

## Investigations

# Phylogenetic Systematics of the Shieldtail Snake Genus *Teretrurus* Beddome, 1886 (Squamata, Uropeltidae) Reveals Extensive Cryptic Diversity and Novel Geographic Spread in the Western Ghats of India

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### Abstract

The genus *Teretrurus* is a small and poorly studied group of uropeltid snakes, known from only a few localities in the Western Ghats of southwest India. Recent taxonomic reviews as well as phylogenetic reconstructions have suggested the presence of cryptic diversity within *Teretrurus*. Here, based on additional collections from previously unsampled regions of the Western Ghats, we expand the geographic range of the genus significantly northwards by ca. 300 km and evaluate species limits between populations. While morphometric analyses indicate that the four currently known species occupy distinct morphospaces, there was no significant difference in the morphospace between the new populations sampled in this study and the four known species. However, phylogenetic species delimitation using multiple methods consistently indicated greater diversity within *Teretrurus* than currently known. Based on these results, we further describe four of these lineages as *Teretrurus albiventer* sp. nov. from Peppara Wildlife Sanctuary, *Teretrurus siruvaniensis* sp. nov. from Siruvani Hills, *Teretrurus periyarensis* sp. nov. from the Periyar plateau and *Teretrurus agumbensis* sp. nov. from Agumbe. The four new lineages can be distinguished by their phylogenetic position, geography and a combination of diagnostic characters. The discovery of these four species further highlights the extensive hidden diversity among fossorial taxa and the role of extensive sampling in uncovering the true diversity within uropeltid snakes.

## Introduction

A robust taxonomy is key to accurate estimation of species richness within groups, and to understand the mechanisms underlying diversity patterns (Bevilacqua et al., 2021; Godfray et al., 2004; Wilson, 2004). Such taxonomic clarity is also necessary for devising effective conservation strategies (Thomson et al., 2018). Delimiting species boundaries was traditionally done using visible morphological characters (DeSalle et al., 2005). However, many evolutionary lineages remain undetected due to morphological similarity, yet are genetically distinct (Bickford et al., 2007; Struck et al., 2018). With the recent and rapid advancement in DNA sequencing technology and phylogenetic species delimitation tools, identifying such cryptic diversity has become far easier and has revolutionized the field of systematics (Fišer et al., 2018). However, relying solely on genetic data can also lead to over-splitting populations into distinct species

(Coates et al., 2018; Sukumaran & Knowles, 2017), calling for multiple lines of evidence (Blair & Bryson Jr., 2017; Hofmann et al., 2019) explicitly including morphology, genetics and geography (Shanker et al., 2017).

India is exceptionally biodiverse, with a significant portion of its biodiversity concentrated in the Western Ghats escarpment, a global biodiversity hotspot along with the adjacent island of Sri Lanka (Gunawardene et al., 2007). The Western Ghats escarpment (8-21°N 73-77°E) is a 1600 km long linear series of hill ranges that extends parallelly along the western coast of the Indian Peninsula. The contemporary landscape of the Western Ghats consists of a series of massifs, chief among which are the following (from south to north): Agasthyamalai (ca. 1800 m asl), Devarmalai (ca. 1900 m asl), Meghamalai (ca. 1900 m asl), Anaimalai-Palni (ca. 2600 m asl), Nilgiris (ca. 2600 m asl), Wayanad (ca. 2500 m asl), Coorg (ca. 1800 m asl), Kudremukh-Mullayan-giri (ca. 1900 m asl), followed further north (>14°N) by



much lower (< 1300m asl) massifs that lack notable relief features. This series of hill ranges are not continuous but are interspersed briefly by three low-elevation (< 400 m asl), dry, “Gaps”, viz. the Sencottah Gap (8°N), the Palghat Gap (10–11°N) and the Goa Gap (15°N) (Biswas & Karanth, 2021). These massifs also experience different rainfall regimes that vary with respect to latitude (southern to northern), with southern ranges getting more rain (Pascal, 1988) and with respect to aspect (windward/western vs. leeward/eastern) with the western aspect getting more rain (Nagendra & Ghatge, 2003). This topographic complexity and environmental variability of the Western Ghats has influenced species diversification of many groups of plants and animals within the region (e.g., Cyriac et al., 2024; Gopal et al., 2023; Robin et al., 2010; Vijayakumar et al., 2016).

Recent phylogenetic analyses on various reptile groups have highlighted the presence of cryptic diversity within several wide-ranging terrestrial species and have led to the description of several new species (e.g., Karanth, 2017). However, establishing species boundaries in many strictly fossorial groups has been more challenging due to long-standing taxonomic instability in some groups and the difficulty in systematically sampling lineages (Sampaio et al., 2023). Shieldtail snakes of the family Uropeltidae are a diverse (65 spp.) assemblage of small-sized (< 800 mm), fossorial, mostly wet-adapted montane snakes endemic to the Indian Peninsula and the adjacent island of Sri Lanka (Cyriac & Kodandaramaiah, 2017; Pyron et al., 2016; Sampaio et al., 2023). As an ensemble of many range-restricted species distributed on individual massifs of the Western Ghats (WG), uropeltids mirror the distribution patterns of some predominantly endemic frog and reptile groups (Chaitanya et al., 2019; Narayanan et al., 2021; Vijayakumar et al., 2016). However, recent phylogenetic reconstructions and attempts at species delimitation in uropeltid snakes have revealed knowledge gaps about their diversity (Cyriac & Kodandaramaiah, 2017; Sampaio et al., 2023). Recent taxonomic efforts have resulted in numerous new species discoveries from the Indian Peninsula and Sri Lanka (e.g. Aengals & Ganesh, 2013; Cyriac et al., 2020; Ganesh et al., 2021; Ganesh & Achyuthan, 2020; Gower, 2020; Gower & Maduwage, 2011; Jins et al., 2018; Sampaio et al., 2020; Wickramasinghe et al., 2020).

The uropeltid genus *Teretrurus* is endemic to the Western Ghats of India (Pyron et al., 2016). It was erected by Beddome (1886) to place *Plectrurus sanguineus* Beddome, 1867 (type species) in a distinct genus based on characters that separated it from other members of *Plectrurus*. Until recently, the genus was considered monotypic, represented only by its apparently ‘widespread’ type species – *T. sanguineus* (see Pyron et al., 2016 and references therein). While phylogenetic reconstruction indicated that *T. sanguineus* included multiple deeply divergent lineages (Cyriac & Kodandaramaiah, 2017), only recently were the two nominal species that remained synonymized under *T. sanguineus* resurrected to the species level (Ganesh & Murthy, 2022). Thus, two more congeners *Teretrurus hewstoni* (Beddome, 1876) from Wayanad and *T. travancoricus* Beddome,

1886 from Agasthyamalai were recognized as valid, while restricting true *T. sanguineus* to the Anamalai Hills. In addition, the genus *Brachyophidium* and its only known species *B. rhodogaster* Wall, 1921, from the Palni Hills was found to be nested within *Teretrurus* (Cyriac & Kodandaramaiah, 2017), and was formally reinstated into *Teretrurus* based on Smith’s (1943) assessment (Ganesh & Murthy, 2022).

Despite recent studies on the *Teretrurus* taxonomy by Ganesh & Murthy (2022) the diversity and distribution of this genus remain only partially documented. Although phylogenetic species delimitation analyses on the group have suggested multiple cryptic lineages (Sampaio et al., 2023), the lack of extensive sampling from across the Western Ghats has restricted taxonomic inferences, and the genus currently contains four allopatric species: *T. hewstoni* from the Wayanad plateau, *T. sanguineus* from the Anaimalai Hills, *T. rhodogaster* from the Palni Hills and *T. travancoricus* from the Agasthyamalai Hills (Ganesh & Murthy, 2022) (Fig. 1). However, there are intervening massifs between the geographic ranges of these four *Teretrurus* species (Fig. 2), which have conducive habitats and could potentially harbour more hidden lineages within this genus. By sampling for *Teretrurus* in these intervening, under sampled massifs in the Western Ghats, we test whether current taxonomy reflects the true diversity within *Teretrurus*. Our work, combining morphological, genetic and geographic data, reveals the presence of extensive cryptic diversity and provides an integrated taxonomic assessment of the genus *Teretrurus*. Based on these results, we describe four additional new species of *Teretrurus*.

## Materials & Methods

We carried out multiple field surveys across different locations in the Western Ghats of Kerala and Karnataka states from 2013 to 2020. Specimens collected were photographed and euthanized. Liver tissue was collected from the specimens for DNA extractions, after which the specimens were fixed in 10% formalin solution and then transferred to 70% ethanol. The specimens were used to record scalation and morphometric data after which they were deposited either at the museum of the Bombay Natural History Society (BNHS), Mumbai, India or the Centre for Ecological Sciences (CES), Bangalore. We also examined other specimens deposited at CES (including vouchers labeled under the VP series maintained at CES), BNHS, and the Zoological Survey of India Western Ghats Regional Center (ZSI-WGRC), Kozhikode, Kerala, India. This also includes the known species of *Teretrurus*, i.e. *T. sanguineus* (n = 7), *T. rhodogaster* (n = 7), *T. hewstoni* (n = 6) and *T. travancoricus* (n = 5). In total, we examined 37 specimens. We followed Cyriac et al. (2020) for scoring morphometric and meristic characters. Ventral scales were counted following Gower & Ablett (2006). We did not determine the sex of the specimens as the only definitive method for uropeltid snakes when the hemipenes are not everted requires examining the urogenital tracts by dissecting specimens (Cyriac et al., 2020; Huntley et al., 2021). All measurements were made to the nearest 0.1 mm using a Yuri Silver digital vernier

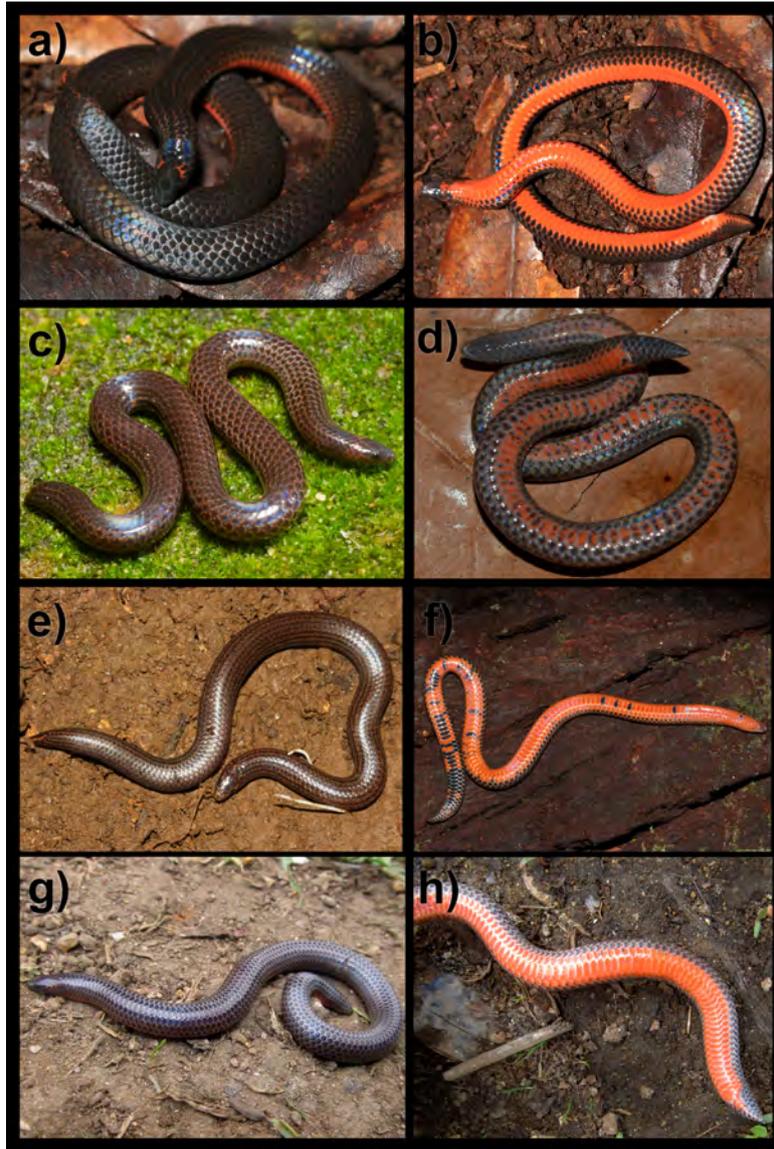


Figure 1. Colouration in life of *Teretrurus* species. A–B: dorsal and ventral view of *T. sanguineus* (Photographs: VPC); C–D: dorsal and ventral view of *T. hewstoni* (Photographs: C – AG; D – VPC); E–F: dorsal and ventral view of *T. travancoricus* (Photographs: David V. Raju); G–H: dorsal and ventral view of *T. rhodogaster* (Photographs: SRG).

caliper, except for snout-vent length, which was measured using a twine and a metal ruler or a measuring tape to the nearest 1 mm.

