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A non-adaptive radiation of viviparous skinks from the seasonal tropics of India: Systematics of *Subdoluseps* (Squamata: Scincidae), with description of a new genus and five cryptic new species

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Abstract

Subdoluseps is a recently described genus of Lygosomine skinks distributed in peninsular India and Southeast Asia. We conduct the first revision of Indian *Subdoluseps* based on range-wide sampling including 89 specimens from 33 localities. We use two mitochondrial and three nuclear markers, 58 morphological characters, and ecological data to reconstruct the evolutionary history of Indian *Subdoluseps* and assess their diversity and distribution, providing insights into lygosominin biogeography. We formally describe the Indian clade as a new genus, *Dravidoseps* **gen. nov.** and name five new species from Tamil Nadu, India in an integrative taxonomic framework – *D. gingeeensis* **sp. nov.**, *D. jawadhuensis* **sp. nov.**, *D. kalakadensis* **sp. nov.**, *D. srivilliputhurensis* **sp. nov.**, and *D. tamilnaduensis* **sp. nov.**. We transfer *Riopa goaensis*, *Subdoluseps pruthi* and *S. nilgiriensis* to the new genus and designate neotypes for the former two. Members of *Dravidoseps* **gen. nov.** are the first known viviparous skinks from peninsular India and the only known viviparous lygosominins apart from a few species of east African *Mochlus*. The Lygosomini have a Southeast Asian origin and began diversifying in the Eocene with three dispersals between India and Southeast Asia. Species level diversification in *Dravidoseps* **gen. nov.** was likely driven by a combination of niche conservatism, paleoclimate and past forest distribution. The discovery of a new genus and five new species reiterates the high levels of diversity and endemism present in peninsular India and how much more remains to be discovered.

Keywords

Asia, biodiversity hotspot, diversification, integrative taxonomy, nuclear DNA, reproductive mode

Introduction

Skinks (Family Scincidae) are among the most diverse squamate clades, with over 1,740 species distributed across tropical and temperate regions, from sea level up to over 4,500 m (Camp 1923; Vitt and Caldwell 2014; Uetz et al. 2023). Skinks have diverse life-history traits, and may be diurnal, cathemeral or nocturnal; and include terrestrial, aquatic, arboreal, fossorial, and rupicolous species (Vitt and Caldwell 2014; Borkin et al. 2018). Over a third of all skink species are viviparous, with numerous independent origins of viviparity and varied levels of matrotrophy (Vitt and Caldwell 2014; Zimin et al. 2022). Their body forms also vary significantly, encompassing a broad range of body sizes (27–350 mm snout to vent length) and multiple instances of limb loss or limb reduction (Vitt and Caldwell 2014); though individual clades are often highly conserved in morphology, making the recognition of cryptic species challenging (e.g. Freitas et al. 2020; Slavenko et al. 2020). The diversity of traits within the Scincidae and their wide distribution make them an excellent system for studies in developmental biology and comparative ecology and evolution (Vitt and Caldwell 2014; Slavenko et al. 2022; Camaiti et al. 2023). We follow Shea's (2021) conception of three subfamilies containing numerous tribes for higher level skink taxonomy.

Peninsular India has a moderate species diversity of skinks with ~40 species including representatives of two of the three global skink sub-families and numerous endemic radiations at the genus or clade level (Karanth 2015; Deuti et al. 2020; Shea et al. 2021; Uetz et al. 2023). These include the limbless genera *Barkudia* Annandale and *Sepsophis* Beddome of the subfamily Scincinae, endemic to the Eastern Ghats (EG); and within the Lygosomidae, *Kaestlea* Eremchenko and Das (Sphenomorphini) and *Ristella* Gray (Ristellini) endemic to the Western Ghats; and clades of *Eutropis* Fitzinger (Mabuyini), *Riopa* Gray and *Subdoluseps* Freitas, Datta-Roy, Karanth, Grismer & Siler (Lygosomini) in peninsular India (Datta-Roy et al. 2012, 2014; Freitas et al. 2019; Ganesh et al. 2021; Deuti et al. 2020). The diversity of Indian skinks is likely a sampling artefact, and just two species – *Dasia johnsinghi* Harikrishnan et al., 2015 and *Subdoluseps nilgiriensis* Ganesh et al., 2021 have been described from peninsular India since the turn of the century, both from the Western Ghats (Harikrishnan et al. 2012; Ganesh et al. 2021). This contrasts against the 141 new species of agamids, geckos and lacertids that have been described from the country over the same timeframe (Uetz et al. 2023). Apart from a single report of embryos in early developmental stages (said to be equivalent to a 3-day old chicken embryo) within the eggs of a dissected *Eutropis carinata* (Schneider) (Seshaiya 1938), no peninsular Indian skinks are known to be viviparous (Zimin et al. 2022).

The genus *Subdoluseps* (type species: *Eumeces bowringii* Günther) was recently erected for species formerly assigned to *Lygosoma* Hardwicke and Gray, which molecular phylogenetic data places sister to *Riopa* from India and Southeast Asia and *Mochlus* Günther from Africa, within the Tribe Lygosomini (Freitas et al. 2019; Shea 2021). Six species of *Subdoluseps* are known from Southeast Asia and two from peninsular India. All genus members are small (35–70 mm snout to vent), oviparous, forest-dwelling skinks that live in leaf-litter or are semi-fossorial, with elongate bodies and relatively short limbs and small heads (Freitas et al. 2019; Ganesh et al. 2021; Grismer et al. 2019; Le et al. 2021; Zimin et al. 2022). The two Indian species, *Subdoluseps pruthi* (Sharma, 1977) and *Subdoluseps nilgiriensis* Ganesh et al., 2023 differ from Southeast Asian *Subdoluseps* by the presence of a transparent window on the lower eyelid, versus a scaly lower eyelid in the latter group (Sharma 1977; Freitas et al. 2019; Ganesh et al. 2021). *Subdoluseps pruthi* was described based on three specimens from the Sitteri Hills of Tamil Nadu, a massif that rises to > 1000 m asl. (Sharma 1977), and has since been recorded, based on uncollected specimens from multiple, isolated hill ranges in Tamil Nadu at elevations of ~ 700–1400 m asl. (Ganesh and Arumugam 2016; Ganesh and Aengals 2018; Ganesh et al. 2019, 2021). However, the type series seems to be lost and only two museum specimens have been referred to this species, from the isolated massifs of Jawadhu Hills and Pachaimalai, >50 km from the type locality, respectively (Fig. 1; Das et al. 1998; Ganesh and Aengals 2018; Ganesh et al. 2021). *Subdoluseps nilgiriensis* was more recently described based on three specimens from two closely spaced localities in the Western Ghats, and its phylogenetic affinities were confirmed based on partial sequences of two mitochondrial genes (Ganesh et al. 2021).

The vast landscape that *Subdoluseps* is distributed in across peninsular India is highly heterogeneous, including the biodiverse Western Ghats and several isolated massifs and uplands. All of these landscapes harbour numerous endemic species and lineages of agamids, geckos and skinks from multiple genera (e.g. Harikrishnan et al. 2012; Deepak et al. 2016; Agarwal et al. 2019a, b; Amarasinghe et al. 2022; Khandekar et al. 2022; Narayanan et al. 2022; Pal and Mirza 2022). This led us to hypothesize that taxonomic diversity within Indian *Subdoluseps* is likely underestimated. In this paper we present a range-wide sampling of the genus from peninsular India including 89 specimens from 33 localities, 58 morphological characters, and two mitochondrial and three nuclear markers. We also investigated the status of *Riopa goaensis*, even though a mitochondrial phylogeny suggests it is sister to *R. guentheri* (Peters), as no morphological data was included in that study (Datta-Roy et al. 2014), and the species closely resembles *Subdoluseps pruthi* and *S. nilgiriensis* in colouration and overall body form. We use these data to reconstruct the evolutionary history of *Subdoluseps* and the timing of its diversification, as well as to assess the diversity and distribution of Indian *Subdoluseps*. We formally describe the Indian clade of *Subdoluseps* as a new genus and recognise five new species from Tamil Nadu, India using an integrative taxonomic framework, and present a dichotomous identification key.

Materials and Methods

Taxon sampling and molecular genetic data

We sampled most reported peninsular Indian localities of *Subdoluseps* spp. (Ganesh and Arumugam 2016; Ganesh and Aengals 2018; Ganesh et al. 2018, 2021; Fig. 1) and similar habitats across Tamil Nadu, as well as *Riopa goaensis* (Sharma) from multiple localities in the northern Western Ghats, during multiple field trips from 2018–2023, sampling over 350 locations in ~ 12 months of total fieldwork by a team of 3–6 workers. Specimens were hand-collected, and photographed using Canon and Nikon DSLR cameras with macro lenses and external flashes, before being euthanized using isoflurane, with liver tissues or tail tips of 1–6 individuals per putative species per locality collected in molecular-grade ethanol and subsequently stored at –20°C for genetic analysis. Collection permits were issued by the Tamil Nadu Forest Department (see acknowledgements) and collection protocols cleared by an inhouse ethics committee. Spec-

