA phylogeny, Fig. S1) with low mtDNA genetic distances within this group (0.2–0.9%, Table S3) and the second *C. scabrum* clade includes animals from western India and adjacent Pakistan that have genetic distances ranging from 1.7–4.9%, with the two clades 4.3–7.6% divergent (Table S3).

Divergence dating

BEAST analyses had converged after 100 000 000 generations with ESS values of more than 150 for all parameters. Tree topology was similar to ML and BI analyses, with slightly different positions for poorly supported inter-relationships (Fig. 3). Divergence dating estimates varied depending on the position of the *Cretaceogekko* prior and root prior, though median age estimates were similar across fossil calibrations (Table 1). The oldest divergences for the combined data set were obtained with the gekkonid/phyllodactylid + squamate root prior and the youngest with the gekkotan + squamate root prior, with estimates from the gekkotan + bird-lizard root prior lying in between, while estimates from nuclear data alone were the most recent (Table 1). Reported in the main text are estimates from gekkotan + bird-lizard analyses, what we consider the most appropriate option. Secondary calibrations resulted in younger divergence estimates than those obtained from the

original publication (Bauer *et al.* 2013), while the use of two different mitochondrial rates of evolution resulted in very different estimates (Table 1).

Divergence date estimates for most deeper nodes were similar to (Bauer *et al.* 2013), and we report only divergence estimates for nodes 1–11 (Table 1, Fig. 2). The most recent common ancestor (mrca) of clades C–F was dated to 32-20 (40–14) mya (Table 1). The split between '*Cyrtopodion*' *kohsulaimanai* and '*Cyrtopodion*' *aravallense* occurred at 18 (26–12) mya, between the north and south clades within '*Cyrtopodion*' *aravallense* at 9 (12–6) mya and subsequent splits between species as recent as 4 (6–2) mya. The mrca of the Peninsular Indian *Hemidactylus* is at 35 (43–26) mya and of the *H. flaviviridis* group at 23 (31–16) mya, while the terrestrial Indian *Hemidactylus* diverged from *H. brookii* about 22 (29–16) mya, began diversifying about 15 (20–10) mya and *H. imbricatus* diverged from Indian species 10 (15–6) mya. Additionally, *M. persicus euphorbiacola* from Sam, India, diverged from the sampled specimens from the pet trade 8 (10–5) mya (Fig. S2).

Ancestral area reconstructions

Palaearctic naked-toed geckos in the subcontinent are distributed across over 1100 km E–W and 1300 km N–S within India, and across the mountains and lowlands of Pakistan (Fig. 1). The ancestor of Palaearctic naked-toed geckos was unambiguously retrieved as being distributed in the Palaearctic, also the most likely distribution for the mrca of clades C–F that include all the species found in the Indus and Peninsular Indian Divisions (Fig. S3). Within this group, *Agamura*, *Bunopus*, *Tenuidactylus*, *Cyrtopodion* sp. Pakistan and '*Cyrtopodion*' *kohsulaimanai* are Palaearctic in distribution, the sampled *Crossobamon* and

Table 1 Node ages (and 95% HPD) in millions of years within select Palaearctic naked-toed geckos

| Node* | Fossil calibrations | | | | Mitochondrial rates secondary calibration | | |
	Squamate + Gekkonid prior	Bird + Gekkotan prior	Squamate + Gekkotan prior	Bird + Gekkotan prior (Nuclear)	0.57% prior	2.05% prior	mrca Palearctic naked-toed geckos [31]
1	38 (25–30)	32 (40–24)	29 (35–23)	23 (29–17)	59 (75–45)	16 (21–13)	33 (42–24)
2	36 (43–30)	30 (38–23)	28 (33–23)	–	57 (73–45)	16 (20–12)	32 (41–23)
3	34 (42–28)	29 (37–22)	27 (33–22)	–	54 (70–42)	15 (19–11)	30 (29–21)
4	24 (30–18)	20 (27–14)	19 (24–14)	16 (22–11)	38 (51–27)	11 (14–8)	22 (29–15)
5	21 (29–14)	18 (26–12)	16 (23–11)	–	33 (47–22)	9 (11–6)	18 (25–12)
6	10 (13–7)	9 (12–6)	8 (10–6)	7 (11–4)	15 (21–11)	4 (6–3)	8 (11–5)
7	42 (49–34)	35 (43–26)	32 (38–26)	27 (34–20)	65 (83–50)	18 (23–14)	–
8	28 (35–21)	23 (31–16)	21 (27–16)	17 (23–12)	45 (60–32)	12 (17–9)	–
9	27 (34–21)	22 (28–16)	20 (26–15)	15 (21–10)	43 (57–31)	12 (16–9)	–
10	18 (23–13)	15 (20–10)	13 (18–10)	10 (15–6)	27 (38–18)	8 (10–5)	–
11	12 (18–7)	10 (15–6)	9 (14–6)	7 (12–2)	17 (25–9)	5 (8–3)	–