### Morphometric analyses

We carried out multivariate analyses on a set of 19 morphometric variables collected from 38 examined adult specimens (see supplementary Table S2–S4) in R v. 4.1.1 (R Core Team, 2020). We first performed a Principal Component Analysis (PCA) on 19 standardised (z-transformed) head variables to identify variables that contribute to the observed variation in the data. We then plotted the main PCs to visually examine the overlap in the morphospaces between species. Since allometry can affect inferences about morphological variation (Klingenberg, 2016), we performed additional PCAs on the standardised head variable after correcting for body size. We accounted for body size by 1)

using the residuals obtained from a least-square regression of each head variable with SVL and 2) by transforming each variable using Thrope's allometric formula (Thorpe, 1975) using the *GroupStruct* package (Chan & Grismer, 2022). We then performed a non-parametric multivariate analysis of variance using PERMANOVA to test for the similarities between the groups' centroid positions using the R package *RVAideMemoire* (Herve, 2023).

### DNA extraction and Phylogenetic reconstruction

Total genomic DNA was extracted from tissue samples of seven specimens of *Teretrurus* using the high salt extraction process following standard protocols (Miller et al., 1988). We then amplified three mitochondrial (16S rRNA, 12S rRNA and NADH dehydrogenase subunit 4: ND4) and one nuclear (oocyte maturation factor: c-mos) marker using

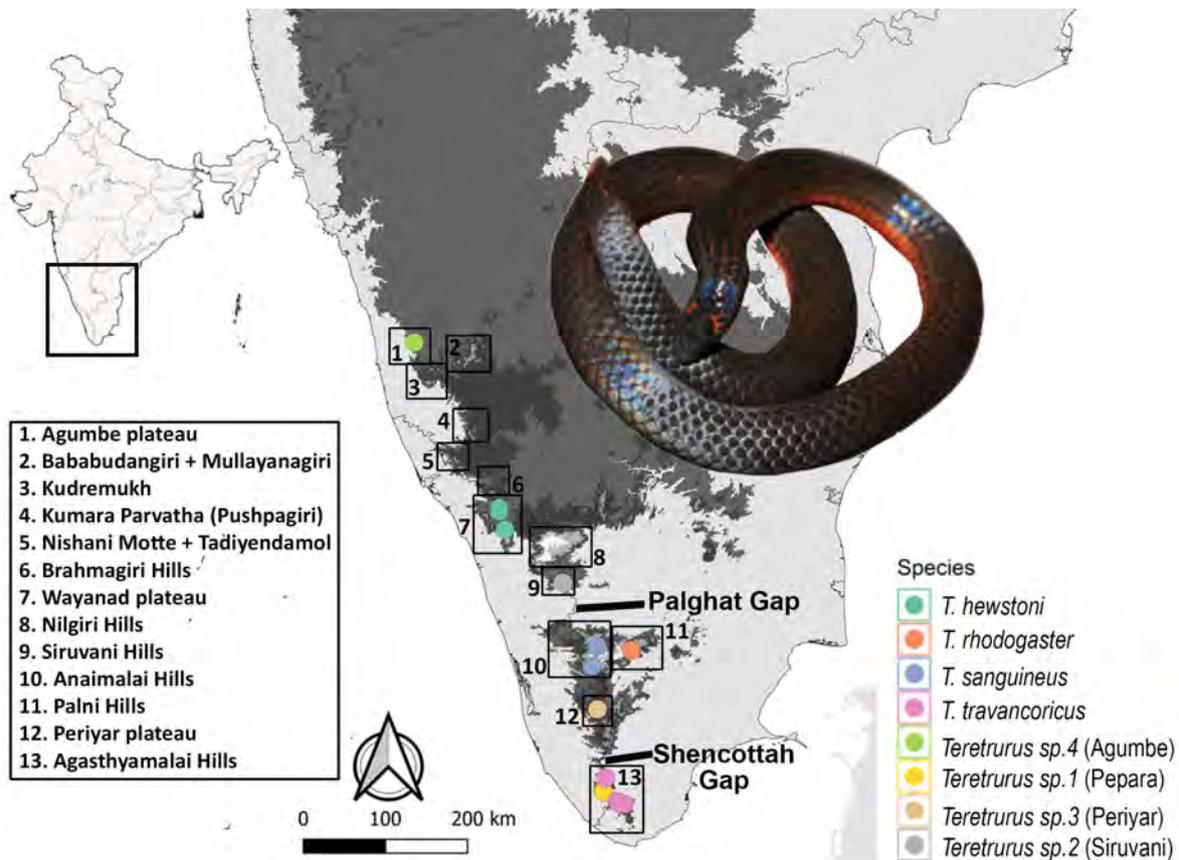


Figure 2. Map of peninsular India showing the distribution of different populations of *Teretrurus*. The black rectangles and the numbers indicate the position of prominent hill clusters and massifs in the Western Ghats. The colour of each species in the map is indicated in the legend.

standard 3-step PCR protocol (Palumbi, 1996) using the primers (supplementary Table S5) and the PCR protocols described in Cyriac & Kodandaramaiah (2017) and Sampaio et al. (2023). PCR products were checked on an agarose gel and Sanger sequenced using the forward and reverse primer tails by Barcode Bioscience, Bangalore.

Sequences of both forward and reverse strands were checked manually and consensus sequences were generated using BioEdit v.7.2.5 (Hall, 1999). We also compiled all available sequences of *Teretrurus* and four outgroups (two species each of *Platyplectrurus* and *Melanophidium*) from GenBank for the four markers mentioned above and for an additional nuclear marker (prolactin receptor: PRLR) (supplementary Table S6). We aligned all the sequences of each marker using the MUSCLE algorithm (Edgar, 2004) implemented in MEGA11 (Tamura et al., 2021). We removed ambiguously aligned positions in the two non-protein coding markers (16S rRNA and 12S rRNA) using Gblocks v.0.91b (Talavera & Castresana, 2007) implemented in Phylosuit v 1.2.2 (D. Zhang et al., 2020). We then concatenated the alignments to build two datasets: 1) a single-locus mitochondrial dataset (mt DNA), 2) a multilocus dataset (mt + nuDNA).

The datasets were partitioned by gene for the non-protein coding markers (12s rRNA and 16s rRNA) and by codon position for the protein-coding markers (ND4, c-mos and PRLR). We carried out phylogenetic inferences using both

Maximum Likelihood (ML) and Bayesian Inference (BI) for both the mitochondrial only dataset (mt DNA) and the multilocus dataset (mt + nuDNA). The ML analysis was performed in IQ-TREE v 2.0.6 (Minh et al., 2020) using the inbuilt ModelFinder to find the best-fit nucleotide substitution model and implementing 1000 ultrafast bootstrap (UFB) replicates to assess branch support. We considered UFB between 90 and 95 as moderate support and UFB > 95 as strong support. The BI was performed in MrBayes v.3.2.7 (Ronquist et al., 2012) using the best-fit partition scheme and nucleotide substitution model identified by Partition-Finder2 v.2.1.1 (Lanfear et al., 2017) (supplementary Table S7). We implemented two independent runs for five million generations sampling every 500 generations. The two runs were checked for convergence by examining the trace plots and ensuring the Effective Sample Size (ESS) values were greater than 200 in Tracer v.1.7.1 (Rambaut et al., 2018). We discarded the first 25% of the trees as burn-in and summarized the remaining trees as a maximum clade credibility (MCC) tree. We considered posterior probability values greater than 0.95 as strong support for branches. The ML and BI trees were used to identify operational taxonomic units and inform species hypotheses for the phylogenetic species delimitation analyses.

## Single-locus species delimitation

We first used the Assemble Species by Automatic Partitioning (ASAP) method (Puillandre et al., 2021) to identify species using the mtDNA dataset. ASAP is a distance-based hierarchical clustering method that successively merges sequences into groups or partitions until all sequences form a single partition. Partitions are evaluated by assessing the probability of a partition ( $n$ ) from its previous partition scheme ( $n-1$ ) and the slope of the ranked distance at a given genetic cut-off (Puillandre et al., 2021). We ran ASAP on the online platform (<https://bioinfo.mnhn.fr/abi/public/asap/>) using Kimura (K80) distance matrices and setting the probability at which a node is split at 0.01. We evaluated the 10 best partitions and selected the partition with the lowest ASAP score.

We then employed two single-locus tree-based methods to delimit species within *Teretrurus* using the mtDNA dataset. First, we used the General Mixed Yule Coalescent (GMYC) method that applies a time threshold to identify the point at which the branching process in an ultrametric tree changes from a Yule process to a coalescent process (Pons et al., 2006). We built an ultrametric tree for *Teretrurus* using \*BEAST in BEAST2 v.2.5. (Bouckaert et al., 2019) under a relaxed lognormal clock and a Yule model as the tree prior. We ran four independent analyses for 500 million generations sampling every 50,000 generations. We checked the runs for convergence by examining the trace plots and ensuring the ESS values were above 200, and then merged the runs using LogCombiner (Bouckaert et al., 2019). We summarized the trees as an MCC tree discarding the first 25% as burn-in using TreeAnnotator (Bouckaert et al., 2019). We used the resulting tree to run GMYC using the R package *splits* (Ezard et al., 2021).

Additionally, we also ran a Bayesian implementation of the Poisson Tree Process (bPTP), which uses the branch lengths from a gene tree as a proxy to identify speciation versus coalescent events (J. Zhang et al., 2013). We used the ML tree from the mtDNA dataset and ran bPTP using the exhaustive ML search option (-m H0) for 1000000 generations sampling every 1000 generations and discarded the first 25% as burn-in.

## Multi-locus species delimitation

We performed a multi-locus species delimitation analysis in Bayesian Phylogenetics & Phylogeography program (Yang & Rannala, 2010). We used the multi-locus dataset (mt + nu DNA) dataset to run the A10 analyses in BPP v.4.6.2 (Flouri et al., 2018) using the operational taxonomic units inferred from the IQ-TREE analysis as a guide tree. Since the selection of the guide tree can impact the results of the BPP analyses (Leaché & Fujita, 2010), we included all geographically separated populations in the guide tree. The posterior probabilities for the BPP models are also sensitive to the prior distribution of the population size ( $\theta$ ) and root age ( $\tau$ ) with large values of  $\theta$  and small values for  $\tau$  favouring more conservative species delimitation (Yang & Rannala, 2010). Thus, we ran four BPP analyses implementing different priors on population size ( $\theta$ ) and divergence time ( $\tau$ ). Prior

values were set as inverse Gamma (IG) distributions for the four BPP analyses assuming 1) large ancestral population sizes [ $\theta \sim \text{IG}(3, 0.2)$ ] and ancient divergences [ $\tau \sim \text{IG}(3, 0.2)$ ]; 2) large ancestral population sizes [ $\theta \sim \text{IG}(3, 0.2)$ ] and recent divergences [ $\tau \sim \text{IG}(4, 0.003)$ ]; 3) small ancestral population sizes [ $\theta \sim \text{IG}(4, 0.003)$ ] and ancient divergences [ $\tau \sim \text{IG}(3, 0.2)$ ]; 4) small ancestral population sizes [ $\theta \sim \text{IG}(4, 0.003)$ ] and recent divergences [ $\tau \sim \text{IG}(4, 0.003)$ ]. These values were set based on previous studies on amphibians and reptiles (Bellati et al., 2015; Gehara et al., 2017; Leaché & Fujita, 2010), including for uropeltid snakes (Sampaio et al., 2023). We ran each of the runs assuming independent rates among loci (symmetric Dirichlet prior:  $\alpha = 5$ ) with an initial 1000000 burn-in and then running 10000 generations sampling every 10 generations. We ran two independent analyses for each of the four prior settings to check for convergence between the runs.

Since the different species delimitation methods produced varying results, we used Bayes Factor Delimitation (BDF) to test alternative species tree hypotheses. We tested three alternate species models that included: 1) four species model (m1), representing the current taxonomy where we considered lineages north of the Palghat gap as *T. hewstoni*, lineages in the Anamalais and Periyar as *T. sanguineus*, lineages in the Palni Hills as *T. rhodogaster* and lineages south of the Shencottah gap as *T. travancoricus*; 2) six species model (m2) recovered by the bPTP-ML wherein the populations from Agumbe, Nilgiris and Siruvani were together a single distinct species and the population from Periyar as another distinct species in addition to the four currently known species; 3) a 10 species model (m3) from the ASAP and BPP analyses. We did not test the species models recovered by GMYC and bPTP-BI since these methods led to over-splitting species (see results). For each of the three species models, we reconstructed the species tree from the mt DNA and two nuclear loci in \*BEAST2 implemented in BEAST2 v.2.5. (Bouckaert et al., 2019) under a relaxed lognormal clock and a Yule tree prior. For all the \*BEAST2 analyses, the clock model and tree priors were unlinked for the mitochondrial loci and the two nuclear loci to account for their independent evolutionary histories. We ran two independent analyses for 500 million generations sampling every 50,000 generations for each species model. We checked the runs for convergence by examining the trace plots and the ESS values and merged the runs using LogCombiner. We then estimated the marginal likelihood using the stepping stone algorithm (Grummer et al., 2014) using the Path Sampler add-on package in BEAST. We ran the Path sampling analyses for 10 million generation for 25 steps and a 10% burn-in. We determined the number of steps in the path sampling analyses by increasing the number of steps by five in subsequent analyses until there was no much difference in the estimated marginal likelihood values. We estimated the Bayes Factor (BF) for species model pairs from the marginal likelihoods and selected the best-fit model following Kass & Raftery (1995), where  $\ln\text{BF} < 3.2$  indicates no support,  $\ln\text{BF} = 3.3\text{--}10$  indicates moderate support and  $\ln\text{BF} > 10$  indicates strong support for a model. We used geographic information from our sampling

to infer possible allopatric separation scenarios, which provides additional support for our species hypotheses.