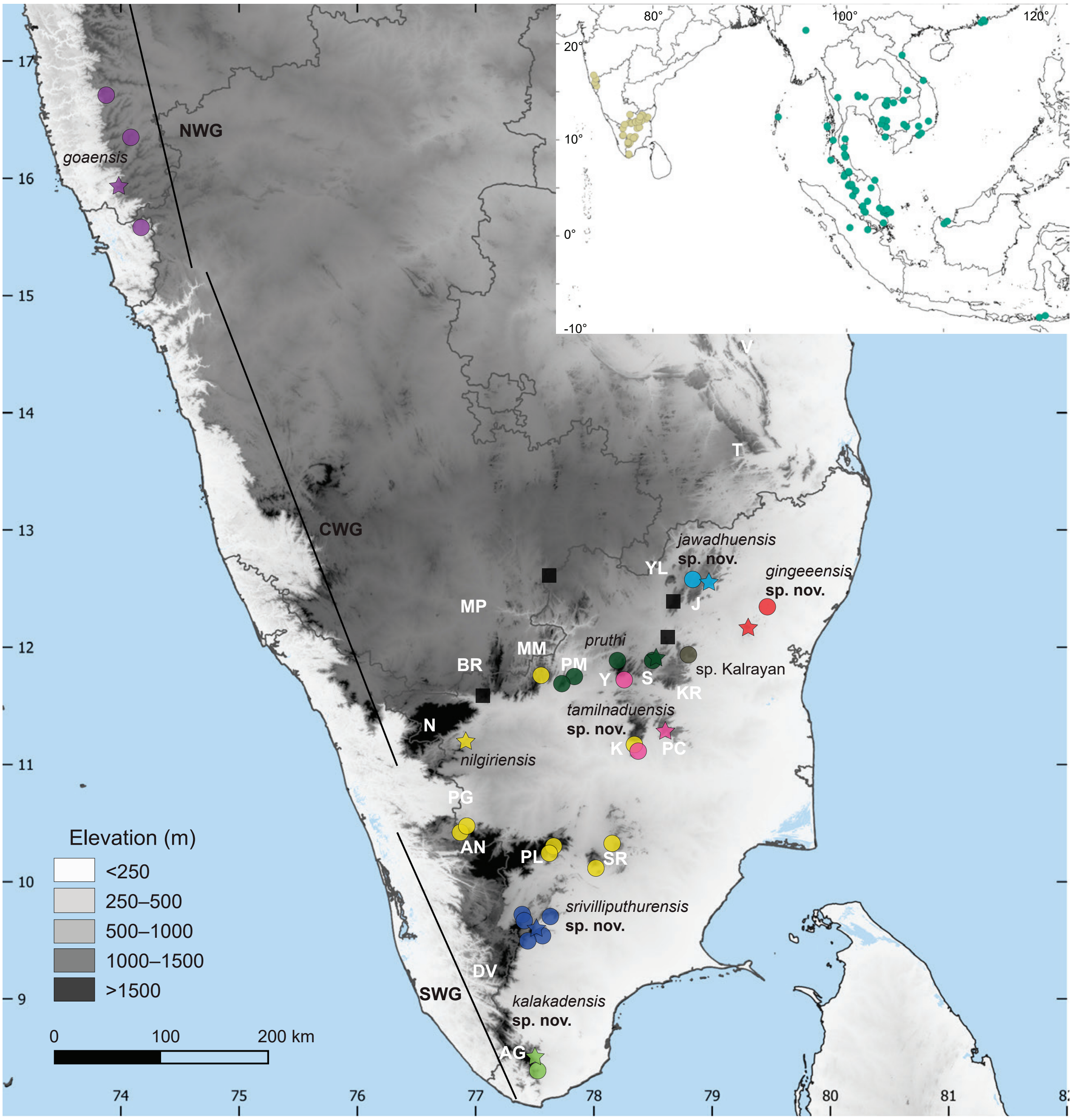

Figure 1. Elevation map showing sampling localities from peninsular India. Stars indicate type localities (neotype locality shown for *Dravidoseps goaensis* **comb. nov.**, original type locality is close to the southernmost point), light blue *D. jawadhuensis* **sp. nov.**, dark blue *D. srivilliputhurensis* **sp. nov.**, light green *D. kalakadensis* **sp. nov.**, dark green *D. pruthi* **comb. nov.**, red *D. gingeeensis* **sp. nov.**, yellow *D. nilgiriensis* **comb. nov.**, pink *D. tamilnaduensis* **sp. nov.**, and grey, *D.* sp. Kalrayan (colour scheme representing species is the same as Figs 3–6), black squares unsampled previously known localities. The approximate extent of the Central Western Ghats (CWG), Northern Western Ghats (NWG), and Southern Western Ghats (SWG) are shown; major hill ranges and features are marked by bold white text, within the Western Ghats: AG, Agasthyamalai; AN, Anaimalai; DV, Devarmalai; N, Nilgiris; PG, Palghat Gap; PL, Palani; and outside the Western Ghats: BR, Biligirangan; J, Jawadhu; K, Kollimalai; KR, Kalrayan; mm, Male Mahadeshwara; MP, Mysore Plateau; PC, Pachaimalai; PM, Palamalai; S, Sitteri; SR, Sirumalai; T, Tirupati; V, Velikonda; Y, Yercaud; YL, Yelagiri. Inset, global distribution of *Dravidoseps* **gen. nov.** (brown) and *Subdoluseps* sensu stricto (green). *Dravidoseps goaensis* = *Riopa goaensis* (see main text).

imens were fixed in 8% formaldehyde for ~12 hours, washed in water and transferred to 70% ethanol for long-term storage. Specimens are deposited in the Museum and Research Collection Facility at National Centre for Biological Sciences, Bengaluru (**NRC-AA**), the Bombay Natural History Society, Mumbai (**BNHS**) and the Zoological Survey of India, Kolkata (**ZSI-R**).

We sequenced 57 *Subdoluseps* tissues from 33 localities (the sample from Kalrayan is a tail-tip only, some others were juveniles or damaged individuals – listed in referred material) across the known range of the group in peninsular India (Fig. 1), including topotypic or near-topotypic material from the two described species (*S. pruthi* and *S. nilgiriensis*) and *Riopa goaensis*, and combined these with other published sequences of *Subdoluseps* from peninsular India and Southeast Asia (Table 1, Table S1; after Freitas et al. 2019; Freitas 2020). We used the Qiagen DNeasy Blood and Tissue kit to extract whole genomic DNA from ethanol preserved liver or tail biopsies and targeted two mitochondrial genes (1538 base pairs (bp): 16S, ~500 bp; ND2, 1038 bp) and three nuclear genes (2246 bp: PRLR, 565 bp; R35, 662 bp; RAG1, 1019 bp) using the primers and annealing temperatures listed in Table 2 for PCR amplification and sequencing (carried out by Barcode BioSciences (Bengaluru). PCR reactions used 2 µl of template, 1 µl primer (~ 2.5 pmol) and 7 µl of EmeraldAmp® GT PCR Master Mix, with the PCR cycle 95°C/3 min, 35 x (95°C/30–35 s, 50–53°C/30–35 s, 72°C/45–60 s), 72°C/3–5 min (the longer cycle was used for nuclear markers). Successful reactions were cleaned up using the QIAGEN QIAquick PCR Purification Kit and sequencing reactions used the BDT v3.1 Cycle sequencing kit on Applied Biosystems™ MiniAmp™ Plus Thermal cycler and were sequenced on the ABI 3730xl. Bidirectional sequence reads were assembled manually using Chromas 2.6.6 (Technelysium Pty Ltd; https://technelysium.com.au) with heterozygous sites determined as overlapping peaks (~70 % each other's height) that were coded using IUPAC nucleotide codes. Sequences were aligned using default settings in ClustalW (Thompson et al. 1994) in MEGA 5.2 (Tamura et al. 2011) and protein coding genes were translated to amino acids which showed no premature stop codons. Uncorrected p-distance was calculated in MEGA 5.2 using the pairwise deletion option (Table 3).

Table 1. Sequences used in this study with voucher and locality information. Voucher collection abbreviations as follows: AK/AK-R Akshay Khandekar field series; BNHS, Bombay Natural History Society, Mumbai; CAS, California Academy of Sciences, San Francisco; CES, Centre for Ecological Sciences, Bangalore; FMNH, Field Museum of Natural History, Gainesville; JAM, Jimmy McGuire field series; KU, University of Kansas Natural History Museum, Lawrence; LSUH, La Sierra University, Riverside, California; MVZ, Museum of Vertebrate Zoology, Berkeley; NRC, National Centre for Biological Sciences, Bangalore; PEMR, Port Elizabeth Museum, Port Elizabeth; ZMKUR, ZSI-R, Zoological Survey of India, Kolkata.

Species	Voucher	Locality	GenBank accession number				
			16S	ND2	PRLR	R35	RAG1
Dravidoseps pruthi **comb. nov.**	NRC-AA-1292 (AK803)	India: Tamil Nadu, Dharmapuri District, Sitteri	OR886462	OR888556	OR888610	OR888646	OR888678
Dravidoseps pruthi **comb. nov.**	NRC-AA-1293 (AK804)	India: Tamil Nadu, Dharmapuri District, Sitteri	OR886463	OR888557	OR888611	OR888647	OR888679
Dravidoseps pruthi **comb. nov.**	BNHS 2525 (AK-R 2197)	India: Tamil Nadu, Salem District, Palamalai	OR886464	OR888558	OR888612	OR888648	OR888680
Dravidoseps pruthi **comb. nov.**	BNHS 2557 (AK-R 2198)	India: Tamil Nadu, Salem District, Palamalai	OR886465	OR888559	/	/	/
Dravidoseps pruthi **comb. nov.**	AK-R 2199	India: Tamil Nadu, Salem District, Palamalai	OR886466	OR888560	OR888613	OR888648	OR888681
Dravidoseps pruthi **comb. nov.**	AK-R 2213	India: Tamil Nadu, Dharmapuri District, Sitteri	OR886467	OR888561	/	/	/
Dravidoseps pruthi **comb. nov.**	NRC-AA-1291 (AK-R 2222)	India: Tamil Nadu, Dharmapuri District, Sitteri		OR888562	OR888614	OR888649	OR888682
Dravidoseps pruthi **comb. nov.**	ZSI-R-28601 (AK-R 2716)	India: Tamil Nadu, Salem District, Vanavasi RF	OR886468	OR888563	/	/	/
Dravidoseps pruthi **comb. nov.**	ZSI-R-28602 (AK-R 2750)	India: Tamil Nadu, Salem District, N slope of Yercaud	OR886469	OR888564	OR888615	OR888650	OR888683
Dravidoseps goaensis **comb. nov.**	NRC-AA-1303 (AK 1052)	India: Maharashtra, Kolhapur District, nr. Ugwai temple	/	OR888565	//	//	//
Dravidoseps goaensis **comb. nov.**	NRC-AA-1304 (AK 1190)	India: Maharashtra, Kolhapur District, Talaye	/	OR888566	/	/	/
Dravidoseps goaensis **comb. nov.**	NRC-AA-1305 (AK 1300)	India: Maharashtra, Kolhapur District, Pandivare	OR886470	OR888567	OR888616	OR888651	OR888684

Species	Voucher	Locality	GenBank accession number				
			16S	ND2	PRLR	R35	RAG1
Dravidoseps goaensis **comb. nov.**	BNHS 2566 (AK 1303)	India: Maharashtra, Kolhapur District, Kapurkada Falls, Washi	OR886471	OR888568	/	/	/
Dravidoseps goaensis **comb. nov.**	BNHS 2567 (AK 1345)	India: Maharashtra, Sindhudurg District, Amboli	OR886472	OR888569	OR888617	OR888652	OR888685
Dravidoseps goaensis **comb. nov.**	NRC-AA-1302 (AK-R 2808)	India: Goa, South Goa District, Ustam	/	OR888570	OR888618	OR888653	/
Dravidoseps goaensis **comb. nov.**	ZSI-R 28612 (AK-R 847)	India: Maharashtra, Sindhudurg District, Amboli	/	OR888571	OR888619	/	OR888686
Dravidoseps nilgiriensis **comb. nov.**	BNHS 2642	India: Tamil Nadu, Coimbatore District, Anaikatti hills	MW353683	/	/	/	/
Dravidoseps nilgiriensis **comb. nov.**	NRC-AA-1295 (AK-R 1854)	India: Tamil Nadu, Dindigul District, Palani Hills, nr. Mangalamkombu	OR886473	OR888572	OR888620	OR888654	OR888687
Dravidoseps nilgiriensis **comb. nov.**	NRC-AA-1296 (AK-R 1877)	India: Tamil Nadu, Dindigul District, Palani Hills, nr. Mangalamkombu	OR886474	OR888573	/	/	/
Dravidoseps nilgiriensis **comb. nov.**	NRC-AA-1297 (AK-R 2022)	India: Tamil Nadu, Coimbatore District, ATR, Aliyar RF	OR886475	OR888574	OR888621	OR888655	OR888688
Dravidoseps nilgiriensis **comb. nov.**	NRC-AA-1298 (AK-R 2023)	India: Tamil Nadu, Coimbatore District, ATR, Aliyar RF	OR886476	OR888575	/	/	/
Dravidoseps nilgiriensis **comb. nov.**	NRC-AA-1299 (AK-R 2080)	India: Tamil Nadu, Coimbatore District, near Mettupalayam	OR886477	OR888576	OR888622	OR888656	OR888689
Dravidoseps nilgiriensis **comb. nov.**	NRC-AA-1300 (AK-R 2081)	India: Tamil Nadu, Coimbatore District, near Mettupalayam	OR886478	OR888577	/	/	/
Dravidoseps nilgiriensis **comb. nov.**	NRC-AA-1301 (AK-R 2172)	India: Tamil Nadu, Erode District, Thamarakarai	OR886479	OR888578	OR888623	OR888657	OR888690
Dravidoseps nilgiriensis **comb. nov.**	(AK-R 2173)	India: Tamil Nadu, Erode District, Thamarakarai	OR886480	OR888579	/	/	/
Dravidoseps nilgiriensis **comb. nov.**	BNHS 2559 (AK-R 2539)	India: Tamil Nadu, Madurai District, Sirumalai Hills, nr. Kutladampatti Falls	/	OR888580	OR888624	OR888658	OR888691
Dravidoseps nilgiriensis **comb. nov.**	BNHS 2560 (AK-R 2540)	India: Tamil Nadu, Madurai District, Sirumalai Hills, nr. Kutladampatti Falls	OR886481	OR888581	/	/	/
Dravidoseps nilgiriensis **comb. nov.**	BNHS 2564 (AK-R 2585)	India: Tamil Nadu, Dindigul District, Karanthamalai Hills	OR886482	OR888582	OR888625	OR888659	OR888692
Dravidoseps nilgiriensis **comb. nov.**	BNHS 2565 (AK-R 2586)	India: Tamil Nadu, Dindigul District, Karanthamalai Hills	OR886483	OR888583	/	/	/
Dravidoseps nilgiriensis **comb. nov.**	ZSI-R-28604 (AK-R 2667)	India: Tamil Nadu, Coimbatore District, ATR, Perunguntru trek	OR886484	OR888584	OR888626	OR888660	OR888693
Dravidoseps nilgiriensis **comb. nov.**	ZSI-R-28605 (AK-R 2668)	India: Tamil Nadu, Coimbatore District, ATR, Perunguntru trek	OR886485	OR888585	/	/	/
Dravidoseps nilgiriensis **comb. nov.**	ZSI-R-28694 (AK-R 2726)	India: Tamil Nadu, Namakkal District, Kolli Hills	/	OR888586	OR888627	OR888661	OR888694
Dravidoseps gingeeensis **sp. nov.**	NRC-AA 8273 (AK-R 147)	India: Tamil Nadu, Villupuram District, Pakkamalai RF	OR886486	OR888587	OR888628	OR888662	OR888695
Dravidoseps gingeeensis **sp. nov.**	BNHS 2568 (AK-R 192)	India: Tamil Nadu, Tiruvannamalai District, Vedal	OR886487	OR888588	OR888629	OR888663	OR888696
Dravidoseps jawadhuensis **sp. nov.**	NRC-AA 8274 (CES 09/ 930)	India: Tamil Nadu, Vellore District, Jawadhu Hills	MK414572	/	MK409470	/	MK409548
Dravidoseps jawadhuensis **sp. nov.**	BNHS 2569 (AK 850)	India: Tamil Nadu, Vellore District, Jawadhu Hills	OR886488	OR888589	OR888630	OR888664	OR888697
Dravidoseps kalakadensis **sp. nov.**	NRC-AA 8276 (AK-R 605)	India: Tamil Nadu, Tirunelveli District, KMTR	OR886489	OR888590	OR888631	OR888665	OR888698
Dravidoseps kalakadensis **sp. nov.**	NRC-AA 8277 (AK-R 606)	India: Tamil Nadu, Tirunelveli District, KMTR	OR886490	/	OR888632	OR888666	OR888699