*Node numbers reference Fig. 2 and Fig. 3. The different priors for dating analyses place *Cretaceogekko* as a gekkonid/gekkotan, with root height fixed as the divergence between gekkotans and squamates/divergence between lizards and birds. Refer to methods for details.

Microgecko are from the Indus Division as are some lineages of *C. scabrum* and *C. kacchensis*. Only two genera have moved into the Peninsular Indian Division – *Cyrtopodion*, with a few intraspecific lineages of *C. kacchensis* and *C. scabrum*; and '*Cyrtopodion*' with a single lineage that has colonized many parts of the Peninsular Indian Division from the Palaearctic, found across the Aravallis, Vindhyas, and Panchmahal Hill ranges and Malwa plateau, in Gujarat, Rajasthan, New Delhi and Madhya Pradesh (Fig. 1). The mrca of '*Cyrtopodion*' was in the Palaearctic (BBM) or Peninsular Indian Division + Palaearctic (S-DIVA) and the mrca of '*Cyrtopodion*' *aravallense* complex in the Peninsular Indian Division.

In contrast, the ancestor of Peninsular Indian *Hemidactylus* and its subclades was in the Peninsular Indian Division. The *H. flaviviridis* group has three sampled species, all in the Indian dry zone, and only *H. flaviviridis* is distributed outside the Peninsular Indian Division. The *H. brookii* group has five sampled species, the widespread *H. brookii* and the terrestrial clade, which includes *H. albofasciatus* from the wet zone, *H. reticulatus* and *H. gracilis* from the Peninsular Indian Dry Zone and *H. imbricatus* from the Indus Division. The mrca of terrestrial *Hemidactylus* was in the Peninsular Indian Division, with a subsequent dispersal into the Indus Division – mrca of *H. imbricatus/H. albofasciatus* distributed in the Peninsular Indian Division + Indus Divisions (SDIVA) or in the Peninsular Indian Division (BBM reconstruction, Fig. S3).

Environmental and ecological data

Members of the '*Cyrtopodion*' *aravallense* complex are small (SVL < 70 mm), nocturnal, scansorial rupicolous geckos found in areas with a mean annual temperature that ranges from 22.7–26.2°C and average annual rainfall from 358–1079 mm. Although sample sizes are low, each of the candidate species are separated in multivariate as well as two-dimensional environmental space, with sister lineages well separated (Fig. S4). This variation does not seem to be a consequence of geographic distance as a correlation of geographic and environmental distance between lineages was non-significant (Pearson's coefficient 0.3, $P > 0.1$). The candidate lineages are morphologically similar, sharing an indistinct speckled brownish dorsum, trihedral dorsal tubercles on the dorsum, limbs and tail, enlarged subcaudals, and both precloacal and femoral pores in males; characters used widely in gekkonid alpha taxonomy (Smith 1935; Szczerbak & Golubev 1996; Khan 2002; Krysko *et al.* 2007). These geckos are scansorial and strictly rupicolous, not observed by us away from rocky habitats, and are also similar in size and behaviour.