## Results

### Morphometric analyses

Principal Component Analysis indicated that most of the variability in morphology was explained by the first three principal components (PCs) in the raw and size-corrected morphometric datasets (70–85 % of the variation) (supplementary Table S2–S4). PC1 explained ca. 66.3 %, 47.2 % and 65.3 % of the variance in the raw, residual and allometry-corrected datasets respectively. PC2 explained ca. 13.5 %, 16.2 % and 14.1 % of the variance, while PC3 explained only 5.1%, 6.7 % and 5.6 % in the raw, residual and allometry-corrected datasets respectively. Plotting the first two PCs indicated differences in the morphospace between the four currently known species. However, there was considerable overlap in the morphospace of the newly sampled populations with the four known species (Fig 3a–c; supplementary Fig S1). The PERMANOVA on the PCs obtained from the three datasets (raw, residual and allometry-corrected) indicated significant differences in the centroids of different species for PC1 (raw:  $F = 8.66$ ,  $df = 7$ ,  $P < 0.001$ ; residuals:  $F = 7.216$ ,  $df = 7$ ,  $P < 0.001$ ; allometry-corrected:  $F = 34.19$ ,  $df = 6$ ,  $P < 0.001$ ) and PC2 (raw:  $F = 68.542$ ,  $df = 7$ ,  $P < 0.001$ ; residuals:  $F = 12.319$ ,  $df = 7$ ,  $P < 0.001$ ; allometry-corrected:  $F = 126.56$ ,  $df = 6$ ,  $P < 0.001$ ). Pairwise comparisons between species indicated that the four currently known *Teretrurus* species occupy significantly distinct morphospaces (Fig 3a–c; Table 1). However, there were no significant differences between *Teretrurus* sp.2 (Siruvani), *Teretrurus* sp.3 (Periyar), *Teretrurus* sp.4 (Agumbe) and *T. hewstoni*, and between *Teretrurus* sp.3 (Periyar) and *Teretrurus* sp.4 (Agumbe) when compared to *T. sanguineus* and *T. rhodogaster* and between *Teretrurus* sp.1 (Peppara) and *T. travancoricus* (Table 1).

### Phylogenetic relationship

The ML and BI analyses recovered similar topologies with most branches being well supported, with both the mtDNA and concatenated dataset (Fig 4; supplementary Fig S2). The topologies indicated three strongly supported clades corresponding to lineages north of the Palghat gap (clade A: *T. hewstoni*, *Teretrurus* sp.2, *Teretrurus* sp.4 & *Teretrurus* sp. MW3447), between Palghat and Shencottah gap (clade B: *T. sanguineus*, *Teretrurus* sp.3 and *T. rhodogaster*) and below Shencottah gap (clade C: *T. travancoricus*, *T. cf. travancoricus*, *Teretrurus* sp.1) (Fig 4). However, there were minor differences in the placement of lineages within clade C between the mtDNA and concatenated dataset, wherein *T. cf. travancoricus* from Shendhurney WLS was sister to *T. travancoricus* with strong support in the concatenated dataset while *Teretrurus* sp.1 from Peppara WLS was sister to *T. travancoricus* with strong support in the mtDNA dataset.

## Species delimitation

All the different species delimitation methods indicated that species richness within *Teretrurus* is underestimated. However, different methods recovered different species models. The distance-based ASAP recovered a 10 species scenario as the best model with the lowest ASAP score (supplementary material Fig S3). The GMYC recovered 14 species, while the bPTP-ML and bPTP-BI recovered six and 13 species respectively (supplementary Fig S4–5). The GMYC and bPTP-BI clearly led to instances of over-splitting wherein samples collected from the same locality were split (e.g. *T. hewstoni*\_VPTS0918094 & 95, *Teretrurus* sp.1 and *T. rhodogaster*). The BPP analyses assuming different population sizes and divergence times also indicated a 10 species model as the best supported with the analyses assuming large population sizes having good support (Posterior probability = 0.84) while the analyses assuming small population sizes had lower support (Posterior probability = 0.63–0.64) (supplementary Table S8).

The multi-locus species validation approach using BFD indicated that the species model m3 with 10 species was the best-fit model (MLE = -6506.96) and was strongly supported against the two other models with less species diversity (lnBF = ca. 24–65) (Table 2).

## Taxonomic accounts

The species delimitation methods used to discover potential species (ASAP, GMYC, bPTP & BPP) consistently indicated that the species diversity within *Teretrurus* was underestimated (Fig. 5). The species validation approach using BFD identified six potentially novel taxa. However, the lack of access to specimens for morphological examination precludes us from describing all six of these potentially new lineages. Based on examining available specimens, we here describe four of these new lineages: *Teretrurus* sp.1 as *T. albiventer* sp. nov., *Teretrurus* sp.2 as *T. siruvaniensis* sp. nov., *Teretrurus* sp.3 as *T. periyarensis* sp. nov. and *Teretrurus* sp.4 as *T. agumbensis* sp. nov.

### *Teretrurus albiventer* sp. nov.

urn:lsid:zoobank.org:act:62D2F11B-9081-4E80-B19E-2476CD3759C4

*Holotype*. BNHS 3756, adult male, Chemungimotta, near Pandipath, Peppara Wildlife Sanctuary, Thiruvananthapuram district, Kerala state, India (8.683614° N, 77.190978° E; 1250 m elevation). Collected by Vivek Cyriac, 27 August 2013.

*Paratypes* ( $n=7$ ). BNHS 3757 (male), same locality as holotype (8.675515° N, 77.195497° E; 1340 m elevation), collected by Vivek Cyriac on the same date as holotype; VPTS0522152 & VPTS0522153, from Chemungimotta, Peppara WLS, collected by Avrajjal Ghosh, Umesh Pavukandy and Vivek Cyriac on 08 May 2015 (8.672438° N, 77.200574° E, 1386 m elevation and 8.673744° N, 77.198339° E, 1370 m elevation respectively). ZSI-WGRC coll no: 19407 (sex unknown), Pandipath, Peppara Wildlife Sanctuary, Thiruvananthapuram district, Kerala state, India, collected by

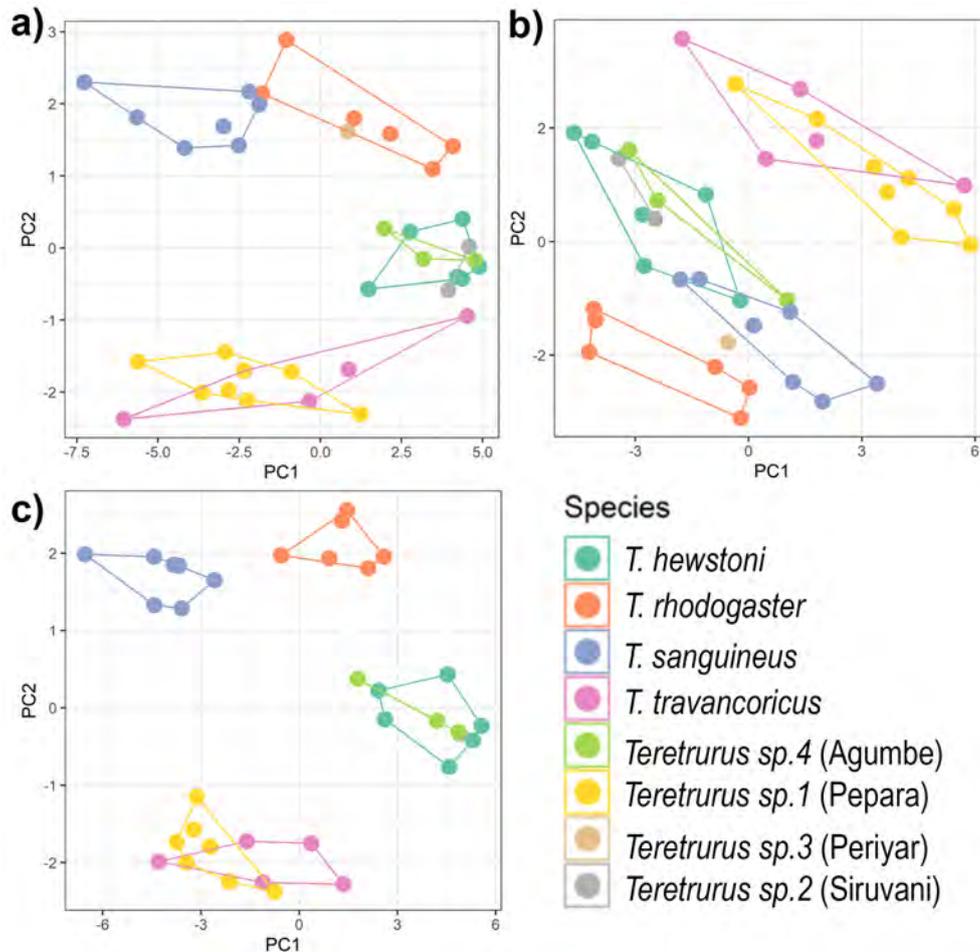


Figure 3. Morphospace occupied by different *Teretrurus* species: a) PCA plot of first two Principal Components (PC1 and PC2) for the raw head measurements, b) PCA plot after size correction using the residuals from a least-square regression with SVL, c) PCA plot after size correction using Thorpe's allometric equation. The colours of each species in all the plots are indicated in the legend.

K.G. Emiliyamma on 14 October 2012. CESS077, CESS118 & CESS120 from Chemungimotta, Peppara WLS, collected by Saunak Pal on 18 April 2010.

**Etymology.** Latin, albus = white, venter = underside, an adjective alluding to the white ventral colouration that is diagnostic of this new species.

**Lineage Diagnosis.** *Teretrurus albiventer* sp. nov. is nested within Clade C and is sister to a clade comprising *T. travancoricus* and *T. cf. travancoricus* in the concatenated multi-locus tree (Fig. 4). It can be diagnosed as a shallow divergent lineage from *T. travancoricus* (16S: 1.1%; 12S: 1.1%; ND4: 3.8–4.0%). Geographically, it is restricted to the Chemunjimotta (and possibly Agasthyakoodam) massif in the western slopes of the Agasthyamalai Hills, while *T. travancoricus* is found on the eastern slopes of Agasthyamalai Hills.

**Diagnosis.** A species of *Teretrurus* inhabiting Agasthyamalai, characterized by: a maximum SVL of 187.4 mm; presence of a supraocular scale; 13–15 dorsal scales rows in the anterior region of the body and 15 dorsal scales rows at mid-body; 130–139 ventral scales, 6–10 paired subcaudal scales; 5–18 posterior most ventrals having 4–7 keels in males; 2–3 rows of the posterior most dorsal scales rows

feebly keeled; anterior subcaudals and lateral scales of tail keeled; and having a uniform greyish brown dorsum and a pale white ventrum with heavy dark black mottling.

*Teretrurus albiventer* sp. nov. differs from *T. rhodogaster* by the presence of a supraocular scale (supraocular fused with ocular scale in *T. rhodogaster*). The new species can be differentiated by the number of ventral scales ranging from 130–139 as opposed to being higher in *T. sanguineus* (143–150), *T. rhodogaster* (138–149) and *T. periyarensis* sp. nov. (152) and being lower in *T. hewstoni* (118–127), *T. siruvaniensis* sp. nov. (127–129) and *T. agumbensis* (116–127). *Teretrurus albiventer* sp. nov. most closely resembles *T. travancoricus* (including *T. cf. travancoricus*) and *T. periyarensis* sp. nov. in having keeled ventral and subcaudal scales. However, the new species can be differentiated from the latter two species by the lack of bright red ventral colouration and the extensive dark black mottling on the belly (vs. belly bright red with or without dark black marking in *T. travancoricus* and *T. periyarensis* sp. nov.).

**Description of holotype** (Figs. 6a–f). See supplementary Table S1 for morphometric and meristic data. Head small (HL 3.9 % of SVL), snout acuminate. Rostral small (RL 8.1% of HL), visible from above, rounded, wider than long, not

Table 1. Results of the non-parametric pairwise PERMONOVA tests used to assess the level of overlap in the morphospaces between *Teretrurus* species. Values in bold indicate P value < 0.05.