Species	Voucher	Locality	GenBank accession number				
			16S	ND2	PRLR	R35	RAG1
Dravidoseps kalakadensis **sp. nov.**	BNHS 2830 (AK-R 700)	India: Tamil Nadu, Tirunelveli District, KMTR	OR886491	OR888591	OR888633	OR888667	OR888700
Dravidoseps kalakadensis **sp. nov.**	BNHS 2831 (AK-R 701)	India: Tamil Nadu, Tirunelveli District, KMTR	/	/	OR888634	/	OR888701
Dravidoseps srivilliputhurensis **sp. nov.**	NRC-AA 8279 (AK-R 1344)	India: Tamil Nadu, Virudhunagar District, SMTR, Ayyanar Kovil Falls	OR886492	OR888592	OR888635	OR888668	OR888702
Dravidoseps srivilliputhurensis **sp. nov.**	NRC-AA 8281 (AK-R 1345)	India: Tamil Nadu, Virudhunagar District, SMTR, Ayyanar Kovil Falls	OR886493	OR888593	/	/	/
Dravidoseps srivilliputhurensis **sp. nov.**	BNHS 2832 (AK-R 1434)	India: Tamil Nadu, Virudhunagar District, SMTR	OR886494	OR888594	OR888636	OR888669	OR888703
Dravidoseps srivilliputhurensis **sp. nov.**	BNHS 2833 (AK-R 1435)	India: Tamil Nadu, Virudhunagar District, SMTR	OR886495	OR888595	/	/	/
Dravidoseps srivilliputhurensis **sp. nov.**	BNHS 2836 (AK-R 1489)	India: Tamil Nadu, Virudhunagar District, SMTR, Atthi Kovil	OR886496	OR888596	OR888637	OR888670	OR888704
Dravidoseps srivilliputhurensis **sp. nov.**	BNHS 2837 (AK-R 1490)	India: Tamil Nadu, Virudhunagar District, SMTR, Atthi Kovil	OR886497	OR888597	/	/	/
Dravidoseps srivilliputhurensis **sp. nov.**	ZSI-R-28617 (AK-R 1516)	India: Tamil Nadu, Theni District, SMTR, Sathuragiri	OR886498	OR888598	OR888638	OR888671	OR888705
Dravidoseps srivilliputhurensis **sp. nov.**	ZSI-R-28618 (AK-R 1716)	India: Tamil Nadu, Theni District, SMTR, Chinna Suruli Falls	OR886499	OR888599	/	/	/
Dravidoseps srivilliputhurensis **sp. nov.**	(AK-R 1717)	India: Tamil Nadu, Theni District, SMTR, Chinna Suruli Falls	OR886500	OR888600	OR888639	OR888672	OR888706
Dravidoseps srivilliputhurensis **sp. nov.**	ZSI-R-28619 (AK-R 1761)	India: Tamil Nadu, Theni District, SMTR, Megamalai View Point	OR886501	OR888601	/	/	/
Dravidoseps srivilliputhurensis **sp. nov.**	ZSI-R-28620 (AK-R 1762)	India: Tamil Nadu, Theni District, SMTR, Megamalai View Point	OR886502	OR888602	/	/	/
Dravidoseps tamilnaduensis **sp. nov.**	NRC-AA 8287 (AK 739)	India: Tamil Nadu, Tiruchirappalli District, Pachaimalai	OR886503	OR888603	OR888640	OR888673	OR888707
Dravidoseps tamilnaduensis **sp. nov.**	NRC-AA 8288 (AK 740)	India: Tamil Nadu, Tiruchirappalli District, Pachaimalai	OR886503	OR888604	OR888641	OR888674	OR888708
Dravidoseps tamilnaduensis **sp. nov.**	NRC-AA 8286 (AK-R 2396)	India: Tamil Nadu, Tiruchirappalli District, Pachaimalai	OR886504	OR888605	OR888642	/	/
Dravidoseps tamilnaduensis **sp. nov.**	ZSI-R-28692 (AK-R 2724)	India: Tamil Nadu, Namakkal District, Kolli Hills	/	OR888606	OR888643	OR888675	OR888709
Dravidoseps tamilnaduensis **sp. nov.**	ZSI-R-28693 (AK-R 2725)	India: Tamil Nadu, Namakkal District, Kolli Hills	OR886505	OR888607	/	/	/
Dravidoseps tamilnaduensis **sp. nov.**	ZSI-R-28695 (AK-R 2734)	India: Tamil Nadu, Salem District, nr. Madu Falls	OR886506	OR888608	OR888644	OR888676	OR888710
Dravidoseps sp. Kalrayan	AK-R 2379 (tissue sample only)	India: Tamil Nadu, Villupuram District, Kalrayan Hills	OR886507	OR888609	OR888645	OR888677	OR888711
Subdoluseps bowringii	FMNH 261839	Cambodia	MK414544	MK414544	MK409442	MK409498	MK409526
Subdoluseps bowringii	JAM 1893	Malaysia	/	JQ610822	/	/	/
Subdoluseps frontoparietalis	ZMKUR 705	Thailand	/	/	MK409454	MK409509	MK409539
Subdoluseps malayana	LSUHC 12098	Malaysia	MG020473	/	MK409456	MK409514	MK409541
Subdoluseps samajaya	CAS 259777	Indonesia	MG020475	/	MK409457	MF981876	MK409542
Eutropis dissimilis	MVZ 248450	Pakistan	KX364958	KX364958			
Eutropis macularia	CAS 247949	Myanmar	KX231450	/			
Eutropis multifasciata	KU 337427	Phillipines	MK414566	MK414566	MK409460	MK409520	KX231381
Trachylepis boulengeri	PEMR 16179	Tanzania	/	/	/	/	MK791864
Trachylepis capensis	CAS 234152	South Africa	MK792005	MG605159	KC345131		
Trachylepis perrotetii	KU 291923	Guinea	/	/	JF498450	JF498450	/

Table 2. Primers and annealing temperature used for PCR amplification and sequencing.

Gene	Primers	Sequence (5' – 3')	Annealing temperature	Source
16S	16Sar-L	CGCCTGTTTATCAAAAACAT	50°C	Palumbi et al. (1991)
	16Sbr-H	CCGGTCTGAACTCAGATCACGT		
ND2	L4437	AAGCTTTCGGGCCCATACC	50°C	Macey et al. (1997)
	H5540	TTTAGGGCTTTGAAGGC		
PRLR	PRLR.F1	GACARYGARGACCAGCAACTRATGCC	53°C	Townsend et al. (2008)
	PRLR.R3	GACYTTGTGRACTTCYACRTAATCCAT		
R35	R35.F	GACTGTGGAYGAYCTGATCAGTGTGG	53°C	Fry et al. (2006)
	R35.R	GCCAAAATGAGSGAGAARCGCTTCTG		
RAG1	RAG1SKF2	TTCAAAGTGAGATCGCTTGAAA	53°C	Portik et al. (2010)
	RAG1SKR1200	CCCTTCTTCTTTCTCAGCAAAA		

Table 3. Uncorrected pairwise ND2 sequence divergence (below diagonal, maximum ND2 intra-lineage divergence in bold along diagonal) and number of differences in concatenated nuclear sequence data (above diagonal) between species of *Dravidoseps* **gen. nov.** and *Subdoluseps bowringii*.

	Species	1	2	3	4	5	6	7	8	9
1	*D. gingeeensis* **sp. nov.**	**1.6**	12	24	25	8	23	16	11	4
2	*D. jawadhuensis* **sp. nov.**	17.0	/	29	30	14	30	21	13	14
3	*D. kalakadensis* **sp. nov.**	19.4	20.7	**1.0**	1	27	34	5	21	27
4	*D. srivilliputhurensis* **sp. nov.**	18.5	19.4	11.5	**3.0**	28	33	5	22	27
5	*D. tamilnaduensis* **sp. nov.**	14.1	14.0	19.5	18.9	**5.0**	28	18	14	5
6	*D. goaensis* **comb. nov.**	18.9	19.1	21.3	19.7	17.4	**3.3**	25	29	28
7	*D. nilgiriensis* **comb. nov.**	21.1	21.2	14.0	13.8	19.5	18.6	**4.3**	13	18
8	*D. pruthi* **comb. nov.**	14.8	14.7	18.3	17.9	14.0	17.1	19.3	**5.1**	12
9	*D.* sp. Kalrayan	14.6	14.5	19.4	17.9	10.5	18.6	19.5	13.7	/
10	*S. bowringii*	21.9	23.7	23.0	21.9	23.3	23.2	23.0	22.2	23.4

Phylogenetic analyses

The monophyly of *Subdoluseps*, and the sister relationship between Indian and Southeast Asian *Subdoluseps* was well supported in previous studies (Freitas et al. 2019; Freitas 2020), and was confirmed in preliminary analyses (see divergence dating section below). We thus restricted phylogenetic reconstructions to *Subdoluseps*, using members of the Mabuyini as outgroups (Table 1; 16S sequence MK414558 for *Subdoluseps frontoparietalis* (Taylor) (ZMKUR705) was excluded as a BLAST search places it with *Riopa* and not *Subdoluseps*).

We subset our molecular datasets for three separate analyses: the first including each marker separately, the second concatenating only nuclear data, and the third concatenating all protein-coding genes genes (ND2 + nuclear DNA). The best-fitting partitioning schemes and models of sequence evolution were calculated for each gene fragment partitioned by codon (with a single partition for 16S) in PartitionFinder 2.1.1 (Lanfear et al. 2016) with linked branch lengths and selection based on the Bayesian information criterion (BIC) (Table S2). We reconstructed phylogenetic relationships using Maximum Likelihood (ML) in RaXML HPC 8.2.12 (Stamatakis 2014) and Bayesian inference (BI) in MrBayes 3.2.7 (Ronquist and Huelsenbeck 2003). ML analyses had the GTR + G + I model applied to the partitioned data, with 10 independent ML runs and support assessed through 1000 rapid bootstraps. Partitioned BI analysis used two parallel runs with four chains each (three hot and one cold) run for 2,000,000 generations, sampling every 200 generations. Convergence was determined based on inspection of log files in Tracer 1.7.2 (Rambaut et al. 2018; available at https://github.com/beast-dev/tracer/releases/tag/v1.7.2) and the standard deviation of split frequencies (<<0.01), the first 25% of trees were discarded as burn-in and a consensus tree was built using the sumt function.

Species delimitation

Our approach to species delimitation integrates multiple independent sources of data to demonstrate that each putative species is an independently evolving lineage (Dayrat 2005; de Queiroz 2007). Lineages had to first have support from both sources of molecular data to be considered putative species – mitochondrial DNA based species delimitation + fixed differences in at least one nuclear marker. All putative species that could then be morphologically diagnosed were considered new species (see below). For mtDNA delimitation, we used ND2 sequence data (16S was excluded on account of missing data) with two tree-based and one distance-based methods to delimit putative species. The tree-based methods, the single and multi-rate Poisson tree process (PTP and MPTP, respectively), attempt to differentiate between intra- and interspecific branching patterns to delimit species (Zhang et al. 2013; Kapli et al. 2017). These analyses were ran using ND2 trees as inputs with their outgroups trimmed and were carried out on web servers (https://mptp.h-its.org/#/tree) with default settings and a P-value of 0.001 for PTP. The distance-based method used a barcoding gap in mtDNA sequence data. Pairwise uncorrected ND2 p-distance for Indian *Subdoluseps* showed no divergence between 5.5–9.7 %, and this was used to determine the upper limit for intraspecific divergence (5.5 %) (see results).