We did not observe any sympatric congenerics in our sampling within India, and Palaearctic naked-toed geckos were sympatric only at Sam, Nabh Dongar and Chohtan in the Thar (Fig. 1) where 2–3 unrelated species co-occurred – *Crossobamon orientalis* (terrestrial, psammophilous), *C. scabrum* (scansorial/terrestrial, rupicolous), and *M. persicus euphorbiacola* (terrestrial, rupicolous; not observed by us at Chohtan, recorded from Barmer District; Sachin Rai pers. comm.). We observed *Hemidactylus* spp. across some sampling sites and *Cyrtodactylus* (*Siwaligekko*) spp. in the lower and greater Himalayas, with the latter sympatric with one species of Palaearctic gecko, *Cyrtopodion mansarulum* at one locality. The rupicolous *Hemidactylus* we observed included two members of the arid-zone radiation (Carranza & Arnold 2006) with one species each in the south Aravallis (Balundara and Mt. Abu) and the Thar (Nabh Dongar), sympatric with *C. scabrum*. The '*Cyrtopodion*' *aravallense* complex is absent from those sites in the south Aravallis and overlapped only with one scansorial rupicolous gecko, the commensal *Hemidactylus flaviviridis*, at some sites. Terrestrial *Hemidactylus* we observed across the Aravallis are members of the *H. brookii* complex.

Discussion

A radiation of cryptic species in the Indian dry zone

This is the first dated phylogeny of multiple taxa from the Indian dry zone and our sampling effort encompasses the geographic range of Palaearctic naked-toed geckos within India. Nuclear and mitochondrial sequence data support the recognition of seven divergent lineages within '*Cyrtopodion*' *aravallense* that began diversifying in the late Miocene and have divergent climatic niches. The discovery of cryptic diversity from the dry zone of India, an area considered homogeneous and species-poor, highlights how poorly the regions' biodiversity is characterized. We were surveying what we thought to be a relatively uniform habitat and sampled broadly across the vast area that '*Cyrtopodion*' *aravallense* is found, and diversity within this group is almost certainly underestimated. Although their ranges are not well characterized, given that several divergent lineages occur allopatrically within 200 km of each other (Fig. 1), it seems likely that many of the candidate species will be found to be narrowly endemic to hill ranges or ridges. The importance of multiple lines of evidence for species delimitation is being increasingly recognized (Sites & Marshall 2004), particularly in the case of cryptic species – with high morphological conservatism (Joshi & Karanth 2012). Our results support the use of multiline evidence (Padial *et al.* 2010), and the integration of molecular data both for delimitation and divergence dating, which allows unprecedented insights into the evolutionary history of species (Oliver *et al.* 2010). A more detailed analysis of morphology is ongoing to identify diagnostic characters and formally describe the divergent lineages as new species.

These candidate species warrant specific conservation attention as the only terrestrial vertebrate radiation known from the Peninsular Foreland (Mani 1974a) of north-western central India. The areas the 'Cyrtopodion' aravallense complex are distributed in correspond to the semi-arid and central highlands provinces of India (4A, 4B, 6A; Rodgers & Panwar 1988); central India (Fig. 1 Smith 1931); or the north-western thorn scrub forests, Kathiarbar-Gir deciduous forests and a part of the Narmada Valley dry deciduous forests (IM1303, IM0206 and IM0207; Olson *et al.* 2001). Just two bird and two mammal (bat) species are endemic to the region (retrieved from http://worldwildlife.org/ecoregions), and these are the first endemic reptiles (Smith 1931, 1935, 1943).

Biogeography of the Indo-Pakistan Palaearctic naked-toed geckos

The role of the India–Asia collision and Miocene climate change. The common ancestor of the Palaearctic naked-toed gecko clade was probably in Central Asia, with the current centre of diversity in the region, and the collision of the Arabian and Indian Plates and resultant mountain orogeny and climate change are likely to have played an important role in diversification within the group (Bauer *et al.* 2013). Our results support this as there are a series of short branches with low support indicative of rapid diversification in the clade that has species distributed on the Indian Plate: Clades C-F (Fig. 2), with each of these lineages having diverged from its sister between 32–29 (40–22) mya, contemporaneous with the closure of the Tethys Sea and Himalayan uplift (Ali & Aitchison 2008).