Species Pairs		P-value		
Species 1	Species 2	Raw	Residuals	Allometry
<i>T. rhodogaster</i>	<i>T. hewstoni</i>	<b>0.021</b>	<b>0.039</b>	<b>0.002</b>
<i>T. sanguineus</i>	<i>T. hewstoni</i>	<b>0.001</b>	<b>0.006</b>	<b>0.001</b>
<i>T. travancoricus</i>	<i>T. hewstoni</i>	<b>0.021</b>	<b>0.006</b>	<b>0.002</b>
<i>Teretrurus</i> sp.4 (Agumbe)	<i>T. hewstoni</i>	0.769	0.534	0.574
<i>Teretrurus</i> sp.1 (Pepara)	<i>T. hewstoni</i>	<b>0.000</b>	<b>0.001</b>	<b>0.001</b>
<i>Teretrurus</i> sp.3 (Periyar)	<i>T. hewstoni</i>	0.143	0.286	NA
<i>Teretrurus</i> sp.2 (Siruvani)	<i>T. hewstoni</i>	0.780	0.967	0.682
<i>T. sanguineus</i>	<i>T. rhodogaster</i>	<b>0.000</b>	<b>0.028</b>	<b>0.000</b>
<i>T. travancoricus</i>	<i>T. rhodogaster</i>	<b>0.033</b>	<b>0.003</b>	<b>0.002</b>
<i>Teretrurus</i> sp.4 (Agumbe)	<i>T. rhodogaster</i>	0.113	0.141	0.014
<i>Teretrurus</i> sp.1 (Pepara)	<i>T. rhodogaster</i>	<b>0.000</b>	<b>0.000</b>	<b>0.001</b>
<i>Teretrurus</i> sp.3 (Periyar)	<i>T. rhodogaster</i>	0.857	0.857	NA
<i>Teretrurus</i> sp.2 (Siruvani)	<i>T. rhodogaster</i>	0.075	0.075	<b>0.039</b>
<i>T. travancoricus</i>	<i>T. sanguineus</i>	<b>0.008</b>	<b>0.002</b>	<b>0.001</b>
<i>Teretrurus</i> sp.4 (Agumbe)	<i>T. sanguineus</i>	<b>0.008</b>	0.080	<b>0.008</b>
<i>Teretrurus</i> sp.1 (Pepara)	<i>T. sanguineus</i>	<b>0.000</b>	<b>0.001</b>	<b>0.001</b>
<i>Teretrurus</i> sp.3 (Periyar)	<i>T. sanguineus</i>	0.125	0.619	NA
<i>Teretrurus</i> sp.2 (Siruvani)	<i>T. sanguineus</i>	<b>0.025</b>	<b>0.025</b>	<b>0.029</b>
<i>Teretrurus</i> sp.4 (Agumbe)	<i>T. travancoricus</i>	0.126	0.126	<b>0.018</b>
<i>Teretrurus</i> sp.1 (Pepara)	<i>T. travancoricus</i>	0.320	0.137	0.103
<i>Teretrurus</i> sp.3 (Periyar)	<i>T. travancoricus</i>	0.500	0.333	NA
<i>Teretrurus</i> sp.2 (Siruvani)	<i>T. travancoricus</i>	0.190	0.143	<b>0.048</b>
<i>Teretrurus</i> sp.1 (Pepara)	<i>Teretrurus</i> sp.4 (Agumbe)	<b>0.006</b>	<b>0.012</b>	<b>0.011</b>
<i>Teretrurus</i> sp.3 (Periyar)	<i>Teretrurus</i> sp.4 (Agumbe)	0.250	0.750	NA
<i>Teretrurus</i> sp.2 (Siruvani)	<i>Teretrurus</i> sp.4 (Agumbe)	0.500	0.700	0.500
<i>Teretrurus</i> sp.3 (Periyar)	<i>Teretrurus</i> sp.1 (Pepara)	0.114	0.114	NA
<i>Teretrurus</i> sp.2 (Siruvani)	<i>Teretrurus</i> sp.1 (Pepara)	<b>0.022</b>	<b>0.022</b>	<b>0.026</b>
<i>Teretrurus</i> sp.2 (Siruvani)	<i>Teretrurus</i> sp.3 (Periyar)	0.333	0.333	NA

strongly projecting rearwards and without a dorsal ridge. Nasals in broad contact with each other (INS 8.1% of HL) and is as long as the rostral when viewed from above. External naris small, subcircular, located slightly above the anteroventral corner of nasal. Nasal contacts supralabials 1 and 2. Frontal irregularly hexagonal, longer than wide (FL 43.5% of HL; FW 25.8% of HL), lateral (ocular) margins slightly converging posteriorly; lateral (ocular) margin shortest, posterolateral edges longest. Prefrontals wider than long (PFL 21% of HL; PFW 27.4% of HL), shorter than frontal and in broad contact with each other along midline (IPFS 14.5% of HL). Supralabials four, first smallest, making the least contribution to margin of mouth; fourth largest. Ocular contacts supralabials 3 and 4. Eye distinct, large (EL 17.8% of HL) taking up more than half the entire anterior region of the ocular (EL 64.7% of OL); pupil subcircular. Paired parietals much longer than wide (PL 41.9% of HL; PW 25.8% of HL), longer and narrower than the frontal, pos-

teriorly slightly rounded, angle between posteromedial and posterolateral edges approximately 90°. Parietals in broad midline contact (IPS 17.7% of HL), much longer than midline contact between prefrontals. Parietals in contact with four scales posteriorly. Mental sub-triangular, smaller than infralabials, contacting only the first infralabials; mental groove absent. Three infralabials on each side; first smallest, second largest.

Body cylindrical having generally evenly sized scales on the body. Dorsal scale rows 12 anteriorly, 15 at mid-body and posteriorly. Ventral scales evenly sized except for the six anteriormost ones, which are narrower; ventrals 139; 10 posteriormost ventrals keeled, the posterior most scales with five keels gradually reducing to three keels. Anal scales paired (right overlying left). Anal scale with five keels and overlaps four (left) and three (right) small scales posteriorly in addition to first subcaudals. Posterior most 1–3 dorsal scale rows adjoining the ventral with three keels. Tail small

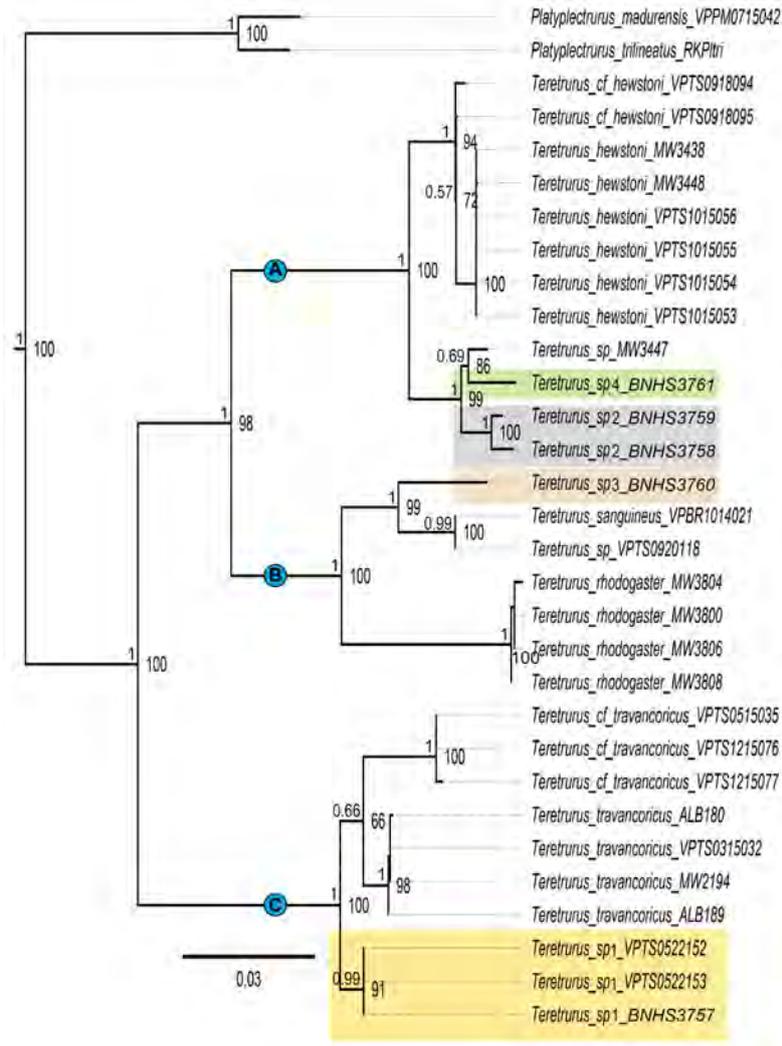


Figure 4. Phylogenetic relationships among *Teretrurus* spp. based on the concatenated mt + nu dataset. Values at the nodes indicate branch support values; posterior probabilities from the Bayesian Inference on the left and Ultrafast bootstrap support values from the Maximum Likelihood analysis on the right. The three main clades (A, B & C) are indicated by the blue circle. Lineages highlighted in colour indicate the newly sampled populations.

Table 2. Marginal-likelihood estimation (MLE) for each species models (M1, M2 and M3) from the Path Sampling analyses and pairwise Bayes factor delimitation (BFD) between tested models. BFD interpretation is as follows:  $\ln(\text{BF}) < 3.2$  is no support,  $\ln(\text{BF}) 3.2-10$  is substantial support and  $\ln(\text{BF}) > 10$  is strong support.

Species models	M1	M2	M3
Species No.	4	6	10
MLE	-6539.26	-6527.04	-6506.96
Model pairs		Supported model	$\ln(\text{BF})$
M1	M2	M2	-24.44
M1	M3	M3	-64.6
M2	M3	M3	-64.6

(TL 5% of SVL), slightly laterally compressed and tapering; terminal scale enlarged and ending in a single point. Ten paired subcaudals, anterior few subcaudals with three keels. A few dorsal and lateral scales on the tail having 2–3 faint keels.

*Colour in alcohol.* Rostrum greyish black. Head shields greyish black with a thin, disrupted, pale brownish-white stripes extending from the nostril to the eye and few pale brownish-white patches on the posterior region of the head. First supralabial scale greyish black, the remaining supralabials greyish black with the basal half of each scale

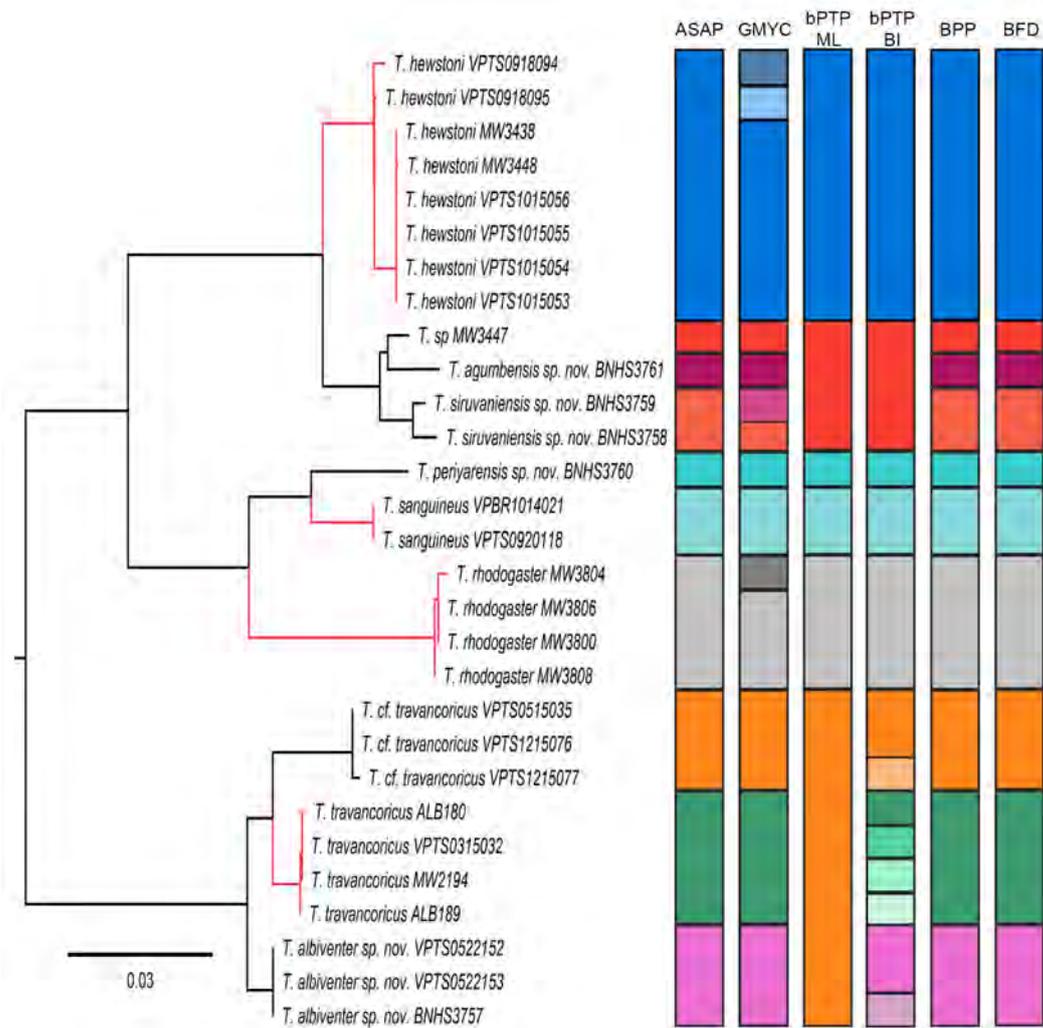


Figure 5. Summary of the results of different species delimitation methods. Clades highlighted in red in the tree indicate the position of the four currently recognized *Teretrurus* species. Each coloured block (left to right) indicates species clusters identified by the species delimitation methods. The first five blocks (ASAP, GMYC, bPTP-ML, bPTP-BI, BPP) implement species discovery approaches and the final block (BFD) implements the species validation approach.

being pale white. Dorsal body colour greyish brown with the anterior and lateral margins of each scale having pale whitish patches. Ventral scales pale whitish overall with several black patches, which are more pronounced on the anterior and posterior regions of the body. Subcaudal scales greyish black with the posterior margins of each scale having pale whitish colourations.