We built median joining haplotype networks for each nuclear marker after excluding missing data with an epsilon setting of zero in Popart 1.7 (Bandelt et al. 1999; Leigh and Bryant 2015). These allowed us to visualize the distribution of nuclear haplotypes among mtDNA lineages that were separated by the barcoding gap/ species delimitation analyses. We additionally analysed the nuclear markers to find variable sites between putative species using DNAdiagnoser (Vences et al. 2021). Nucleotide positions used in diagnoses are relative to published sequences of *Subdoluseps samajaya* (Karin, Freitas, Shonleben, Grismer, Bauer & Das) (PRLR: MK409457; RAG1: MK409542; R35: MF981876).

Divergence dating

The molecular dataset for divergence dating included a single lineage each per putative species of Indian *Subdoluseps*, with a relatively dense sampling of the Lygosomini (after Freitas et al. 2019; Freitas 2020), and representatives of most skink subfamilies and tribes (after Shea 2021) and the Cordyliformes (Cordylidae, Gerrhosauridae + Xantusiidae) for ND2 and partial fragments of 16S, PRLR, and RAG1 (R35 was excluded because of large amounts of missing data) for a total of 62 taxa (Table S1). We used chimeric sequences for some outgroup taxa when the same individual or species did not have data for all four genes (Table S1). We used seven fossils as calibration points for the most recent common ancestor (MRCA) of various nodes within the Scincidae, assigning exponential prior distributions and an arbitrary mean of 10. The root was calibrated using the oldest Scincoidea fossils (*Eoscincus*, *Microtera*; 150–145 Mya; Brownstein et al. 2022); the MRCA of cordyliformes (Contogeniidae; 99.6–93.5 Mya; Noonan et al. 2013; Blair et al. 2015); the MRCA of Scincidae (based on a partial dentary of a possible scincid DMNH EPV.119554 from the lower Kirtland formation (75 Mya); Woolley et al. 2020); the MRCA of *Oligosoma* Girard (based on the oldest material from the St. Bathans formation; 19–16 Mya; Lee et al. 2009); the MRCA of *Chalcides* Laurenti (*Chalcides augei*; 16–13.7 Mya; Čerňanský et al. 2019); the MRCA of *Egernia* Gray (*Egernia gillespieae*; 14.8 Mya; Thorn et al. 2019); and the MRCA of *Tropidophorus* Duméril & Bibron (*Tropidophorus bavaricus*; 16 Mya; Bohme 2010). Genes were not partitioned by codon due to a lack of convergence after even >100 million generations (ESS < 200, not shown) and instead the dataset was partitioned by gene (with ND2 3rd codon position in a separate partition) resulting in five partitions varying in length from 346–1021 bp. The optimal partitioning scheme and models of sequence evolution were selected in PartitionFinder2 with linked branch lengths and selection based on BIC (Table S2; Lanfear et al. 2016). Divergence times were estimated in BEAST 1.10.4 (Drummond et al. 2012; Suchard et al. 2018) using a Yule speciation tree prior, linked trees, and a separate substitution model and uncorrelated relaxed lognormal clock model for each partition, with 50 million generations sampled every 5,000. Convergence was determined using the criteria ESS>200 by examining log files in Tracer 1.7.2, after removing the first 25% of trees as burn-in. A maximum clade credibility tree was built in TreeAnnotator v1.10.4 (Drummond et al. 2012) using the post burn-in trees. Median ages rounded off to the nearest million years are presented with 95 % HPD in parentheses.

Niche evolution and ancestral area reconstructions

We extracted climate data using BIOCLIM variables (WorldClim version 2.1 climate data for 1970–2000; Booth et al. 2014; Fick and Hijmans 2017) and canopy cover (Hansen et al. 2013) for *Subdoluseps* in order to contrast the environmental regimes occupied in India and Southeast Asia, with localities sourced from our collections and GARD 2.0 (Global Assessment of Reptile Distributions group; http://www.gardinitiative.org; an updated version of Roll et al. 2017). We excluded two published *Subdoluseps* localities from Bangladesh which we reidentified as *Riopa albopunctata* Gray based on photographs (Mahony and Reza 2007; Rabbe et al. 2022) and all localities for Southeast Asian *Subdoluseps* that are unpublished (e.g. from VertNet/ iNaturalist/ GBIF) as there is inadequate sampling for *Subdoluseps* across Southeast Asia and it is unclear if all these records represent *Subdoluseps* or potentially *Lygosoma* and *Riopa* species. In total we retained 44 unique localities for India and 84 for Southeast Asia (Table S3). We also checked localities individually against satellite imagery on Google Maps (https://www.google.com/maps) and moved some locations in Southeast Asia from the ocean/water bodies to the nearest point on land, and deleted imprecise type localities and points in cities. Our resultant distribution closely matches the map in Freitas (2020: 168, fig. 1). Climate variables were selected that describe the mean, range and variability of temperature and precipitation: BIO1 (annual mean temperature), BIO4 (temperature seasonality), BIO5 (maximum temperature of the warmest month), BIO6 (minimum temperature of the coolest month), BIO12 (annual precipitation), and BIO15 (precipitation seasonality). Boxplots in conjunction with an ANOVA and Tukey HSD tests were used to visualize positions of Indian and Southeast Asian *Subdoluseps* in climate space and to determine if these are significantly different for climatic variables describing temperature (average, extreme and variability) and precipitation (annual and variability).

We designated three ancestral areas for the Lygosomini – India (the Indian subcontinent west of Myanmar), Southeast Asia (all areas east of Myanmar), and Africa using trimmed trees from the divergence dating analysis for biogeographic analyses. *Riopa albopunctata* was coded as being distributed in India, where it has a wide distribution, as no sequences or voucher specimens are available to confirm records from Southeast Asia (Geissler et al. 2011). A subset of 1000 trees were used to build a consensus tree using 100 random trees in RASP 4.3 (Yu et al. 2015). We reconstructed ancestral areas using the Bayesian Binary Markov Chain Monte Carlo (MCMC) model (BBM; Yu et al. 2015) with fixed state frequencies, equal among site variation, temperature of 0.1 and 10 chains with a sample frequency of 1000 across 1,000,000 generations with a 10% burn-in. We considered an ancestral area well-supported when its highest probability was at least two-times higher than the next ranked area.

Morphological data

The morphological dataset comprises 58 characters from 89 specimens from Maharashtra and Tamil Nadu including topotypical material for *S. nilgiriensis*, *S. pruthi* and *L. goaensis* and the type series of *S. nilgiriensis*. The types of *S. pruthi* and *R. goaensis* could not be traced in the collection of the ZSIK (Das et al. 1998; Ganesh et al. 2021; Pratyush Mohapatra pers. comm. 2023), and we designate neotypes for these species to stabilize the taxonomy of the group and permit comparisons. We recorded colour pattern from live photographs of specimens and a single observer (AK) recorded morphological data under a ZEISS Stemi 305 stereo dissecting microscope on the left side of the body whenever possible, with bilateral scale counts taken on both sides of the head, and measurements taken using a Mitutoyo digital calliper (to the nearest 0.1 mm). When summarizing morphological data, means (in mm) are presented ± standard deviation (range). Scale nomenclature follows Grismer et al. (2019) (Fig. 2). We took the following measurements (after Grismer et al. 2019): snout vent length (**SVL**, from tip of the snout to cloacal opening); tail length (**TL**, from cloaca to tail tip); tail width (**TW**, measured at tail base); forearm length (**FL**, from elbow to distal end of wrist); crus length (**CL**, from knee to heel); axilla to groin length (**AGL**, from posterior margin of forelimb insertion to anterior margin of hindlimb insertion); body height (**BH**, maxi-

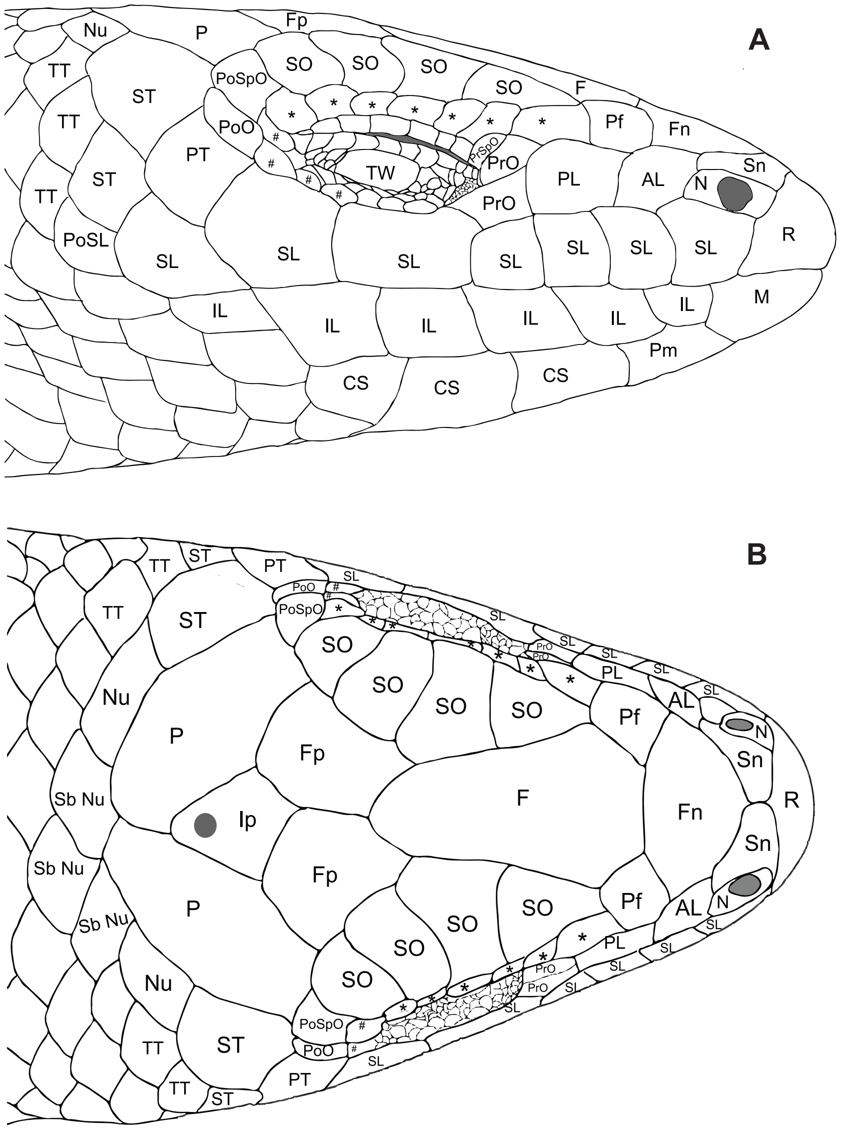

Figure 2. Line drawing of head of *Dravidoseps pruthi* **comb. nov.** (neotype, NRC-AA-1291): **A** dorsal and **B** lateral view. Scale nomenclature is after Grismer et al. (2019). AL = anterior loreal, CS = chin shields; F = frontal, Fn = frontonasal, Fp = frontoparietal, IL = infralabial, Ip = interparietal, M = mental, N = nasal, Nu = nuchal, P = parietal, Pf = prefrontal, PL = posterior loreal, Pm = postmental, PrO = preocular, PT = primary temporal, PoSL = postsupralabial, PoSpO = postsupraocular (maybe homologous to the last superciliary of Taylor (1935), PoO = postocular, R = rostral, SL = supralabial, SO = supraocular, ST = secondary temporal, and TT = tertiary temporal. * = superciliary and # = postsubocular. This specimen is missing the presubocular on this side of the head.

mum height of body); body width (**BW**, maximum width of body); head length (**HL**, distance between retroarticular process of lower jaw and snout tip); head width (**HW**, maximum width of head); head height (**HH**, maximum height of head); eye diameter (**ED**, greatest horizontal diameter measured between median canthus); transparent window diameter (**TWD**, greatest horizontal diameter of transparent window on lower eyelid); eye to ear distance (**EE**, distance from anterior edge of ear opening to posterior margin of eye); ear length (**EL**, maximum length of ear opening); eye to snout distance (**ES**, distance between anterior margin of eye and tip of snout); eye to nares distance (**EN**, distance between anterior margin of eye and posterior edge of nostril); internarial distance (**IN**, distance between nares); interorbital distance (**IO**, shortest distance between left and right supraciliary scale rows in front of orbit).