Our results support the diffuse biogeographic boundary recognized between the Indus and Peninsular Indian Divisions based on mammalian distribution (Corbet & Hill 1992). However, there are no current or known past geological/physical barriers to gene flow, and a climatic barrier may have limited dispersal eastward for some arid-zone groups. The Indus Division is currently much drier than the Peninsular Indian Division and apart from the mountains in the north receives <400 mm of rainfall annually, with this difference surmised to go as far back as the Oligocene (~30 mya, Fig. 22A; Chatterjee *et al.* 2013). Palaearctic naked-toed geckos began diversifying in the Eocene of Central Asia, which was dry with limited monsoons (Zhang *et al.* 2012). This arid-zone group was present in the Indian Subregion by the Oligocene and has high diversity in Pakistan, across both the mountains and lowlands (Khan 2002), but since then only a single lineage has been able to extensively colonize the Peninsular Indian Division, in the late Miocene. If indeed high rainfall was limiting, our results imply that the Indus Division began drying much earlier than the rest of India or was historically more arid.

Divergence dating. The three different fossil-calibration approaches we used differed with respect to the *Cretaceogekko* and root calibration, and while deeper nodes varied in age, the 95% HPD of divergences within our group of interest was similar and we are confident that these are representative of the broad biogeographic history of this group. A range of different mitochondrial rates, often calibrated using geological events (Macey *et al.* 1999; Carranza *et al.* 2000, 2002, 2008) and secondary calibrations are now available in the literature and have been widely used for divergence dating, often without explicit justification, and a more prudent approach where a range of approaches are compared is only sometimes used (Oliver & Sanders 2009; Dubey & Shine 2010). Dates estimated from secondary calibrations were consistently younger (than Bauer *et al.* 2013) and dates from the two mitochondrial calibrations varied widely. The mtDNA substitution rate of 0.57% per million years (Macey *et al.* 1999) resulted in unrealistically high divergence estimates (Table 1; also noted by Siler *et al.* 2012 in their *Cyrtodactylus* phylogeny). Gómez-Díaz *et al.* (2012) used a range of mitochondrial rates for CYTB and 12S from many distantly related lizards derived from mostly geological calibrations, and their median estimates of the divergence between *H. flaviviridis* and *H. turcicus* do not overlap with the lower bound of our estimate (Table 2). Our divergence estimates are very similar, however, to the results from the analyses that have used similar or overlapping fossil calibrations (Gamble *et al.* 2011; Wood *et al.* 2012; Bauer *et al.* 2013) and also to some estimates using alternate fossil calibrations (Table 2, Fig. S2). Estimates of the median age of the mrca of Peninsular Indian *Hemidactylus* are similar to Bansal & Karanth (2013); though their median estimate for the divergence of *Hemidactylus* (*Dravidogecko*) *anamallensis* from *Hemidactylus* is above the higher bound of our estimate (Table 2). The 95% HPD from both studies overlap though this is not unexpected given how broad the estimates from the previous work are (SD 9, 12 vs. 5, 7 in this study); and while also used by Gamble *et al.* (2011), the use of the Helodermatidae/Anguidae divergence as a calibration for divergence dating in geckos is questionable, given that these groups have been separated from gekkotans for about 200 million years (Vidal & Hedges 2005). The availability of multiple gekkotan fossils (Daza *et al.* 2014) makes these the most appropriate calibration priors for divergence estimates within the Gekkota (e.g. Gamble *et al.* 2008; Oliver & Sanders 2009; Heinicke *et al.* 2011; Pepper *et al.* 2011). Oliver & Sanders (2009) compared the use of multiple fossil calibration priors, and our results are similar for the mrca of pygopodoids and the split between pygopodoids vs. other gekkotans (Table 2). Consideration of multiple calibration approaches and congruence with fossil-calibrated divergence

Table 2 Node ages (and 95% HPD) in millions of years comparing age estimates for gekkotan nodes from this study to published estimates using different calibrations