**Colour in life (Figs. 7a–b).** Dorsum overall greyish brown, with the anterior and lateral margins of each scale having pale orangish patches. Head shields greyish brown with a thin, disrupted, orangish stripes extending from the nostril to the eye. Temporal, supralabial and infralabial regions with light orange markings. Ventral scales mostly white with most scales having some amount of black mottling or patches, the black patches being more pronounced in the anterior-most and posterior most ventral scales. Dorsal scales of tail greyish brown with an interrupted orangish mid-dorsal strip extending to the tip of the tail. Ventral scales of the tail black with each scales having a white posterior margin.

**Variation.** All paratypes are in good condition. Meristic and morphometric data are provided in [Table 1](#). The number, arrangement and overlapping of head shields are similar to the holotype except for the prefrontals being wider than long in all other paratypes and the frontal length being greater than the snout length in BNHS 3756, VPTS0522152 and CESS118. The nasals in VPTS0522152 make more substantial midline contact (INS 11.5 % of HL vs INS 7.8 % of HL in holotype) and is only slightly smaller than the midline contact between the prefrontals.

Ventrals 130–139, subcaudals 6–10. There is considerable variation in how many of the posteriormost ventrals are keeled. Individuals that had greater tail lengths (TL ca. 5% of SVL), 9–10 subcaudal scales and are presumably males (males tend to have longer tails and greater number of subcaudal scales compared to females: see Huntley et al., 2021) had 6–18 posteriormost ventrals keeled. The only exception was CESS077 which had a short tail (TL 3.5% of SVL) and 7 subcaudals had very feeble keels on the posteriormost five ventral scales. VPTS0522152 and CESS118 hav-

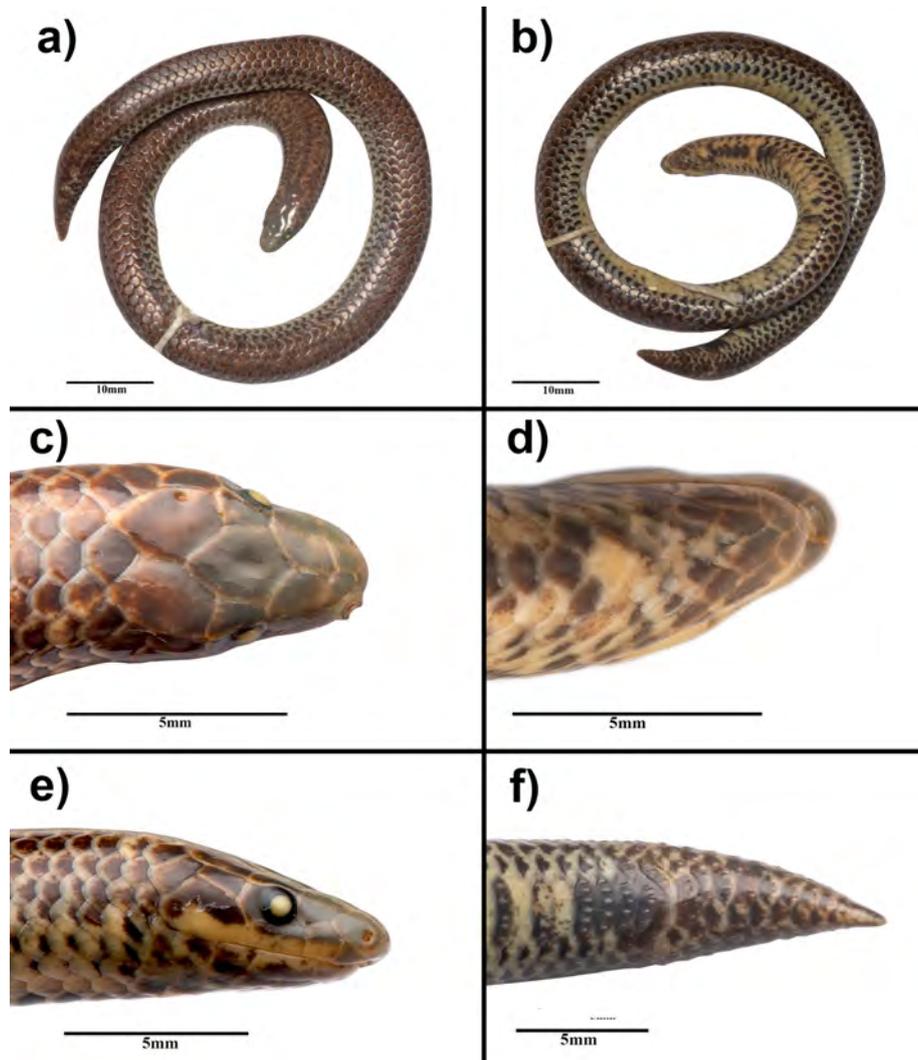


Figure 6. Holotype of *Teretrurus albiventer* sp. nov. A – dorsal view of whole specimen; B – ventral view of whole specimen; C – dorsal view of head; D – ventral view of head; E – lateral side of head; F – ventral view of tail.

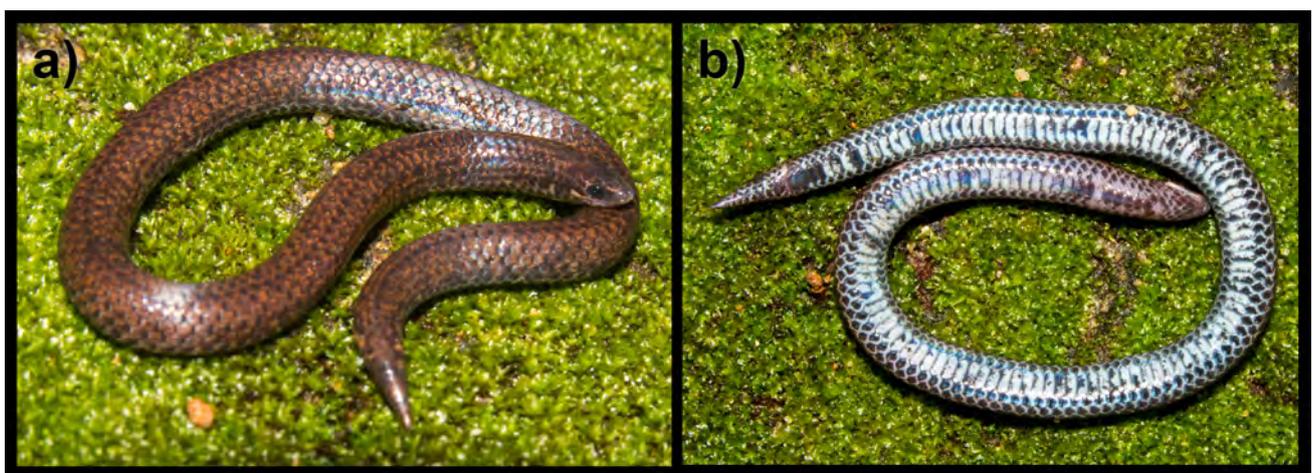


Figure 7. Photograph of *Teretrurus albiventer* sp. nov. in life (Photographs: VPC). A – Dorsal view; B – ventral view.

ing short tails (TL 3.3–3.4% of SVL) and 6 subcaudal scales (presumably females) (see Huntley et al., 2021) had smooth ventral scales. The number of keels on the ventrals scales varied from 3–7 between and within individuals, increasing

in number towards the posterior end. Colour pattern similar to holotype except for minor variation in the degree of black mottling on the venter.

*Distribution and natural history.* *Teretrurus albiventer* sp. nov. is known only from the vicinity of Chemunjimotta in Peppara Wildlife Sanctuary in Thiruvananthapuram District of Kerala state, at approximately 1100–1350 m elevation. All individuals were found in dense evergreen shola forests close to the edge of grasslands. While our extensive surveys in the southern WG have not yielded this species from other localities, we still consider the possibility of finding this species in adjacent localities around Peppara WLS and Agastyaarkoodam peak. Currently, the new species is likely to qualify for Data Deficient status under IUCN Red List criteria.

The holotype was found at 22:00, moving on the surface of a forest trek path in a dense evergreen forest patch. Paratype BNHS 3756 was found at 11:00 at the edge of a shola forest patch, under a fallen, moderately decomposed log at 15–20 cm below the soil. The paratypes VPTS0522152 and VPTS0522152 were found at around 10.00–10.50 hrs from under a decomposed log and a small rock on the forest floor respectively. The new species occurs in sympatry with other uropeltids such as *Uropeltis rubrolineata*, *U. liura* and *Melanophidium* cf. *punctatum* and may also partially overlap with *U. myhendrae*, which is generally found in lower elevations in the same hill ranges.

### ***Teretrurus siruvaniensis* sp. nov.**

urn:lsid:zoobank.org:act:9B8E1966-A951-4413-9191-DD3F1C856347

*Holotype.* BNHS 3758, adult male, base of Elival Malai, Siruvani Hills (10.9671507° N, 76.6343686° E; 996 m elevation), a part of the Nilgiri Hill Complex, situated just north of the Palghat Gap, in Palakkad district, Kerala, India. Collected by Avrajjal Ghosh and Vivek Cyriac, 24 September 2014.

*Paratypes* ( $n = 1$ ). BNHS 3759 (female), same locality as holotype (10.9671507 N, 76.6343686 E; 996 m elevation), collected by Avrajjal Ghosh on the same date as holotype.

*Etymology.* Toponym, alluding to the type locality located within Siruvani Hills in the Nilgiri biosphere reserve.

*Lineage Diagnosis.* *Teretrurus siruvaniensis* sp. nov. is nested within Clade A and is sister to a clade comprising *T. agumbensis* sp. nov. and *Teretrurus* sp. (MW3447) from near Silent Valley in the Nilgiri Hills (Fig. 4). It can be diagnosed as a shallow to moderately divergent lineage from *T. agumbensis* sp. nov. (16S: 0.2–0.4%; 12S: 1.7–1.8%; ND4: 5.6–5.9%) and *T. hewstoni* (16S: 1.0–1.5%; 12S: 1.8–2.8%; ND4: 7.5–8.3%). Geographically, *T. siruvaniensis* sp. nov. is restricted to the Siruvani Hills, while *T. hewstoni* is restricted to the Wayanad plateau and *T. agumbensis* sp. nov. is restricted to the Agumbe plateau.

*Diagnosis.* A species of *Teretrurus* inhabiting Siruvani Hills, characterized by: a known maximum SVL of 134.5 mm; presence of a supraocular scale; 13–15 dorsal scales in the anterior region of the body, 15 dorsal scales rows at mid-body and posterior regions; 127–129 ventral scales, 6–8 paired subcaudal scales; nasals in narrow contact with each other; parietal scales in broad contact with each other; smooth scales on ventral regions of the body and tail; and having a uniform greyish brown dorsum with reddish

colourations on the lateral margins of the scales and uniform pale reddish ventrum with very sparse black spots or mottling.

*Teretrurus siruvaniensis* sp. nov. differs from *T. rhodogaster* by the presence of a supraocular scale (supraocular fused with ocular scale in *T. rhodogaster*). The new species can be differentiated by the lower number of ventral scales ranging from 127–129 as opposed to being higher in *T. sanguineus* (143–150), *T. rhodogaster* (138–149), *T. travancoricus* (130–142), *T. albiventer* sp. nov. (130–139) and *T. periyarensis* sp. nov. (152) and by the absence of keeled scales on the posteriormost scales of the ventrals and the subcaudals (vs. keeled scales on posteriormost ventrals and subcaudals in *T. travancoricus*, *T. albiventer* sp. nov. and *T. periyarensis* sp. nov.). *T. siruvaniensis* sp. nov. most closely resembles *T. hewstoni* and *T. agumbensis* sp. nov. but can be differentiated from *T. hewstoni* by the higher number of ventrals ranging from 127–129 (vs. 118–127), and by the nasals having a comparatively narrower contact with each other (INS 33–36% of NL) (vs. broad contact between nasals (INS 44–50% of NL) in *T. hewstoni*). The new species can be differentiated from *T. agumbensis* sp. nov. by its broad interparietal contact (IPL 36.8% of PL) and its uniform reddish belly (vs. narrow inter-parietal contact (IPL 17.3% of PL) and the belly sparsely reddish and heavily mottled with black spots in *T. agumbensis* sp. nov.).