Meristic data recorded were supraoculars (**SO**, number of supraocular scales); supraoculars contacting frontoparietal (**SO** contacting **FP**, number of supraoculars in contact with frontoparietal); Nuchals (**Nu**, number of elongated scales behind parietals and between first secondary temporals, excluding smaller scales forming continuous paravertebral rows behind the parietals); scales between nuchals (**Sb Nu**, number of transverse paravertebral scales behind parietals counted between enlarged, elongated nuchals); supraciliary scales (**SC**, number of supraciliary scales counted between prefrontal and post-supraocular above eye); loreals (**LO**, number of loreal scales); pre-supraoculars (**PrSpO**, number of pre-supraoculars); preoculars (**PrO**, number of preoculars); pre-suboculars (**PrSbO**, number of pre-suboculars); post-supraoculars (**PoSpO**, number of post-supraoculars); postoculars (**PoO**, number of postoculars); post-suboculars (**PoSbO**, number of post-suboculars); post-supralabials (**PoSL**, number of scales posterior to and contacting last supralabial, excluding temporals); primary temporals (**PT**, number of primary temporals – scales behind eye and above SL); secondary temporals (**ST**, number of secondary temporals – scales in contact with PT but excluding PoSL); tertiary temporals (**TT**, number of tertiary temporals – scales in contact with ST excluding Nu); the number of supralabials and infralabials (**SL** and **IL**, from rostral and mental, respectively, to the posterior-most enlarged scale at the mouth opening; number indicated by Roman numerals); ear lobules (**Elo**, number of ear lobules); chin shields (**CS**, number of enlarged chin shields); paravertebral scales (**PVT**, number of scales between the nuchals/parietals to immediately above the cloaca counted in a straight line immediately left or right of the vertebral column); round the body scales (**RBS**, number of scales around the body counted at mid-body); ventral scales (**VS**, number of scales counted in a straight line between the first pair of chin shields to the anterior border of the cloaca); scales on precloacal row (**SPCLR**, number of enlarged scales on the last row above the cloaca counted between hindlimb insertions); round the tail scales (**RTS**, number of scales around the tail counted at the 10^{th} subcaudal scale); transverse subdigital lamellae which are wider than high, counted from the base of the digits to the apical end on finger 1 (**LamF1**), finger 4 (**LamF4**), toe 1 (**LamT1**), and toe 4 (**LamT4**).

Additional categorical characters evaluated were supranasals/ prefrontals/ nuchals in contact with each other or separated, frontoparietal/ nasal divided or undivided, presence or absence of transparent disk on lower eyelid, enlarged supralabial below eye, and smooth versus keeled scales on body/ tail dorsum/ lateral sides of tail base.

We also dissected a number of specimens to determine sex and examine the presence of developing eggs/ embryos. Individuals with a yellow throat and flank colouration in life were determined to be adult males.

We cleared and stained one adult female and three subadult Indian *Subdoluseps* in order to determine the nature of the secondary palate (open versus closed, sensu Greer 1977) following the protocols of Hanken and Wassersug (1981). We compared the palatine and pterygoid bones in these specimens with figures in Greer (1977) as well as photographs of the skull of *Subdoluseps bowringii* (Günther) from the Field Museum of Natural History, (FMNH 196173). It turns out that the vial bearing the number FMNH 196173 contains three skulls that appear similar, but we were unable to determine individual specimen numbers (Joshua Mata, pers. comm).

Morphological analyses

We searched for diagnostic morphological characters between lineages that fulfilled the mtDNA and nucDNA species delimitation criteria (see species delimitation section above) that were represented by specimens (all lineages except the tail-tip from Kalrayan). Every locality we sampled had a single *Subdoluseps* mtDNA + nucDNA lineage except for the Kolli Hills (Namakkal District, Tamil Nadu), which included two. Non-genotyped specimens from all populations were assigned to their respective mtDNA lineage, except for NRCAA-8289 (AK-R 2727) from the Kolli Hills which could not be confidently assigned to a population based on morphology. We included only what we considered adults (> 70% of maximum SVL for all species or ≥ 40 mm, n = 64) for analyses of mensural data, which included the characters SVL, AGL, CL, EE, ES, HL, HW and IO. Mensural data were allometrically size-adjusted using Thorpe's (1975) equation that standardizes variables by SVL using the formula: $X_{adj} = \log(X) - b[\log(SVL) - \log(SVL_{mean})]$, where X_{adj} = adjusted value; X = measured value; b = unstandardized regression coefficient for each population; and SVL_{mean} = overall average SVL of all populations in the R 4.1.3 (R Core Team 2021) package GroupStruct (available at https://github.com/chankinonn/GroupStruct) (Chan and Grismer 2021, 2022). We used SVL across all species combined as this clade comprises similarly sized species (maximum SVL of all lineages 50–58 mm) and pooled sexes because there was no apparent sexual dimorphism (sexes did not separate in analyses of single species with high sample sizes, not shown). A principal component analysis (PCA) was conducted to determine separation of lineages in multivariate morphospace based on the size-corrected mensural data using the ez_pca() function in GroupStruct. For meristic characters that showed variation (LAM4T, PVS, RBS, RTS, SPCLR, VS) we visualized the data using boxplots and compared means using a one-way ANOVA followed by a Tukey HSD test to determine which populations differed significantly. Only characters with non-overlapping ranges, and/or significantly different means were used in species diagnoses.

Results

Phylogenetic relationships and patterns of distribution

Analyses of the concatenated molecular dataset, with an expanded sampling of skinks, recovered a well-supported Lygosomini and a monophyletic *Subdoluseps* (Figs 3, S1). The same broad clades were recovered as by Freitas et al. (2019), including *Lamprolepis* Fitzinger in Treitschke, *Lygosoma*, *Mochlus*, *Riopa*, and *Subdoluseps*. *Subdoluseps* was consistently recovered as the sister taxon to the clade comprising *Mochlus* + *Riopa*, with southeast Asian *Subdoluseps* reciprocally monophyletic with respect to Indian *Subdoluseps* (Figs 3, S1, S2). A basal split within Indian *Subdoluseps* separates a Western Ghats clade from another clade which includes *R. goaensis* from the Northern Western Ghats as the sister taxon to five divergent mitochondrial lineages from hills of peninsular India including *S. pruthi* (Figs 3, 4). The Western Ghats clade include three divergent mitochondrial lineages from the Central and Southern Western Ghats, including the named species *S. nilgiriensis*. The 16S tree recovers a similar topology to the ND2 tree, except that one individual from the Srivilliputhur-Megamalai Tiger Reserve (SMTR) lineage falls outside the Western Ghats clade, and the Jawadhu lineage is nested within *S. pruthi* (Fig. S2). Trees based on the concatenated nuclear data and individual nuclear markers are discussed below (see Species Delimitation).

The Indian *Subdoluseps* clade includes nine lineages (Figs 3, 4). The lineage from the Kalrayan Hills is known from a single locality; a lineage in Jawadhu Hills and another in Gingee are known from two closely spaced lo-

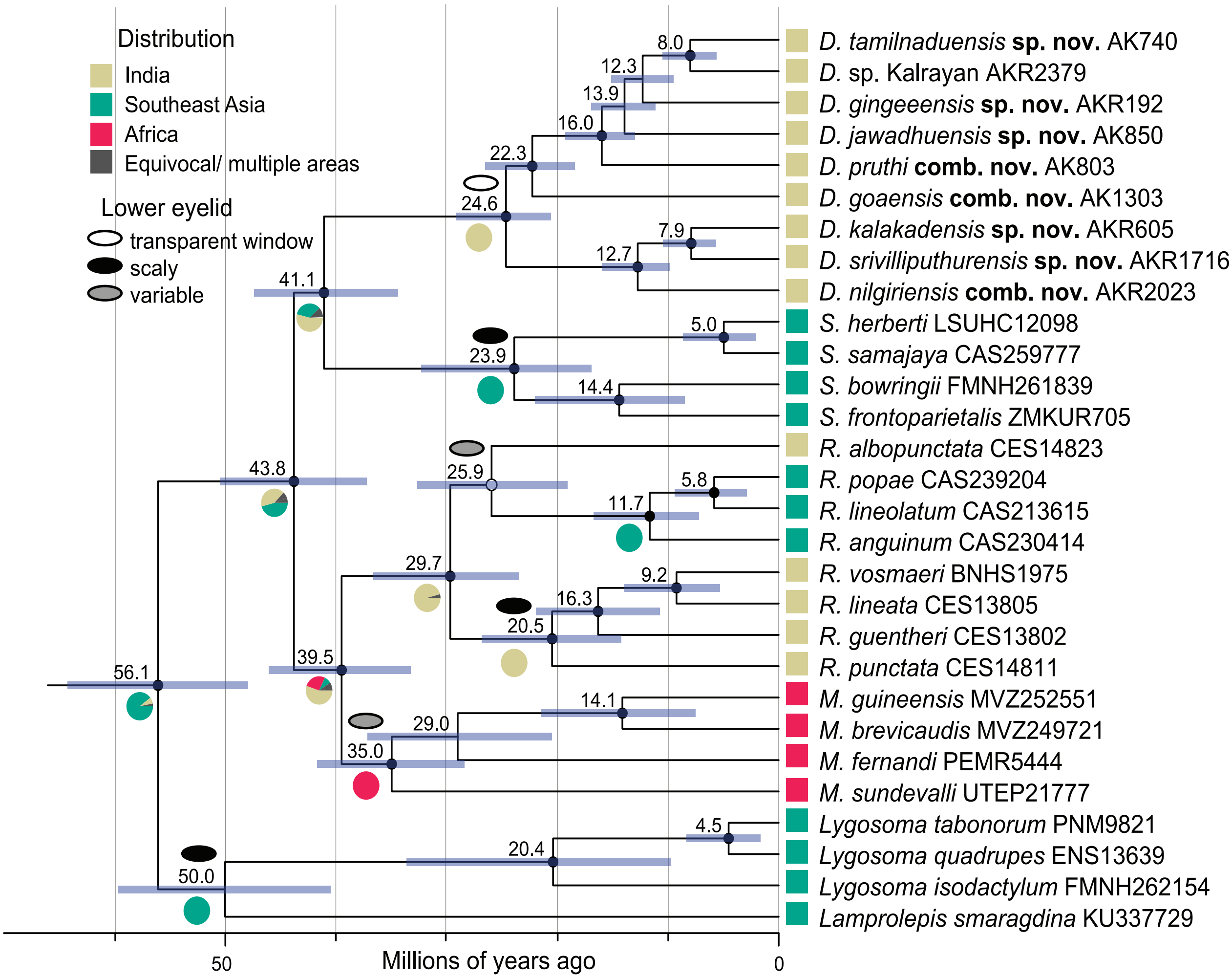

Figure 3. Timetree for the Lygosominae. Numbers at nodes are median node age and bars 95 % HPD; solid black circles indicate posterior probability ≥0.99 + bootstrap support ≥ 80% and open circle posterior probability 0.97 + no bootstrap support; colored circles below nodes represent reconstructed ancestral areas and colored squares indicate distributional ranges; ovals indicate condition of the lower eyelid.

calities each (3 km and 27 km apart, respectively); another lineage is spread across the isolated massifs of Kolli, southern Yercaud and Pachaimalai; *S. pruthi* was recorded from Sitteri, northern slopes of Yercaud, Palamalai and Vanavasi; *R. goaensis* from four localities in southern Maharashtra and Goa including close to the type locality; one of the Western Ghats lineages from six localities around SMTR; a second from Kalakad-Mundanthurai Tiger Reserve (KMTR); and finally *S. nilgiriensis* is the most widely distributed lineage, represented by eight localities from Sirumalai, the Palani, Anaimalai, and Nilgiri hills, the southern edge of the Mysore Plateau, and even the Kolli Hills (Fig. 1).