Description of node	This study	Published estimates	Source	Calibration
Stenodactylus vs. *Tropiocolotes*	26 (35–18)	88 (121–57)	Fujita & Papenfuss (2011)	mtDNA rate
Hemidactylus flaviviridis vs. *H. turcicus*	39 (49–31)	~23	Gómez-Díaz *et al.* (2012)	mtDNA rate
mrca Peninsular Indian *Hemidactylus*	35 (43–26)	36 (53–20)	Bansal & Karanth (2013)	Multiple fossil + geological
Hemidactylus anamallensis vs. *Hemidactylus*	53 (63–42)	69 (93–45)	Bansal & Karanth (2013)	Multiple fossil + geological
mrca pygopodoids	61 (78–45)	79 (102–58)	Oliver & Sanders (2009)	Multiple fossil + geological
Pygopodoids vs. other gekkotans	114 (133–97)	125 (156–97)	Oliver & Sanders (2009)	Multiple fossil + geological

estimates suggests that our estimates are a reasonable approximation of divergence dates within this group. Given the vital importance of dating estimates in biogeographic reconstructions, it seems pertinent that studies assess the use of different calibration priors even for preliminary estimates of species' histories, given inconsistencies in secondary calibrations and mitochondrial rates (Sauquet 2013).

The history of the Indian dry zone as told by geckos

Dry zone taxa have been considered relatively recent entrants into-India (Mani 1974b; Karanth 2003), though there is evidence of seasonality going as far back as the early Miocene, with increased aridity in the late Miocene (Clift *et al.* 2008). Our analyses included Palaearctic naked-toed geckos and *Hemidactylus*, two independently derived groups with endemics in the Indian dry zone and different histories in the Indian subcontinent. These groups were in the Indian Subregion by the Oligocene, but while Palaearctic naked-toed geckos have a hyperarid Palaearctic origin, Peninsular Indian *Hemidactylus* originated in peninsular India when wet forests covered much of the peninsula (Pound *et al.* 2012). The ancestor of '*Cyrtopodion*' *aravallense* moved into the Peninsular Indian Division in the middle Miocene with subsequent late Miocene diversification. Conversely, the *H. flaviviridis* group that includes only dry zone species and the terrestrial *Hemidactylus* clade that includes mainly dry zone species began diversifying in Peninsular India in the early-middle Miocene, with a late Miocene dispersal into the Indus Division and only a single known descendant species (Khan 2004). The divergence of western Indian *Microgecko* from specimens from Pakistan is also in the late Miocene (Fig. S2). These results provide a number of important insights into the formation of the Indian dry zone: (i) the middle Miocene of north-western central India was dry enough for arid-zone groups to move in from the Indus Division, (ii) the dry zone of peninsular India was dry enough by the early-middle Miocene for current-day dry zone groups to have evolved, (iii) Late Miocene intensification in aridity is congruent with diversification within the '*Cyrtopodion*' *aravallense* complex and with dispersal of the ancestor of *Hemidactylus imbricatus* into the most arid region

within which any Peninsular Indian *Hemidactylus* species is found.

Indian dry zone taxa and consequently the dry zone itself potentially date back to at least the Miocene, and increasing aridity from the middle Miocene onward may have been a driver of diversification besides allowing dispersal between the Peninsular Indian dry zone and Indus Division. A thorough geographic sampling of diverse taxa found across Peninsular India will help understand true patterns of diversity and thus the history of the Indian dry zone.

Evolutionary history of an endemic dry zone radiation

*Diversification of '*Cyrtopodion*' – a role for one of the most diverse gekkonid genera in India?.* Although the exact sequence of diversification within '*Cyrtopodion*' cannot be determined by our sampling, and '*Cyrtopodion*' *kohsulaimanai* may not be the closest relative of the *aravallense* group, some broad patterns are clear. The ancestor of '*Cyrtopodion*' *kohsulaimanai* and the '*Cyrtopodion*' *aravallense* group diverged from its sister group in the Oligocene-early Miocene. Subsequently, in the middle-late Miocene, a time of increasing aridity, the ancestor of '*Cyrtopodion*' *aravallense* crossed the Indus River and came into India. Basal divergences within the '*Cyrtopodion*' *aravallense* complex are between 9–4 mya, a time of severe aridification across the north-western Indian subcontinent (Ganjoo & Shaker 2007; Nelson 2007; Molnar & Rajagopalan 2012). The Aravallis and other ranges this complex has diversified across are weathered remnants of some of the oldest hill ranges in the world (Valdiya 2010), and the inherent isolation of rocky areas may have played a role in diversification in this group. The complex is distributed north of the Narmada River, and although suitable habitats in the form of dry, rocky areas exist south of the Narmada, niche models had low predictions indicating climatic conditions may not be suitable.