*Description of holotype* (Figs. 8a–f). See supplementary Table S1 for morphometric and meristic data. Head small (HL 3.9% of SVL), snout pointed. Rostral small (RL 7.7% of HL), visible from above, rounded, wider than long, not strongly projecting rearwards and without a dorsal ridge. Nasals in broad contact with each other (INS 7.7% of HL) and is as long as the rostral when viewed from above. External naris small, subcircular, located slightly above the anteroventral corner of nasal. Nasal contacts supralabials 1 and 2. Frontal irregularly hexagonal, longer than wide (FL 38.5% of HL; FW 23.1% of HL), lateral (ocular) margins slightly converging posteriorly; lateral (ocular) margin shortest, posterolateral edges longest. Prefrontals longer than wide, shorter than frontal (PFL 26.9% of HL; PFW 19.2% of HL) and in broad contact with each other along midline (IPFS 17.3% of HL). Supralabials four, first smallest, making the least contribution to margin of mouth; fourth largest. Ocular contacts supralabials 3 and 4. Eye distinct, large (EL 17.3% of HL) taking up more than the entire anterior region of the ocular (EL 75% of OL); pupil subcircular. Paired parietals much longer than wide (PL 36.5% of HL; PW 21.2% of HL), shorter and narrower than the frontal, posteriorly slightly rounded, angle between posteromedial and posterolateral edges approximately 90°. Parietals in moderate midline contact (IPS 13.5% of HL), much shorter than the midline contact between prefrontals. Parietals in contact with four scales posteriorly. Mental sub-triangular, smaller than infralabials, contacting only the first infralabials; mental groove absent. Three infralabials on each side; first smallest, second largest.

Body cylindrical having generally evenly sized scales on the body. Dorsal scale rows 15:15:15. Ventral scales evenly sized except for the seven anteriormost ones, which are

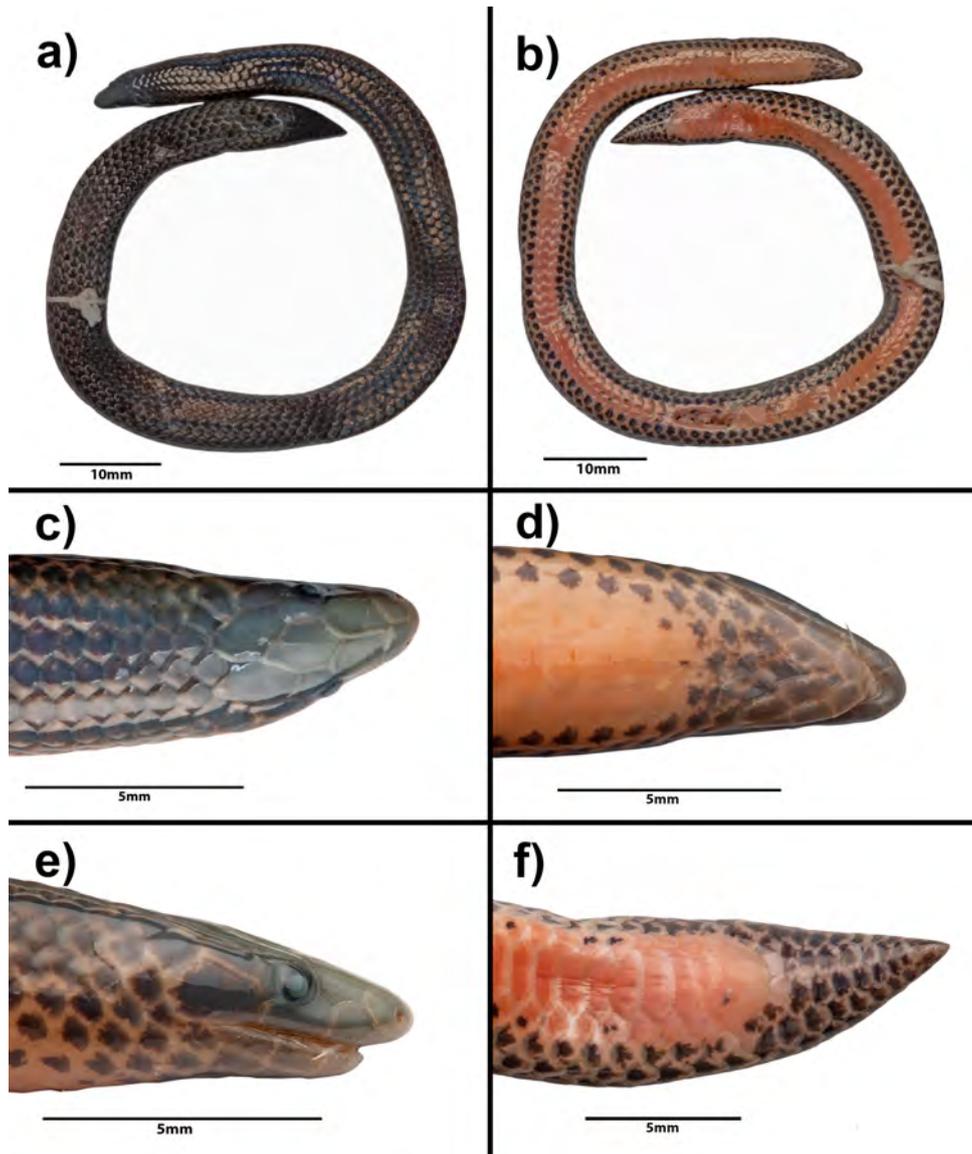


Figure 8. Holotype of *Teretrurus siruvaniensis* sp. nov. A – dorsal view of whole specimen; B – ventral view of whole specimen; C – dorsal view of head; D – ventral view of head; E – lateral side of head; F – ventral view of tail.

narrower; ventrals 127; wider than long and smooth throughout. Anal scales paired (right overlying left) and smooth. Anal scale overlaps four small scales posteriorly on the left and right side in addition to first subcaudals. Tail small (TL 4.8% of SVL), slightly laterally compressed and tapering; terminal scale enlarged and ending in a single point. Eight paired and smooth subcaudals. Dorsal and lateral scales on tail, smooth.

*Colour in alcohol.* Dorsal body colour blackish with the later sides of each scale margins being pale brownish. Head shields greyish black. Supralabial scales greyish black. Infralabials and scales on the throat are brownish grey with posterior scales of the throat and neck having pale reddish or brownish margins. Ventral scales uniformly pale reddish throughout. First two to three dorsal scales on either sides of the ventral scales black with the scale margins being pale reddish. Subcaudals and other ventral scales of the tail black with pale brownish margins.

*Colour in life (Figs. 9a–b).* Dorsum overall blackish brown with the lateral margins of each scale distinctly orangish. Head shields blackish brown. Supralabial scales black. Infralabials and scales on the throat are blackish brown with posterior scales of the throat and neck having orangish margins. Ventral scales uniformly scarlet orange throughout with few ventral scales having one or two small black spots. First two to three dorsal scales on either sides of the ventral scales black with the scale margins being pale reddish. Subcaudals and other ventral scales of the tail blackish brown with orange margins.

*Variation.* The paratype is in good condition; meristic and morphometric data are provided in [Table 1](#). The number, arrangement and overlapping of head shields are similar to the holotype. Ventrals scales in BNHS 3759 is 129, subcaudals 6. Colour pattern in life similar to that of the holotype.

*Distribution and natural history.* *T. siruvaniensis* sp. nov. is known only from Siruvani Hills in Palakkad district of Ker-



Figure 9. Photograph of *Teretrurus siruvaniensis* sp. nov. in life (Photographs: AG). A – Dorsal view; B – ventral view.

ala state, India at approximately 996 m elevation. Both individuals were found in dense evergreen forest. The holotype was found under a stone beneath a large tree, while the paratype was found under a rotting log on the forest floor. Another uncollected individual of the same species was found in the same area while digging in humus soil in between the buttresses of a tree. The new species is likely to qualify for Data Deficient status under IUCN Red List criteria. The new species occurs in sympatry with *Uropeltis cf. ceylanica*.

### *Teretrurus periyarensis* sp. nov.

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*Holotype* (by monotypy). BNHS 3760, adult, Vandiperiyar (9.583839° N, 77.129894° E; 1083 m elevation), in Periyar Tiger Reserve, Idukki district, Kerala, India. Collected by S. Kalesh & Vivek Cyriac on 06 March 2014.

*Etymology*. Toponym, alluding to the type locality located within Periyar Tiger Reserve from where the new species is discovered.

*Lineage Diagnosis*. *Teretrurus periyarensis* sp. nov. is nested within Clade B and is sister to *T. sanguineus* (Fig. 4). It can be diagnosed as a moderately divergent lineage from *T. sanguineus* (16S: 1.9%; 12S: 2.2%; ND4: 6.6%). It is restricted to the Periyar plateau in the Cardamom Hills, as opposed to *T. sanguineus*, which is distributed in the Anaimalai Hills.

*Diagnosis*. A species of *Teretrurus* inhabiting Periyar Plateau, characterized by: a known maximum SVL of 146.7 mm; presence of a supraocular scale; nasals in broad contact with each other; 15 dorsal scales rows at mid-body; 152 ventral scales, 9 paired subcaudal scales; 10 posteriormost ventral scales having 6–9 keels; three dorsal scale rows adjoining the 10–15 posteriormost ventral scales with three keels; the anal scales with four keels; first pair of subcaudal keeled, the rest smooth; and having a uniform greyish brown dorsum with each scale having a paler margin, and uniform reddish ventrum without any black mottling.

*Teretrurus periyarensis* sp. nov. differs from *T. rhodogaster* by the presence of a supraocular scale (supraocular fused with ocular scale in *T. rhodogaster*). The new species can be differentiated from other *Teretrurus* by the high number of ventral scales (152) as opposed to being lower in *T. rhodogaster* (138–149), *T. travancoricus* (130–142), *T. albiventer* sp. nov. (130–139), *T. hewstoni* (118–127), *T. siruvaniensis* sp. nov. (127–129) and *T. agumbensis* sp. nov. (116–127); by the presence of keeled scales on the posteriormost ventral scales (vs. smooth ventral and subcaudal scales in *T. hewstoni*, *T. siruvaniensis* sp. nov., *T. agumbensis* sp. nov. and *T. rhodogaster*). *T. periyarensis* sp. nov. can also be differentiated from *T. travancoricus*, *T. albiventer* sp. nov., all of which have keeled ventral scales, by the uniform reddish ventral surface (vs. ventral surface of the body red or white with several large black patches in *T. travancoricus* and *T. albiventer* sp. nov.). *T. periyarensis* sp. nov. most closely resembles *T. sanguineus* in overall colourations, but can be easily differentiated by the larger number of ventral scales (152), keeled ventral scales and the relatively extensive inter-prefrontal contact (IPFS 70% of PFL) (vs. 143–150 smooth ventral scales and a relatively narrower inter-prefrontal contact (IPFS 52.3–57.1% of PFL) in *T. sanguineus*).

*Description of holotype* (Figs. 10a–f). See Table 1 for morphometric and meristic data. Head small (HL 3.7% of SVL), snout acuminate. Rostral small (RL 9.1% of HL), visible from above, rounded, wider than long, not strongly projecting rearwards and without a dorsal ridge. Nasals in narrow contact with each other (INS 5.4% of HL) and is much shorter than the rostral when viewed from above. External naris small, subcircular, located slightly above the anteroventral corner of nasal. Nasal contacts supralabials 1 and 2. Frontal irregularly hexagonal, longer than wide (FL 45.4% of HL; FW 25.4% of HL), lateral (ocular) margins slightly converging posteriorly; lateral (ocular) margin shortest, posterolateral edges longest. Prefrontal's only slightly longer than wide, shorter than frontal (PFL 30.9% of HL; PFW 27.3% of HL) and in extensive contact with each other along midline (IPFS 21.8% of HL). Supralabials four,