Species delimitation

Uncorrected pairwise ND2 sequence divergences between Southeast Asian and Indian *Subdoluseps* range from 21.9–23.7 %, and up to 21.3 % within Indian *Subdoluseps*. A barcoding gap is seen between 5.5–9.7 %, suggesting a total of nine putative species with sequence divergence ≥ 5.5 % (Fig. 4, Table 3). The tree-based species delimitation methods suggested 9–11 lineages (Fig. 4). Each of the nine putative species recognized in the barcoding analysis and by PTP delimitations methods have fixed differences from all other lineages in at least one nuclear marker (Fig. 4; Table 3, Table S4). The KMTR and SMTR lineages share PRLR and R35 haplotypes, and sp. Kalrayan shares PRLR and R35 haplotypes with the Kolli-Pachaimalai-Yercaud lineage and RAG-1 haplotypes with the Gingee lineage. *Subdoluseps nilgiriensis* does not share any nuclear haplotypes with other lineages and is paraphyletic in PRLR and RAG-1 networks with respect to the two other southern Western Ghats clade species. The same pattern is seen in the concatenated nuclear tree, where all species are monophyletic except for *S. nilgiriensis* (Fig. S1). There are 29 fixed differences in the nuclear dataset between peninsular India and Southeast Asian *Subdoluseps* (Table S4).

Divergence times

The time of divergence between the Scincidae and the Cordyliformes was estimated at 147 (154–145) Mya, and the most recent common ancestor (MRCA) of the Scincidae at 101 (113–89) Mya (Fig. S1). The Lygosomini began diversifying 56 (64–48) Mya and the clade including *Lepidothryis*, *Mochlus*, *Riopa*, and *Subdoluseps* 44 (50–37) Mya (Fig. 3). Southeast Asian and Indian *Subdoluseps* shared a MRCA 41 (47–34) Mya and diversification within each subclade began concurrently, 24 (32–17) Mya and 25 (29–21) Mya, respectively. The Western Ghats clade began diversifying 13 (16–10) Mya and the KMTR and SMTR populations split 8 (10–6) Mya, *S. goaensis* split from the remaining species in southern India 23 (27–18) Mya, and diversification within southern India is from 16–8 Mya. Our estimated divergence dates overlap with various skink and squamate phylogenies (e.g. Wiens et al. 2006; Skinner et al. 2011; Zheng and Wiens 2016; Freitas 2020; Brownstein et al. 2022) as do the estimated mean mtDNA rates (16S, 0.294 % per Mya; ND2 cp1+cp2 0.246 % per Mya; ND2 cp3 2.17 % per Mya versus ND2 0.47 % Mya in Portik et al. 2011; 0.48–1.31% Mya Barley et al. 2015); but are considerably older than a recently published genus level timetree that used secondary calibrations (Ghosh et al. 2023).

Niche evolution and ancestral area reconstructions

Indian and Southeast Asian *Subdoluseps* occupy significantly different climate space based on ANOVA and Tukey HSD tests. In general, Indian *Subdoluseps* occur in regions with cooler average temperatures (BIO1, median 24.5°C versus 26.4°C), higher temperature seasonality and extremes, lower annual precipitation (BIO12, median 942 versus 2251) and higher precipitation seasonality, and canopy cover that ranges from 0–85 (median 33; 0–100 in Southeast Asia, median 90) (Fig. 5A–C), but overlapping summer temperatures (BIO 10, median 27.5°C versus 27.4°C).

The ancestral area of the Lygosomini was reconstructed as being Southeast Asia (probability 0.90), with equivocal reconstructions for the MRCA of *Mochlus* + *Lygosoma* and Indian and Southeast Asian *Subdoluseps* (Southeast Asia 0.46, India 0.41) and the MRCA of Indian and Southeast Asian *Subdoluseps* (India 0.56, Southeast Asia 0.32); while the MRCA of *Mochlus* + *Riopa* was reconstructed as being distributed in India (0.56) as was the MRCA of *Riopa* (0.95) (Fig. 3).

Morphology

The PCA of size-corrected mensural data showed no separation between the eight sampled lineages (the ninth lineage sp. Kalrayan was represented by a tail-tip only and is thus excluded from morphological analyses) of peninsular Indian *Subdoluseps* (Fig. 5D) across the first three principal components, which cumulatively explained 90 % of variance in the data, and neither did a PCA using simple ratios (trait/ SVL, not shown). Of the 39 meristic and categorical characters evaluated, 25 are either entirely conserved or non-informative within peninsular Indian *Subdoluseps*. The ANOVA and Tukey HSD showed that a few meristic characters vary consistently across lineages, the most important of which are Elo, PoSbO, PoSL, RBS, RTS and SPCLR (Fig. 6, Table 4).

Taxonomic account

All specimens of Indian *Subdoluseps* lineages and species that we sampled have a transparent window in the lower eyelid (Fig. 2), a historically important genus level diagnostic character in skinks (e.g. Mittleman 1952; Siler et al. 2011; Karin et al. 2016). The secondary palate of

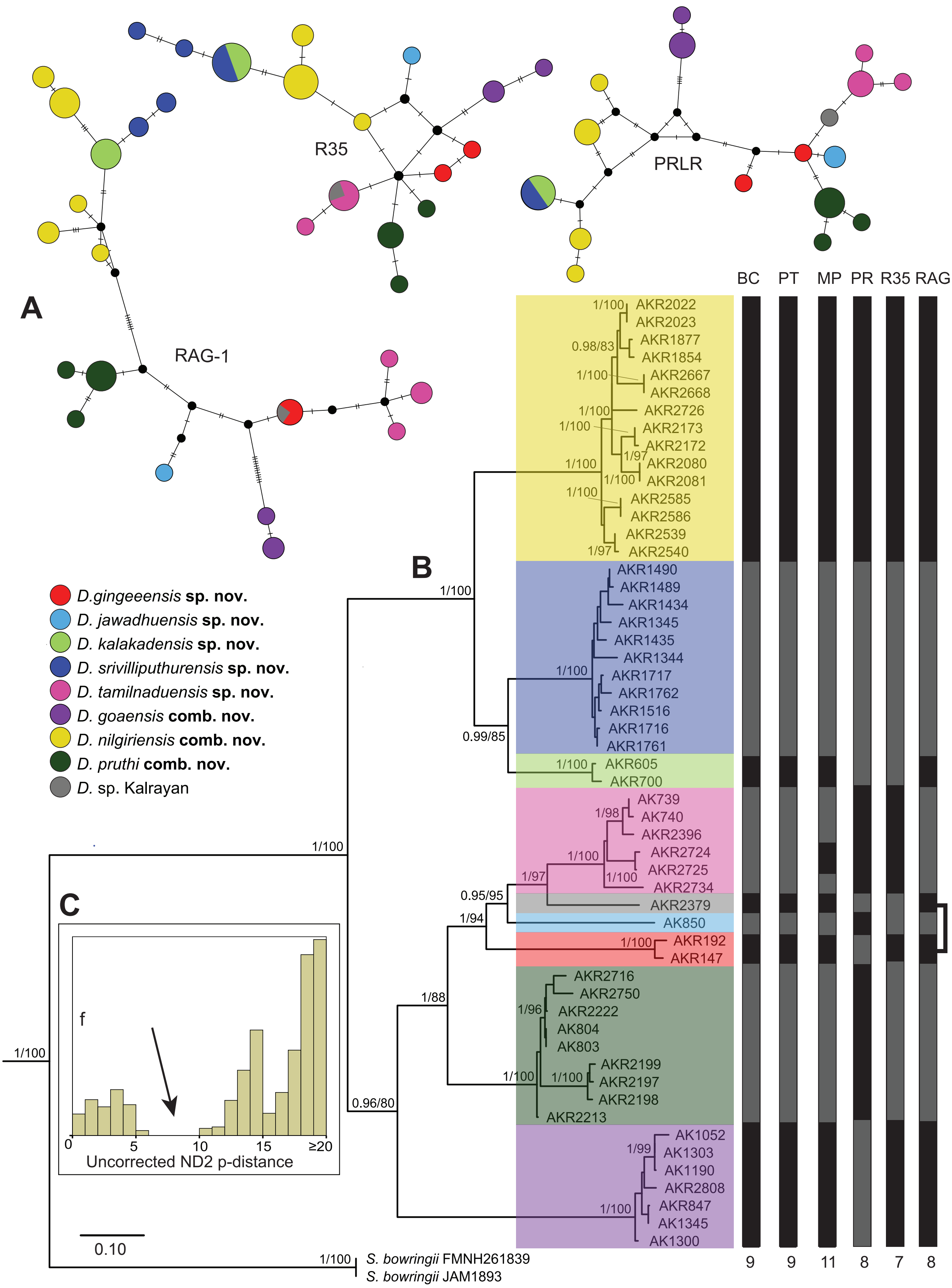

Figure 4. A Median joining networks of *Dravidoseps* **gen. nov.** for three nuclear markers, nodes scaled by haplotype frequency, hatch marks on connecting lines indicate mutations and black circles indicate unsampled intermediate haplotype states. **B** Maximum likelihood ND2 phylogeny of *Dravidoseps* **gen. nov.** with posterior probability/ bootstrap support shown at nodes (outgroups not shown) and species delimitation results shown by alternating black and grey bars with total putative species below (BC, barcoding gap; PT, PTP; MP, mPTP; PR, PRLR; RAG, RAG-1), (square bracket indicates the two separated black squares are a single species). **C** Histogram of uncorrected pairwise ND2 sequence divergence within *Dravidoseps* **gen. nov.** with the barcoding gap marked by an arrow. Putative species are coloured as in Figure 1 on the networks and with transparent boxes on the mtDNA tree.

Indian *Subdoluseps* has the deep emargination of the palatal rami noted by Greer (1977: fig. 3) for the open palate (Fig. 7A) while three skulls in the vial of FMNH 196173 (Fig. 7D shows the skull in best condition) are similar to the closed palate. The deep emargination of the palatal rami is not seen in the subadults (Fig. 7B, C). The palatine bones do not project beyond the inner edge of the pterygoid, resembling *Mochlus tanae* (Loveridge, 1935) and *M. mabuiiformis* (Loveridge, 1935) (Greer 1977: fig. 3). The palatines are also not in contact, unlike in Greer's (1977) illustrations and FMNH 196173, perhaps an artefact of dried skulls (that Greer used) versus clear and stained specimens (AM Bauer pers. comm.) Additionally, we herein report the first instance of viviparity within peninsular Indian skinks and Indian Lygosomini. Of 23 adult specimens dissected representing five putative species, 16 turned out to be gravid females containing 2–4 embryos each, varying from early stages of development to almost fully developed (Fig. 8). Indian and Southeast Asian *Subdoluseps* show 29 fixed differences across the three nuclear markers and are consistently reciprocally monophyletic (Figs 3, S1, S2).