Hemidactylus is the dominant scansorial rupicolous gecko across most of India, with the Peninsular Indian radiation having diversified in the Indian Subregion over the last 35 million years (Fig. 3, Table 2) with over 25 species including many large (SVL > 90 mm) scansorial rupicolous forms

(Smith 1935; Giri & Bauer 2008). Apart from *H. flaviviridis*, a widespread commensal, *H. gujaratensis* in south-western Gujarat (Giri *et al.* 2009) and some species of the arid-zone clade (Carranza & Arnold 2006) to the extreme west, there are no large scansorial rupicolous geckos in India north of the Narmada and south of the Himalayas (Smith 1935). *Hemidactylus flaviviridis* is the common house gecko across north India and also distributed further west through the Middle East into the Arabian Peninsula and North Africa (Das *et al.* 2011; Uetz 2013). Genetic diversity within this species is low (Carranza & Arnold 2006; Bansal & Karanth 2010; Bauer *et al.* 2010a; Gómez-Díaz *et al.* 2012), and an analysis of combined CYTB data from these publications has one group with <1% divergence between samples from across India (Sam, Lucknow, Hospet), Yemen, Oman and the UAE (Table S4), consistent with human-mediated transport. This species was not formerly known from South and Northeast India (Smith 1935), but we have observed the species in urban Karnataka, and it has been recently introduced in Northeast India (Das *et al.* 2011), suggesting *H. flaviviridis* was formerly absent from parts of its current range.

Members of the *'Cyrtopodion'* aravallense are also rupicolous and scansorial and are smaller (SVL < 70 mm) than most non-terrestrial Peninsular Indian *Hemidactylus* spp. (Smith 1935). Apart from the commensal *H. flaviviridis*, members of the *'Cyrtopodion'* aravallense complex did not overlap with any other scansorial rupicolous geckos in our sampling and were absent from localities in the south Aravallis (Mt. Abu and Balundara) where a large scansorial rupicolous member of the arid-zone *Hemidactylus* is distributed. Niche models for the entire *'Cyrtopodion'* aravallense complex (not shown) had high predictions at these localities in the south Aravallis, indicating the absence of this group from those regions is not due to unsuitable conditions.

The right time and the right place?. The ancestor of the *'Cyrtopodion'* aravallense complex came into the nascent Indian dry zone and subsequently radiated across the Peninsular Foreland (Mani 1974a), and does not seem to have dispersed south of the Narmada, where the Peninsular Indian *Hemidactylus* are most diverse (Smith 1935; Bansal & Karanth 2010). The absence of other endemic scansorial rupicolous geckos in the Peninsular Foreland suggests the nocturnal, scansorial, rupicolous niche may have been historically unoccupied. This radiation across an area with no known vertebrate radiations may simply be an artefact of the first systematic sampling across this region; though allopatry, low levels of morphological divergence and the fact that sister clades are not geographically (Fig. 1, Fig. 2) or environmentally proximate (Fig. S4) are indicative of

dispersal to empty niches (Walker & Valentine 1984; Moore & Donoghue 2007; Yoder *et al.* 2010). Although teasing apart the relative roles of vicariance and dispersal are challenging (Kodandaramaiah 2009), our model of the ancestor of *'Cyrtopodion'* aravallense coming into-India in the absence of any competitors (sympatric scansorial rupicolous geckos) and then colonizing a number of vacant areas can serve as a potential null model against which the relative role of more neutral processes can be assessed. Such speculations are preliminary and a finer scale; more thorough sampling is needed across the geographic range of this complex to fully understand its evolutionary history.