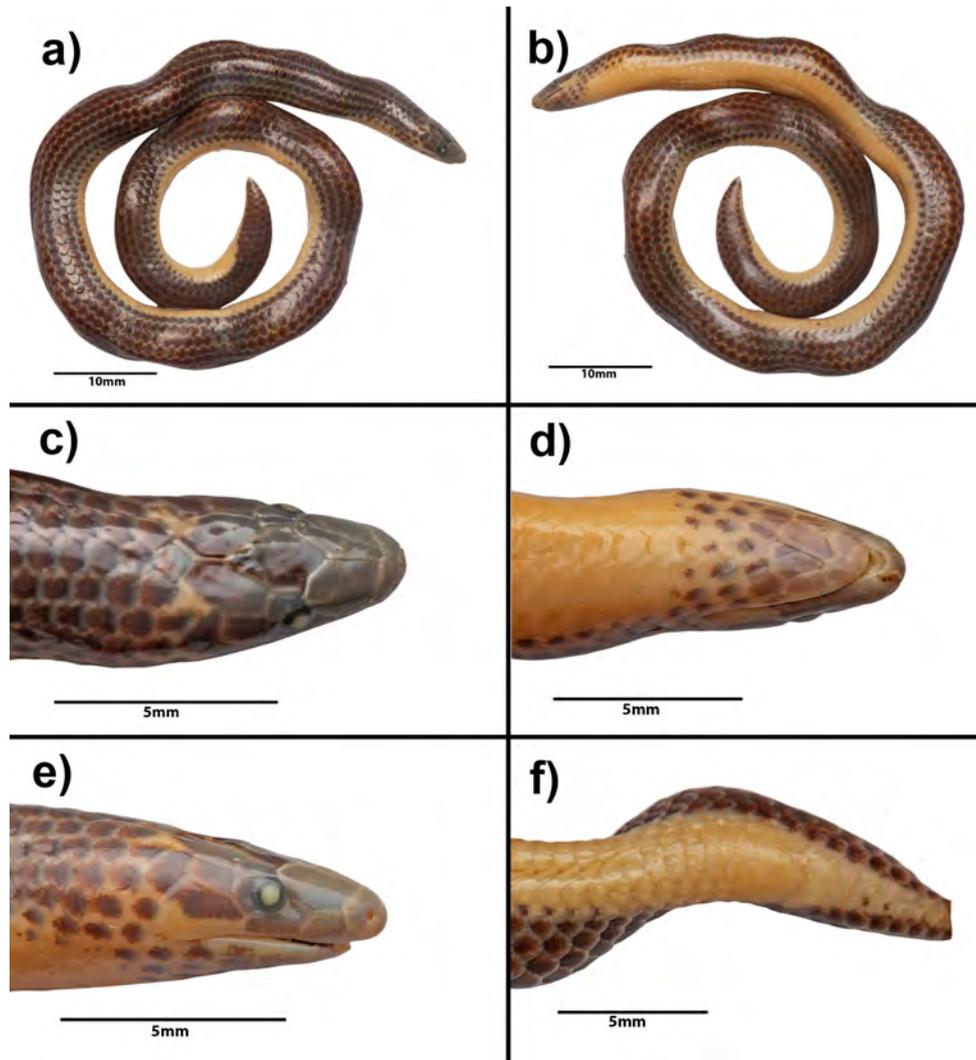


Figure 10. Holotype of *Teretrurus periyarensis* sp. nov. A – dorsal view of whole specimen; B – ventral view of whole specimen; C – dorsal view of head; D – ventral view of head; E – lateral side of head; F – ventral view of tail.

first smallest, making the least contribution to margin of mouth; fourth largest. Ocular contacts supralabials 3 and 4. Eye distinct, large (EL 16.3% of HL) occupying more than half of the anterior region of the ocular (EL 64.2% of OL); pupil subcircular. Parietals longer than wide (PL 38.2% of HL; PW 20% of HL), shorter and narrower than the frontal, posteriorly pointed, posteromedial and posterolateral edges acutely angled. Parietals in broad midline contact with each other (IPS 10.9% of HL), about half the midline contact between prefrontals. Parietals in contact with four scales posteriorly. Mental sub-triangular, smaller than infralabials, contacting only the first infralabials; mental groove absent. Three infralabials on each side; first smallest, second largest.

Body cylindrical having generally evenly sized scales on the body. Dorsal scale row formula 13:15:15. Ventral scales evenly sized and wider than long, except for the five anteriormost ones, which are as long as or longer than wide; ventrals 152; 10 posteriormost ventral scales with 6–9 keels; three dorsal scale rows on either side of the 10–15 posteriormost ventral scales with three keels; Anal scales paired (right overlying left) and with four keels each; each scale

overlaps four small scales posteriorly on the right and left side in addition to first subcaudals. Tail small (TL 5% of SVL), slightly laterally compressed and tapering; terminal scale enlarged and ending in a single point. Seven paired and smooth subcaudals; first pair of subcaudals feebly keeled, the rest smooth.

*Colour in alcohol.* Dorsal body colour blackish with the later sides of each scale margins being pale brownish giving the appearance of nine thin, faint vertical lines. Head shields greyish black with a pale orangish collar on the nape, which is interrupted in the middle. Supralabial scales greyish black, except for the fourth, which has a pale orangish colour on the ventral margins. Infralabials and scales on the throat are brownish grey with posterior scales of the throat and neck having pale orangish colourations on the posterior margins. Ventral scales and first two adjacent dorsal scales uniformly pale orangish throughout. Subcaudals uniformly pale orangish.

*Distribution and Natural History.* This species is currently known with certainty only from Vandiperiyar within Periyar Tiger Reserve in Idukki District of Kerala, India. The species likely has a broader range in mid to high-elevation forests

in the Periyar landscape. Given the lack of information on its distributional range, it is likely to qualify for Data Deficient status under IUCN Red List criteria. Although *Teretrurus* has been reported from Peermed in Idukki (fide Ferguson, 1895), which is just about ca. 15 Km from the type locality of *T. periyarensis* sp. nov., we were unable to verify the species as the voucher specimen (BNHS S106) is severely damaged and in pieces. This species also occurs in sympatry with *Uropeltis* cf. *ceylanica* and *U. madurensis*.

### ***Teretrurus agumbensis* sp. nov.**

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**Holotype.** BNHS 3761, adult, Agumbe (13.575378° N, 76.6343686° E; 697 m elevation), in the Malnad region of the Central Western Ghats, in Shivamogga district, Karnataka, India. Collected by Daimler Pereira on 25 June 2021.

**Paratypes** ( $n = 2$ ). BNHS 3762 and VPTS1023191, adults collected from the same locality as holotype on 30 July 2021 and 05 October 2021 respectively.

**Etymology.** Toponym, alluding to the type locality Agumbe from where the new species is discovered.

**Lineage Diagnosis.** *Teretrurus agumbensis* sp. nov. is sister to *Teretrurus* sp (MW3447) from near Silent Valley in the Nilgiri Hills and is nested within the larger Clade A comprising *T. hewstoni* and *T. siruvaniensis* sp. nov. (Fig. 4). It can be diagnosed as a moderate to strongly divergent lineage from *T. hewstoni* (16S: 0.8–1.1%; 12S: 2.3–3.5%; ND4: 8.1–8.9%) and shallow to moderately divergent from *T. siruvaniensis* sp. nov. (16S: 0.2–0.4%; 12S: 1.7–1.8%; ND4: 5.6–5.9%). This lineage is restricted to the Agumbe plateau in Karnataka, while *T. hewstoni* and *T. siruvaniensis* sp. nov. are restricted to the Wayanad plateau and Siruvani Hills respectively.

**Diagnosis.** A species of *Teretrurus* inhabiting Agumbe, characterized by: a known maximum SVL of 128.3 mm; presence of a supraocular scale; 15 dorsal scales rows at mid-body; 116–127 ventral scales, 7–8 paired subcaudal scales; nasals in narrow contact with each other; large parietal scales in narrow contact with each other; smooth scales on ventral regions of the body and tail; and having a uniform greyish brown dorsum and pale reddish ventrum with extensive black mottling.

*Teretrurus agumbensis* sp. nov. differs from *T. rhodogaster* by the presence of a supraocular scale (supraocular fused with ocular scale in *T. rhodogaster*). The new species can be differentiated by the lower number of ventral scales (116–127) as opposed to being higher in *T. sanguineus* (143–150), *T. rhodogaster* (138–149), *T. travancoricus* (130–142), *T. albiventer* sp. nov. (130–139) and *T. periyarensis* sp. nov. (152); by the absence of keeled scales on the posteriormost scales of the ventrals and the subcaudals (vs. keeled scales on posteriormost ventrals and subcaudals in *T. travancoricus*, *T. albiventer* sp. nov. and *T. periyarensis* sp. nov.). *T. agumbensis* sp. nov. most closely resembles *T. hewstoni* and *T. siruvaniensis* sp. nov. but can be differentiated from *T. hewstoni* and *T. siruvaniensis* sp. nov. by the relatively larger parietal scales and the narrow inter-parietal contact (PL 36.2–42.6% of HL and IPS 17.4–20.0% of

PL) (vs. smaller parietal length and broader inter-parietal contact in *T. hewstoni* (PL 34.7–37.8% of HL and IPS 29.4–35.2% of PL) and *T. siruvaniensis* sp. nov. (PL 36.5–38% of HL and IPS 36.8% of PL)). The new species can be differentiated from *T. hewstoni* and *T. siruvaniensis* sp. nov. by the highly reduced reddish colouration on the ventrals with extensive black mottling (vs extensive reddish colouration on belly with sparse black mottling in *T. hewstoni* and *T. siruvaniensis* sp. nov.).

**Description of holotype** (Figs. 11a–f). See Table 1 for morphometric and meristic data. Head small (HL 4.2% of SVL), snout acuminate. Rostral small (RL 9.2% of HL), visible from above, rounded, wider than long, not strongly projecting rearwards and without a dorsal ridge. Nasals in narrow contact with each other (INS 7.4% of HL) and is shorter than the rostral when viewed from above. External naris small, subcircular, located slightly above the anteroventral corner of nasal. Nasal contacts supralabials 1 and 2. Frontal irregularly hexagonal, about twice as longer than wide (FL 50% of HL; FW 24.1% of HL), lateral (ocular) margins slightly converging posteriorly; lateral (ocular) margin shortest, posterolateral edges longest and strongly projecting rearwards. Prefrontal's longer than wide, shorter than frontal (PFL 27.8% of HL; PFW 22.2% of HL) and in broad contact with each other along midline (IPFS 16.7% of HL). Supralabials four, first smallest, making the least contribution to margin of mouth; fourth largest. Ocular contacts supralabials 3 and 4. Eye distinct, large (EL 14.8% of HL) occupying slightly more than half of the anterior region of the ocular (EL 57% of OL); pupil subcircular. Large parietals, much longer than wide (PL 42.6% of HL; PW 18.5% of HL), shorter and narrower than the frontal, posteriorly slightly rounded, posteromedial and posterolateral edges acutely angled. Parietals in narrow midline contact (IPS 7.4% of HL), less than half the midline contact between prefrontals and equal to the length of the contact between the nasals. Parietals in contacts with four scales posteriorly. Mental sub-triangular, smaller than infralabials, contacting only the first infralabials; mental groove absent. Three infralabials on each side; first smallest, second largest.

Body cylindrical having generally evenly sized scales on the body. Dorsal scale row formula 14:15:15. Ventral scales evenly sized and wider than long, except for the six anteriormost ones, which are longer than wide; ventrals 127 and smooth throughout. Anal scales paired (right overlying left) and smooth. Anal scale overlaps three small scales posteriorly on the right and left side in addition to first subcaudals. Tail small (TL 4.4% of SVL), slightly laterally compressed and tapering; terminal scale enlarged and ending in a single point. Seven paired and smooth subcaudals. Dorsal and lateral scales on tail, smooth.

**Colour in alcohol.** Dorsal body colour blackish throughout. Head shields greyish black without a pale collar on the nape. Supralabial scales greyish black. Infralabials and scales on the throat are brownish grey with the posterior margins of each scale being pale whitish brown. Ventral and subcaudal scales blackish with the posterior margins of each scale having pale whitish brown colourations, which become slightly reddish towards the posterior region. The

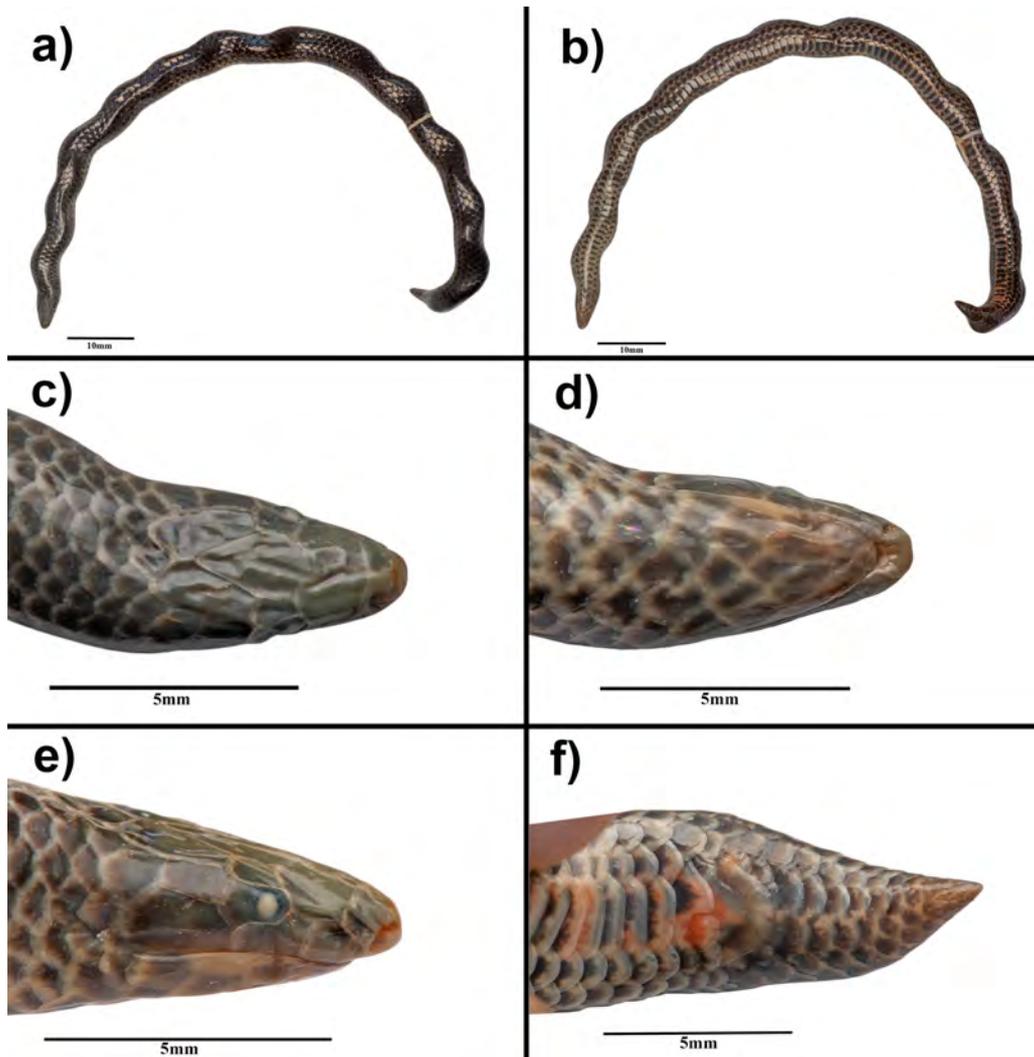


Figure 11. Holotype of *Teretrurus agumbensis* sp. nov. A – dorsal view of whole specimen; B – ventral view of whole specimen; C – dorsal view of head; D – ventral view of head; E – lateral side of head; F – ventral view of tail.

first two costal scales bordering the ventral scales are black with the lateral margins having pale whitish colouration giving the appearance of a thin lateral stripe.