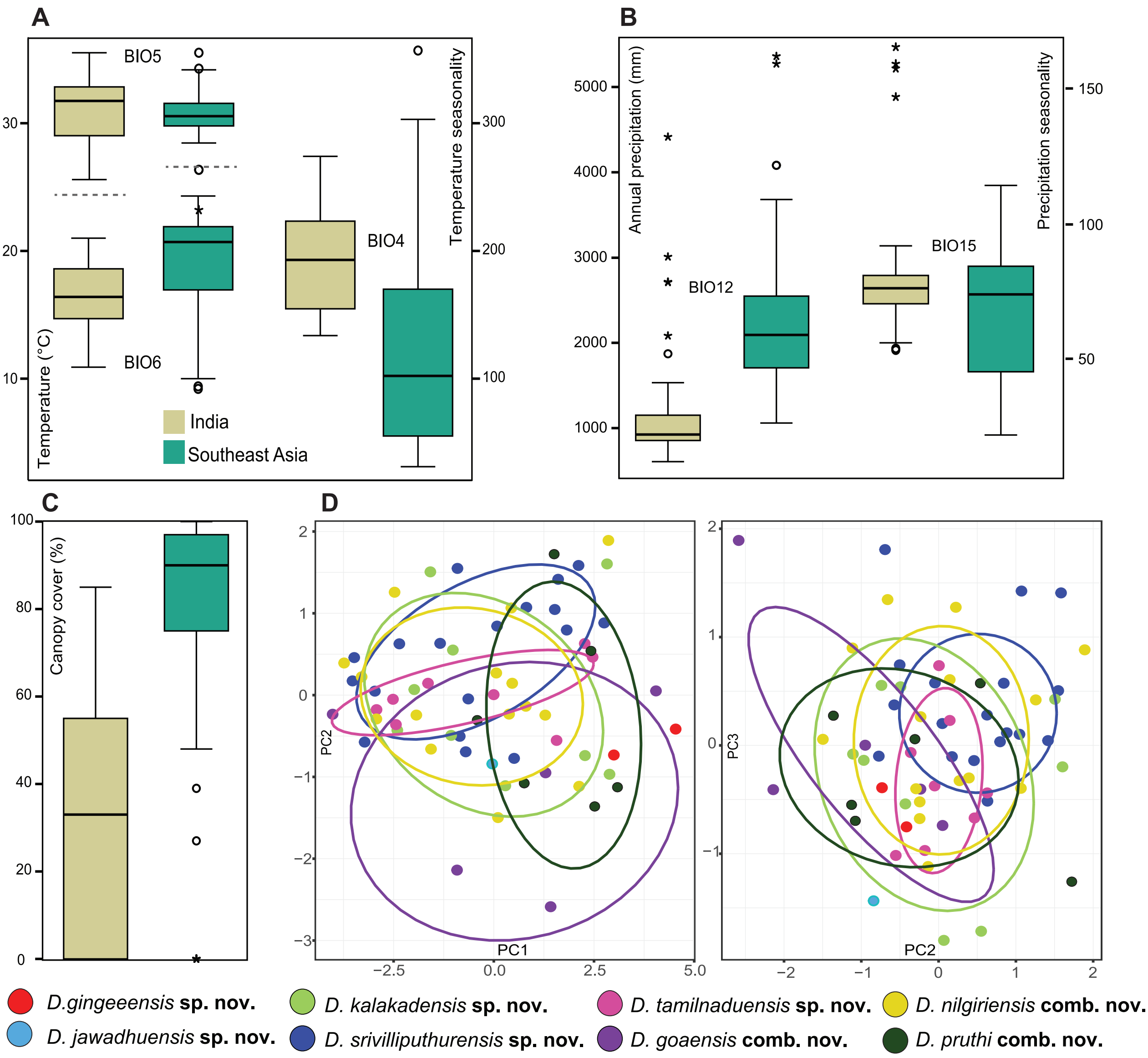

Figure 5. Boxplots of climate and canopy cover for *Dravidoseps* **gen. nov.** and *Subdoluseps*: **A** temperature; **B** precipitation; **C** canopy cover (circles are mild outliers and * are extreme outliers; dashed grey line in (A) is median annual temperature); and **D** plot of the first three Principal Components from a PCA of size-corrected mensural data for *Dravidoseps* **gen. nov.**

We recognize nine Indian lineages of *Subdoluseps*, supported both by the species delimitation analyses as well as fixed differences from all other lineages in at least one nuclear marker. We thus treat these nine lineages as representatives of putative species (apart from the lineage sp. Kalrayan, which does not include a voucher). Taken together, the phylogenetic, morphological, and ecological evidence all demonstrate that the Indian clade of *Subdoluseps* is highly divergent from the Southeast Asian clade, which includes the type species of the genus *S. bowringii*. We thus describe the Indian clade as a new genus and describe five new species below.

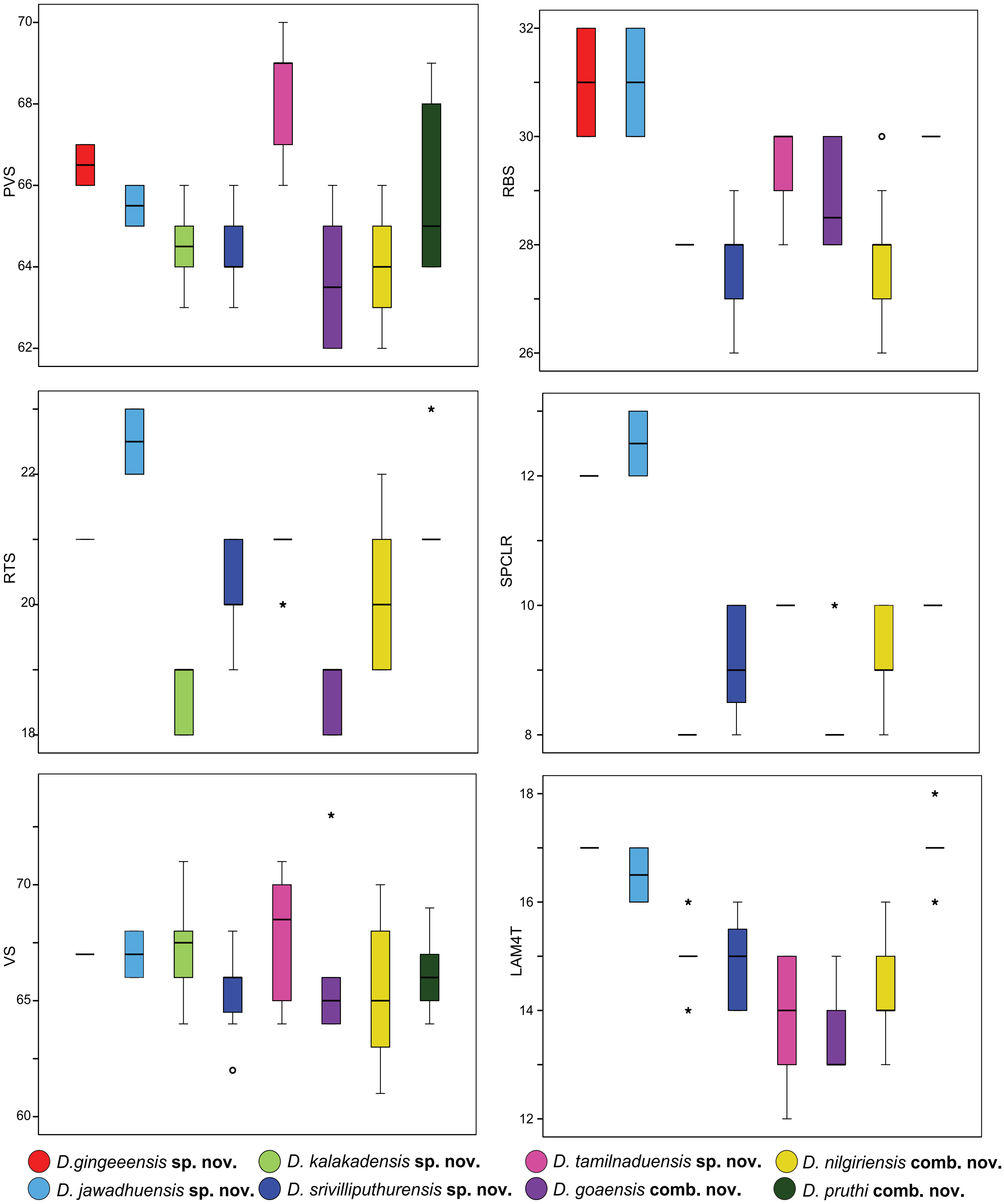

Figure 6. Boxplots of meristic data. Abbreviations as in methods.

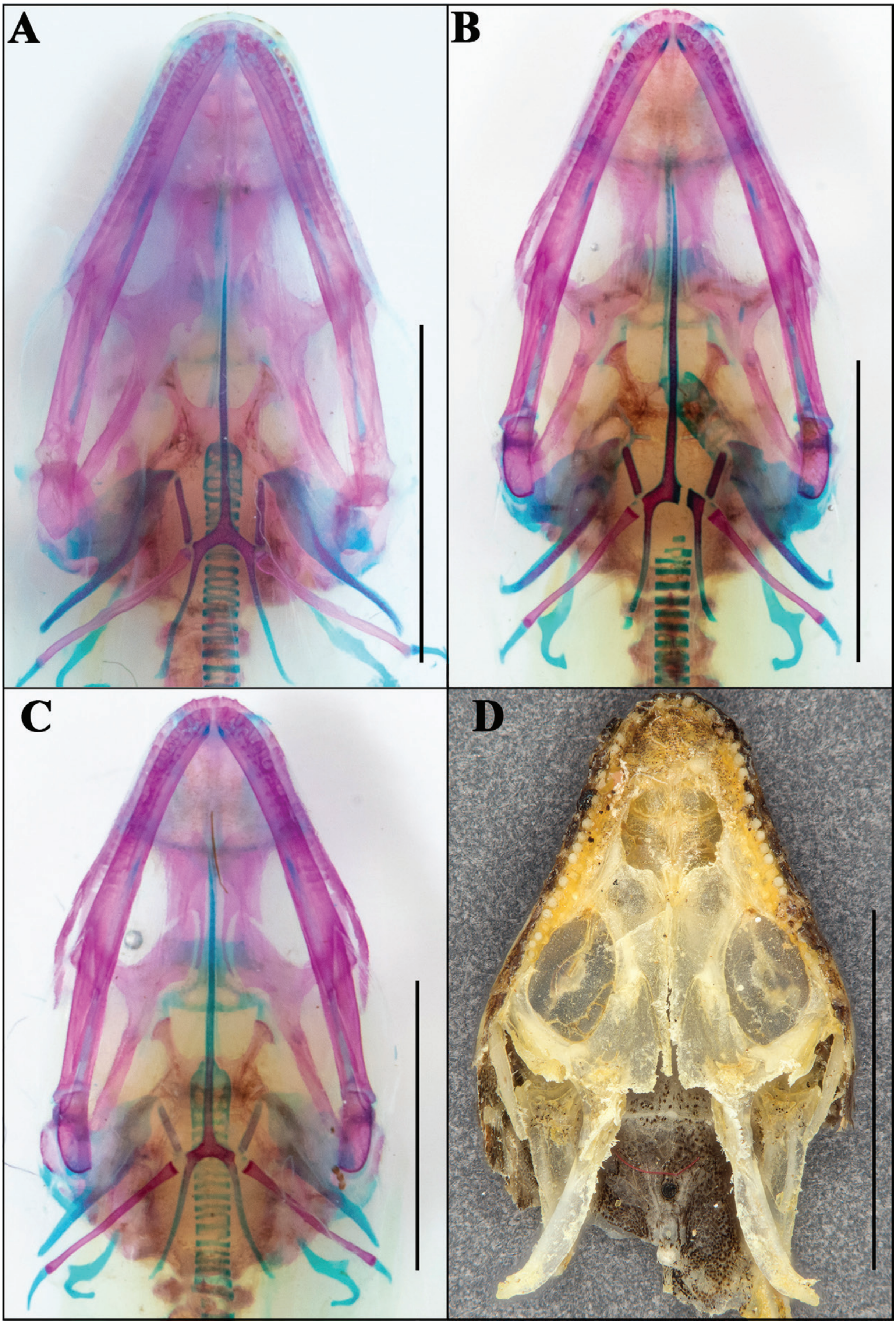

Figure 7. Ventral photos of cleared and stained specimens and one dry skull: **A** adult female *Dravidoseps nilgiriensis* **comb. nov.** (AKR 2586); **B** subadult *Dravidoseps srivilliputhurensis* **sp. nov.** (AKR 1763); **C** subadult *Dravidoseps srivilliputhurensis* **sp. nov.** (AKR 1717); **D** dry skull preparation of *Subdoluseps bowringii* (FMNH 196173). Photos by Akshay Khandekar (A–C) and Stephanie Ware (D).