A case of human-mediated dispersal

Cyrtopodion scabrum is widely distributed, recorded from North Africa through Egypt (type locality, Sinai), across the Arabian Peninsula, Turkey, Iraq, east through Iran, Afghanistan, Pakistan and western India (Uetz 2013). It is unclear which areas represent its native range, as *C. scabrum* has been introduced in at least Israel (Roll *et al.* 2008), Jordan (Khoury *et al.* 2012) and the USA (Witmer *et al.* 2007). We observed this species in and around human habitation only at Sam, on the historical border trade route to the Middle East. Our expanded mtDNA phylogeny of *C. scabrum* revealed two monophyletic groups, the first including two samples from around Sam, India, collected from human habitation, a specimen from SW Iran ~ 2000 km straight line distance from Sam, collected from sand (no other collection data, Jan Červenka pers. comm.) and a specimen from Egypt (>3500 km from Sam, animal from the pet trade with no specific collection data apart from the locality). The second *C. scabrum* group has higher genetic diversity and includes animals from relatively undisturbed rocky areas in western India and adjacent Pakistan, including Nabh Dongar just 20 km east of Sam (Fig. 1, Table S3).

Genetic distances of <1% across 2000–3500 km within one clade that at least in India are represented by collections from commensal habitats, and genetic distances five times higher within 200 km in the sister clade of the same species are indicative of the potential role of human-mediated dispersal in *C. scabrum*. It seems likely that geckos representing the sampled populations from Sam, Egypt and Iran have been moved around by people in the past whereas other Indian localities represent part of the native range of *C. scabrum*, but our conclusions are limited without better sampling from Pakistan and further west across the species' distribution. Our results confirm that even commensal species can show phylogeographic structure within their native range (Bauer *et al.* 2010b; Rato *et al.* 2011).

Taxonomic implications

This work fleshes out parts of the phylogeny presented by Bauer *et al.* (2013) and our sampling of genes allowed us to add species sampled by Červenka *et al.* (2008). We conservatively accept the more thorough recent taxonomic work of Bauer *et al.* (2013) and only indicate additions to or conflicts with their taxonomic decisions based on our phylogenetic results. Our analyses did not support the monophyly of *Altiphylax*. Published *Altiphylax stoliczkai* RAG1 sequences (Bauer *et al.* 2013) did not match our *A. stoliczkai* sequences (3.9–7.5% divergent) or each other (7.9% divergent) and analyses including these RAG1 sequences resulted in an altered position for and the non-monophyly of *A. stoliczkai*. A BLAST search (http://blast.ncbi.nlm.nih.gov/) revealed these are likely erroneous, one sequence similar *to A. levitoni* and the other to *Lygodactylus* spp. Our RAG1 sequences of *A. stoliczkai* were generated from tissue samples from two localities (Table S1) in independent batches of extraction and PCR amplification and are 0.6% divergent from each other, sharing a unique 3-bp deletion absent in the published *Altiphylax* sequences. While our results indicate the monophyly of *Altiphylax* may be an artefact of data quality and *Asiocolotes levitoni* is phylogenetically distinct from *Altiphylax stoliczkai*, a formal resurrection of *Asiocolotes* requires additional sampling, especially of the type species of both genera to resolve the taxonomy of this historically confounding group. Bauer *et al.* (2013) included *Indogekko* as a subgenus of *Cyrtopodion*. Our results indicate that *Indogekko* is monophyletic and additional sampling may reveal that the divergent sister lineage to *Cyrtopodion sensu stricto* 'Cyrtopodion' *kohsulaimanai* has been included in *Cyrtopodion sensu stricto* (Khan 2008a; Bauer *et al.* 2013), though Bauer *et al.* (2013) noted that additional sampling may change the position of 'Cyrtopodion' *kohsulaimanai*. This is confirmed by our analyses, 'Cyrtopodion' *kohsulaimanai* and the 'Cyrtopodion' *aravallense* complex forming a divergent lineage, for which no generic name seems available. Members of this group all have precloacal and femoral pores, a character shared with some species assigned to *Cyrtopodion* and *Tenuidactylus* (Khan 2008b) and a more complete sampling from Pakistan may reveal allied species for which an alternate generic name has been assigned, taking priority.