**Colour in life** (Figs. 12a–b). Dorsal body colour deep brown overall. Head shields brown with lighter shades near scale edges. Rostrum pale brown. No pale collar on the nape. Supralabial scales pale brown. Infralabials and scales on the throat are pale brown with the posterior margins of each scale being greyish. Ventral and subcaudal scales grey brown with the posterior margins of each scale having pale whitish brown colourations, which become slightly reddish towards the posterior region. The first two costal scales bordering the ventral scales are black with the lateral margins having pale whitish colouration giving the appearance of a thin ventro-lateral stripe.

**Variation.** The paratype is in good condition; meristic and morphometric data are provided in Table 1. The number, arrangement and overlapping of head shields are similar to the holotype except in BNHS 3762, where the contact between the parietals is slight larger than the contact between the nasals (IPS 7.7% of HL; INS 5.8% of HL) and in VPTS1023191 where prefrontals are as long as wide (PFL

& PFW 25.5% of HL). Ventrals scales range from 116–127; subcaudals range from 7–8. Colour pattern in life of both the paratypes are similar to that of the holotype.

**Distribution and Natural History.** This species is currently known with certainty only from the vicinity of Kalinga Centre for Rainforest Ecology in Agumbe, Shivammoga district, Karnataka. Additional observations of *Teretrurus* sp. that resemble *T. agumbensis* sp. nov. have been reported by citizen scientists on the Shieldtail Mapping Project ([https://indiabiodiversity.org/group/Shieldtail\\_Mapping\\_Project](https://indiabiodiversity.org/group/Shieldtail_Mapping_Project)), a citizen science initiative, from other localities close to Agumbe such as Thirthalli and Mookambika Wildlife Sanctuary in Shivammoga district. However, these observations need further verification. The holotype was found actively moving on the ground at 01.00 hrs next to a cabin in a small wooded patch. The paratype BNHS 3762 was found in a 1m deep roadside pit at 19.30 hrs while VPTS1023191 was found moving actively across a muddy path in a wooded patch at about 20.00 hrs. The new species is likely to qualify for Data Deficient status under IUCN Red List criteria. The species occurs in sympatry with *Melanophidium* cf. *wynau-dense*, *Uropeltis* cf. *jerdoni* and *U. cf. ceylanica*.



Figure 12. Photograph of colouration of *Teretrurus agumbensis* sp. nov. (Photographs: A – Daimler Pereira; B – SRG). A – Dorsal view in life; B – close-up of ventral scales at mid-body.

### Key to species of *Teretrurus*

Here we provide an updated version of the taxonomic key of *Teretrurus* presented by Ganesh & Murthy (2022) incorporating new data for the four known species and the four new species described here.

1. Supraocular fused with ocular shield...2
  - Supraocular separated from ocular shield...3
2. Ventrals 138–149; ventrals uniformly unpatterned or orange red...*T. rhodogaster*
3. Ventral scales of body and tail smooth...4
  - Posteriormost ventral scales, subcaural scales and adjacent 1–2 costal scales with three to seven keels...7
4. Ventral scales 143–150...*T. sanguineus*
  - Ventrals scales 116–129...5
5. Belly orangish mottled with few black spots; small parietals in broad contact with each other...6
  - Belly sparsely orangish and heavily mottled with black spots; large parietal scales in narrow contact with each other...*T. agumbensis* sp. nov.
6. Nasal scales in narrow contact with each other...*T. siruvaniensis* sp. nov.
  - Nasals in broad contact with each other...*T. hewstoni*
7. Ventral scales 130–142...8
  - Ventral scales 152...*T. periyarensis* sp. nov.
8. Belly orangish-red with few prominent black patches...*T. travancoricus*
  - Belly pale white with extensive black markings and patches...*T. albiventer* sp. nov.

### Discussion

From 1867, when the first species of *Teretrurus* was described from the Anaimalai Hills, until 1921 when the last congener was described from the Palni Hills, a period of over half a century (54 years), there were only five taxonomic studies on the group (Beddome, 1867, 1876, 1886; Theobald, 1876; Wall, 1921). This also includes at least

one redundant invalid description of a species (*Plectrurus scabricauda* Theobald, 1876) and a genus (*Brachyophidium* Wall, 1921). From 1921 to 2022, for a whole century, the taxonomy of *Teretrurus* had remained unattended rather than ‘stable’ (Ganesh & Murthy, 2022). Our work, using both morphometric and molecular data from *Teretrurus* samples collected from several poorly sampled regions, reveals further diversity within this genus.

While our morphometric analyses indicated that the four currently known geographically allopatric ensemble of species (*T. sanguineus*, *T. rhodogaster*, *T. hewstoni* and *T. travancoricus*) occupied distinct morphospaces, the new populations sampled from other regions showed significant overlap with the above species. However, the species delimitation analyses consistently recovered greater species diversity than current taxonomy and indicated that the total diversity within *Teretrurus* ranged from 6–14 species. These results are similar to earlier attempts at phylogenetic species delimitation in uropeltid snakes, albeit with limited sampling, with different methods suggesting 7–12 species within *Teretrurus* (Sampaio et al., 2023). However, some species delimitation methods (GMYC and bPTP-BI) clearly indicated over-splitting wherein morphologically similar samples collected from the same locality were split as distinct species. For example, the two samples of *T. hewstoni* (VPTS0918094 and 095) collected less than a meter from each other in Meppadi, Wayanad were split as two distinct species in the GMYC analysis. Similar instances of over-splitting were seen within *T. travancoricus*, *T. cf. travancoricus* from Pandimotta and *T. albiventer* sp. nov. in the bPTP-BI analysis. There were also possible instances of under-splitting in the bPTP-ML analysis. For instance, *T. siruvaniensis* sp. nov., *T. agumbensis* sp. nov. and *Teretrurus* sp. (MW3447) were recovered as a single species in the bPTP-ML analysis, which seems unlikely given the geographic distribution pattern between these lineages. *T. siruvaniensis* sp. nov. and *Teretrurus* sp. (MW3447) are both distributed in the Nilgiri landscape and are separated from *T. agumbensis* sp. nov. in the Agumbe plateau by about 300 Km with the

intervening regions occupied by *T. hewstoni* in the Wayanad plateau. Nevertheless, our species validation approach with Bayes Factor Delimitation rejected these models as well as the species – model based on current taxonomy, and strongly supported the 10 species model, of which we describe four new species. Although we use multiple specimens to describe three species, we describe *T. periyarensis* sp. nov. based on a single specimen. While *T. periyarensis* sp. nov. shows several distinct morphological characters that distinguish it from all other congeners, the lack of additional specimens hindered detailed analyses of morphological variation. Nonetheless, all the phylogenetic species delimitation methods consistently identified *T. periyarensis* sp. nov. as a distinct lineage. However, additional samples of *T. periyarensis* sp. nov. , and others will be required to fully understand morphological variation within and between *Teretrurus* species.

Our phylogenetic hypothesis and species delimitation of *Teretrurus* indicate that lineages are largely separated according to geography. The tree topologies recovered three main clades corresponding to lineages north of the Palghat gap (clade A), between Palghat and Shencottah gaps (clade B) and below Shencottah gap (clade C) (Fig 4). The Palghat and Shencottah gaps are two main biogeographic barriers and have influenced lineage splitting in many groups of endemic amphibians and reptiles and have resulted in similar phylogenetic patterns as seen in *Teretrurus* (e.g. Chaitanya et al., 2019; Mallik et al., 2020, 2021; Van Bocxlaer et al., 2012; Vijayakumar et al., 2016). Within each of these three main clades, most lineages show allopatric distributions. In clade A, which are distributed north of the Palghat Gap, *T. siruvaniensis* sp. nov. is distributed in the Siruvani Hills. Further north, the *Teretrurus* population in the Nilgiri Hills has not been systematically resolved, despite reports (see Murthy, 1993). North of the Nilgiris, in the Wayanad plateau, occurs *T. hewstoni* (Ganesh & Murthy, 2022). *Teretrurus agumbensis* sp. nov. occurs still north in the Agumbe plateau, which forms the northern limit of the distribution of *Teretrurus*. Within clade B, two congeners *T. sanguineus* and *T. rhodogaster* occur in the Anaimalai-Palni landscape (Ganesh & Murthy, 2022), while *T. periyarensis* sp. nov. occurs in the Periyar plateau. However, in clade C, the three lineages identified from our analyses (*T. travancoricus*, *T. cf. travancoricus* and *T. albiventer* sp. nov.) seem to have split within a seemingly contiguous landscape with no apparent geographic barriers. Nonetheless, two lineages—*T. travancoricus* and *T. albiventer* sp. nov., are distributed on the eastern and western slopes of the Agasthyamalai Hills respectively. Studies have indicated east-west variation in climate and vegetation cover wherein the western slopes experience greater rainfall and have denser vegetation cover compared to the eastern slopes (Murugan et al., 2008; Nagendra & Ghate, 2003). Such climatic factors could also lead to local adaptations and eventual isolation of populations and speciation in these snakes. Similar patterns wherein closely related species are distributed on an east-west gradient have been reported in some groups of geckos (Agarwal et al., 2022; Chaitanya et al., 2019). For instance, *Dravidogecko smithi* and *D. douglasadamsi* are two

sister species of Western Ghats endemic geckos found on either side of the Agasthyamalai Hills, with *D. smithi* found on the western slopes while the other is distributed on the eastern slopes (Chaitanya et al., 2019). In general, the distribution pattern of *Teretrurus* mirrors that of *Xylophis*, another group of endemic fossorial snakes in the Western Ghats, with two distinct species – *X. captaini* and *X. deepaki* – distributed more or less parapatrically in the Agasthyamalai Hills (Narayanan et al., 2021), one potential species in the Periyar-Meghamalai landscape (see Chaitanya et al., 2018), two species in the Anamalai landscape (Deepak et al., 2020), and one species in the Nilgiri Hills (Narayanan et al., 2021).

## Conclusion

Overall, our study highlights the presence of extensive cryptic diversity within *Teretrurus* and describes four new species. Systematically sampling uropeltid snakes is challenging due to their fossorial habits and a lack of adequate information on their natural history and distribution (Sampaio et al., 2023). However, as our work shows, there is clearly a need for extensive fine-scaled sampling of uropeltid snakes across the Western Ghats. While we have broadly expanded the geographic extent of our sampling in this study compared to previous studies, there are still several regions that remain unexplored. For instance, between the ranges of *T. hewstoni* and *T. agumbensis* sp. nov. are a series of tall massifs viz. Brahmagiri, Tadiyendamol, Nishani Motte, Kumara Parvatha, Kudremukh, Mullayangi and Baba Budangiri. While we have surveyed some of these intervening regions for uropeltid snakes, we are yet to find any *Teretrurus* populations. However, the presence of *T. agumbensis* sp. nov. as far north as Agumbe is compelling evidence that *Teretrurus* populations may be present in these intervening massifs. Additionally, known populations of *Teretrurus* from Coonoor, Nilgiris (fide Murthy, 1993) still await formal taxonomic studies. For now, due to lack of adequate data, we refer to them provisionally as *Teretrurus* sp. Future systematic sampling focusing on reducing these sampling gaps is required in all these localities to further discover (and describe) novel populations or species and allow us to uncover the biogeographic history of uropeltid snakes in the tropical montane sky island systems of the Western Ghats.

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## Supporting Information

The supplementary file is available on Zenodo:  
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