At the species level, we sampled the type localities of *Altiphylax yarkandensis*, 'Cyrtopodion' *aravallense*, *Cyrtopodion kachhense* and *C. mansarulum* (Fig. 1). *Altiphylax stoliczkai* from Ladakh, India, the type locality of *A. yarkandensis*, and from Pakistan have low mtDNA divergences, indicating *A. stoliczkai* may be a widely distributed species. Our samples of the relict *M. persicus euphorbiacola* from India are divergent from the captive samples used in Bauer *et al.* (2013) and suggest they have been separated for 9 million years (16–4, Fig. 3). While the provenance of the captive specimens is unknown, the type locality of *M. persicus euphorbiacola* is near Karachi (Minton *et al.* 1970), about 400 km south-west of the Indian locality in the Thar, and we suspect that this is closer to the source of the captive stock. These two areas are largely distinct in their saurofauna (Minton 1966), and the Indian specimens are likely to represent an undescribed cryptic *Microgecko*. The original description of *Cyrtopodion mansarulum* (Duda & Sahi 1978) consists of a single paragraph (the entire paper was never published, Sahi pers. comm.); however, the authors did formally diagnose the species and the nomen is thus valid. Molecular data suggest that *C. mansarulum* may be conspecific with *C. rohtasfortai*, called the commonest sandstone gecko in Pakistan (Khan 2008b), in which case the name *C. mansarulum* (Duda & Sahi 1978) has priority. However, morphological comparisons of material assigned to both species preclude any formal action. Sequences of *C. kachhense* from different localities were similar and suggest a single widely distributed species. As mentioned earlier, 'Cyrtopodion' *aravallense* is a species complex with seven genetically and environmentally divergent lineages, with ongoing taxonomic work to describe them as new species. Records of *Cyrtopodion/Tenuidactylus fedtschenkoi* from India (Sharma 2002) are likely to represent members of the 'Cyrtopodion' *aravallense* complex.

Conclusions

Our work has provided insights into the biogeographic history of the Indian dry zone from two independently derived dry zone gekkonid groups and revealed the first vertebrate radiation in north-west central India, from areas not known to be biodiverse. Taxa of the Indian dry zone may date back to at least the Miocene and a fine-scale sampling of diverse groups will allow us to understand generalities in the biogeographic history of the Indian dry zone. Mountain uplift and Miocene climate change postcollision of the Indian and Eurasian Plates are likely to have played a major role in the diversification of the Palaearctic geckos and indicate a potential historical climatic barrier between the peninsular Indian Division and Indus Division. Diversification of Peninsular Indian *Hemidactylus* was around the same time, indicating the dry zone of peninsular India may have formed by the middle Miocene. The discovery of cryptic diversity from the dry zone of India, with a radiation of at least seven lineages that are genetically and environmentally distinct, supports the use of multiline evidence for species delimitation and the integration of molecular data for divergence dating to gain insights into the evolutionary history of taxa. These candidate species warrant specific conservation attention as the only vertebrate radiation known from north-western central India and highlight how little is known of the biodiversity of the region. Divergence dating and data

on sympatric geckos allow us to speculate that the ancestor of '*Cyrtopodion*' *aravallense* came into India in the Middle Miocene into the nascent Indian dry zone and may have diversified in the absence of sympatric nocturnal scansorial rupicolous geckos.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Fig. S1. Bayesian phylogeny of Palaearctic naked-toed geckos (mtDNA, ND2 + CYTB). Nodes with high support are indicated by black circles (ML bootstrap ≥ 75, Bayesian PP ≥ 0.95), nodes with moderate support only from Bayesian analyses by grey circles (Bayesian PP ≥ 0.90, ML bootstrap < 75), and nodes with support only from ML analyses by white circles (ML bootstrap ≥ 75, Bayesian PP < 0.95). Major clades marked by a letter correspond to those from Fig. 2.

Fig. S2. Complete BEAST chronogram from divergence dating analyses. Bars above nodes indicate 95% HPD.

Fig. S3. Ancestral area reconstructions in RASP; BBM, SDIVA on the left and right respectively.

Fig. S4. Scatter plot of maximum temperature of warmest month (BIO5) vs. annual precipitation (BIO12) showing the seven candidate lineages and 1000 random points from within the geographic range of the 'Cyrtopodion' aravallensis complex.

Table S1. Samples used in this study giving voucher specimen/tissue sample number, locality and GenBank accession numbers.

Table S2. Genetic distances within the 'Cyrtopodion' aravallense complex.

Table S3. Genetic distances within *Cyrtopodion scabrum*.

Table S4. Genetic distances within *Hemidactylus flaviviridis*.