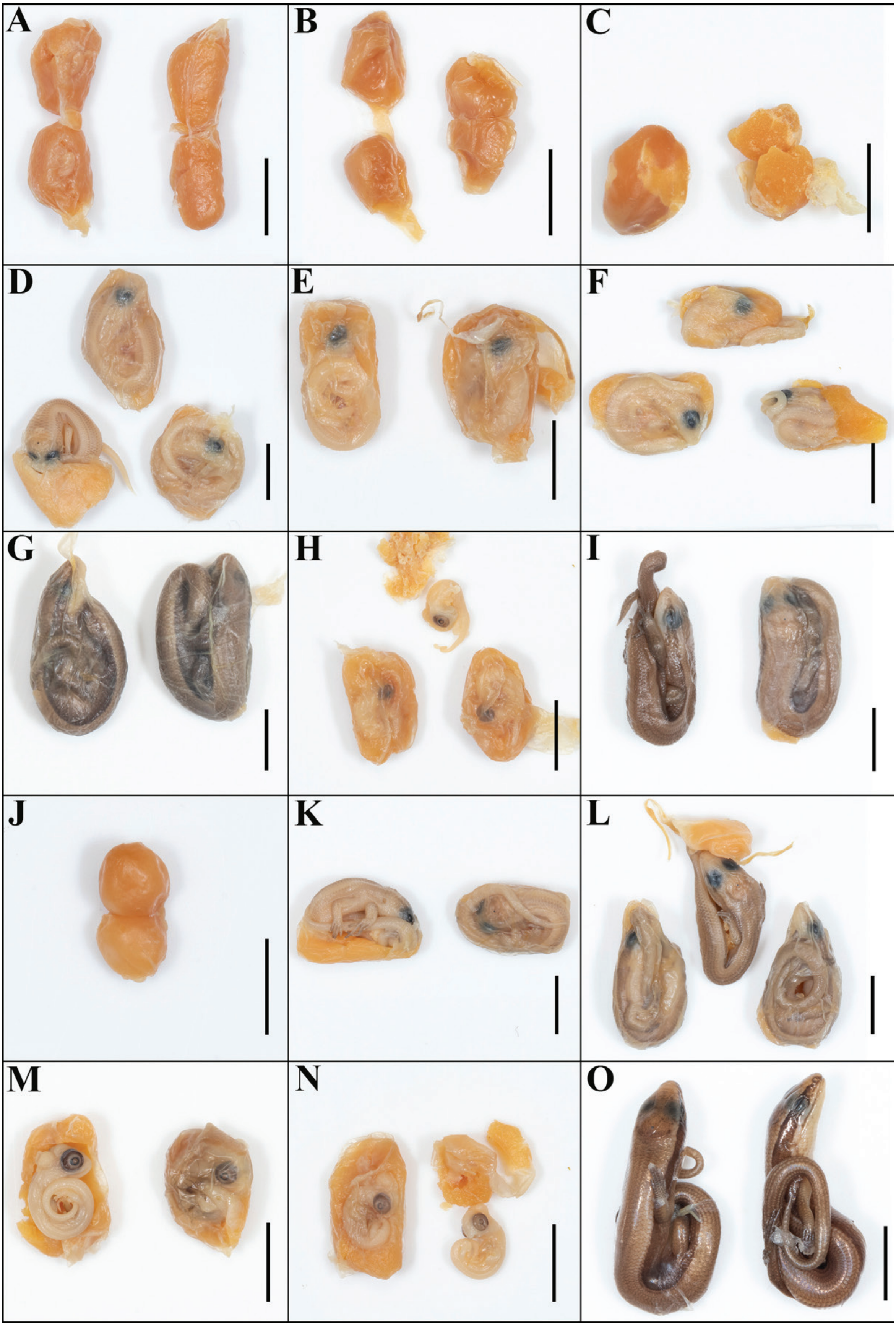

Figure 8. Embryos of *Dravidoseps* **gen. nov.** at different development stages: **A** two pairs in *D. goaensis* **comb. nov.** in early developmental stages (neotype, BNHS 2567); **B** two pairs in *D. gingeeensis* **sp. nov.** in early developmental stages (holotype, NRC-AA-8273); **C–E** various development stages of *D. kalakadensis* **sp. nov.** (paratypes, BNHS 2829, ZSI-R-28613, and ZSI-R-28615 respectively); **F–N** various development stages of *D. srivilliputhurensis* **sp. nov.** (paratypes, BNHS 2832, BNHS 2834, BNHS 2835, BNHS 2837–2839, NRC-AA-8284, NRC-AA-8285, ZSI-R-28618); **O** two almost completely developed in *D. tamilnaduensis* **sp. nov.** (paratype, BNHS 2859). Scale bars = 5 mm; photos by Akshay Khandekar.

Table 4. Summary of maximum SVL (mm) and meristic data for the eight lineages of *Dravidoseps* **gen. nov.**.

	D. gingeeensis **sp. nov.**	*D. jawadhuensis* **sp. nov.**	*D. kalakadensis* **sp. nov.**	*D. srivilliputhurensis* **sp. nov.**	*D. tamilnaduensis* **sp. nov.**	*D. goaensis* **comb. nov.**	*D. nilgiriensis* **comb. nov.**	*D. pruthi* **comb. nov.**
SVL	56.6	46.6	56.0	55.6	55.2	55.2	57.1	56.0
n	2	2	10	20	12	7	25	10
PVS								
mean ± SD	66.5 ± 0.71	65.5 ± 0.71	64.6 ± 0.97	64.5 ± 1.05	68.0 ± 1.48	64.1 ± 1.95	65.0 ± 2.03	66.7 ± 2.00
range (n)	66–67 (2)	65–66 (2)	63–66 (10)	63–66 (20)	66–70 (12)	62–67 (7)	62–70 (25)	64–69 (10)
RBS								
mean ± SD	31.0 ± 1.41	31.0 ± 1.41	28.0 ± 0.00	27.8 ± 0.79	29.6 ± 0.79	29.0 ± 1.00	28.1 ± 0.86	30.0 ± 0.00
range (n)	30–32 (2)	30–32 (2)	28 (10)	26–29 (20)	28–30 (12)	28–30 (7)	26–30 (25)	30 (10)
LAM4T								
mean ± SD	17.0 ± 0.00	16.5 ± 0.71	14.9 ± 0.57	14.8 ± 0.97	13.7 ± 1.07	13.4 ± 0.79	14.4 ± 0.76	16.1 ± 1.20
range (n)	17 (2)	16–17 (2)	14–16 (10)	13–17 (20)	12–15 (12)	13–15 (7)	13–16 (25)	14–18 (10)
VS								
mean ± SD	67.0 ± 0.00	67.0 ± 1.41	67.5. ± 2.12	65.7 ± 1.89	67.7 ± 2.42	66.2 ± 3.49	65.7 ± 2.70	67.0 ± 2.12
range (n)	67 (2)	66–68 (2)	64–71 (10)	62–70 (20)	64–71 (12)	64–73 (6)	61–71 (23)	64–70 (10)
SPCLR								
mean ± SD	12.0 ± 0.00	12.5 ± 0.71	8.0 ± 0.00	9.2 ± 0.77	10.0 ± 0.00	8.3 ± 0.76	9.2 ± 0.60	10.0 ± 0.00
range (n)	12 (2)	12–13 (2)	8 (10)	8–10 (20)	10 (10)	8–10 (7)	8–10 (21)	10 (10)
RTS								
mean ± SD	21.0 ± 0.00	22.5 ± 0.71	18.7 ± 0.52	20.3 ± 0.78	20.8 ± 0.40	18.7 ± 0.52	20.1 ± 1.07	21.4 ± 0.89
range (n)	21 (2)	22–23 (2)	18–19 (6)	19–21 (12)	20–21 (11)	18–19 (6)	19–22 (14)	21–23 (6)
PoSbO								
mean ± SD	3.5 ± 0.71	5 ± 0.00	3.7 ± 0.48	4.0 ± 0.22	3.8 ± 0.45	4.0 ± 0.00	3.9 ± 0.28	4.0 ± 0.00
range (n)	3–4 (2)	5 (2)	3–4 (10)	3–4 (20)	3–4 (12)	4 (7)	3–4 (25)	4 (10)
PoSL								
mean ± SD	2.0 ± 0.00	2.0 ± 0.00	2.0 ± 0.00	2.0 ± 0.00	2.0 ± 0.00	1.7 ± 0.49	2.0 ± 0.00	1.0 ± 0.00
range (n)	2 (2)	2 (2)	2 (10)	2 (20)	2 (12)	1–2 (7)	2 (25)	1 (10)
Elo								
mean ± SD	2.0 ± 0.00	2.5 ± 0.71	1.1 ± 0.32	2.2 ± 0.52	1.9 ± 0.29	1.7 ± 0.76	1.14 ± 0.35	2.3 ± 0.48
range (n)	2 (2)	2–3 (2)	1–2 (10)	1–3 (20)	1–2 (12)	1–3 (7)	1–2 (22)	2–3 (10)

Systematics

Dravidoseps gen. nov.

https://zoobank.org/D8825033-C908-4C22-B246-6DE3AD538D30

Type species. *Lygosoma pruthi* Sharma, 1977

Chresonymy.
Riopa – Sharma (1976, 1978)
Lygosoma – Das (1996)
Subdoluseps – Freitas et al. (2019), Ganesh et al. (2021)

Diagnosis. Medium-sized skinks (adult SVL < 58 mm; n = 89), original tail equal to or slightly longer than body. Dorsal scales on body and tail smooth, cycloid, imbricate; ventrals similar except marginally larger on pectoral and precloacal region; scales on lateral tail base smooth or tricarinate; 62–70 scales in paravertebral rows; 26–32 scales around mid-body; 61–73 ventral scales (rarely 76, n = 1/89); 8–12 enlarged precloacal scales (rarely 13, n = 1/89); and 18–23 scales round the tail. Supranasals in contact with each other behind rostral (rarely not in contact, n = 1/89); single frontonasal; prefrontals relatively small, widely separated on midline; frontal elongate, bell-shaped; four supraoculars; three supraoculars in contact with frontoparietal (rarely two, n = 4/89); frontoparietal divided; interparietal diamond-shaped, eyespot in posterior projection; parietals large, in medial contact posterior to interparietal; 2–4 nuchals, either in contact behind parietals or separated medially by 1–3 paravertebral scales. Nasal divided; two loreals; a single pre-supraocular; two preoculars (rarely three, n = 4/89); and a single sub-preocular (rarely absent, n = 5/89); 6–8 supraciliaries (rarely nine, n = 1/89); lower eyelid with enlarged, transparent central window; a single post-supraocular and postocular; and three or four sub-postoculars (rarely five, n = 3/89); a single primary, two secondary (rarely three, n = 1/89), and three tertiary (rarely four, n = 1/89) temporals. Six or seven supralabials and infralabials; fourth or fifth supralabial elongate, below eye; one or two post-supralabials; 1–3 ear lobules; three enlarged pairs of chin shields. Pentadactyl; limbs well-developed; subdigital lamellae unpaired, smooth to weakly keeled; 4–7 lamellae under digit I of manus and pes, 9–12 lamellae under digit IV of manus and 12–17 lamellae under digit IV of pes (rarely 18, n = 1/89). Viviparous, litter size

2–4. Dorsum light coconut to dark chocolate brown; thick dark band from rostrum to tail speckled with light spots; supralabials with a white streak; males with yellow on lower parts of forebody and flanks, sometimes extending onto belly; venter white with some darker markings (Fig. 9).

Dravidoseps **gen. nov.** differs from *Subdoluseps* by the presence of a transparent central window in the lower eyelid (versus no transparent central window in the lower eyelid), by the presence of an open secondary palate (versus a closed secondary palate) and by being viviparous (versus oviparous) (Freitas et al. 2019; Zimin et al. 2021).

Content. *Dravidoseps goaensis* **comb. nov.**, *Dravidoseps pruthi* **comb. nov**., *Dravidoseps nilgiriensis* **comb. nov.**, and five species described below.

Phylogenetic definition. This genus comprises species that share a more recent common ancestor with *Dravidoseps pruthi* **comb. nov.** than with *Subdoluseps bowringii*.

Etymology. A combination of the Sanskrit 'Dravida', referring to the original inhabitants of southern India and Sri Lanka, and the Ancient Greek 'seps', for a snake-like creature that has been previously used in skink generic names (e.g. Erens et al. 2017; Freitas et al. 2019). The gender of the genus is masculine and the suggested common name is Indian leaf-litter skinks.

Distribution and natural history. The three known species and five unnamed lineages (described below) are distributed in peninsular India, including the northern Western Ghats, central and southern Western Ghats, the edge of the Mysore Plateau and isolated massifs in Tamil Nadu (Fig. 1). Members of the genus are diurnal (sometimes seen moving in the litter soon after dark) and are terrestrial and partially fossorial.

Dravidoseps pruthi Sharma, 1977 comb. nov.

Figures 9A, 10, Table 5

Chresonymy.
Riopa pruthi – Sharma (1977)
Lygosoma pruthi – Das (1996, 2003)
Subdoluseps pruthi – Freitas et al. (2019), Ganesh et al. (2021)

Holotype. ZSI 22393, unsexed adult, "Chitteri range, lat. 11°50′N, long. 78°25′E, Salem District, Tamil Nadu, India [= Sitteri, Dharmapuri District, Tamil Nadu, India; ~11.833°N, 78.417°E] ", collected by Dr. H. S. Pruthi in 1929 (Sharma 1977). Considered lost (Das et al. 1998; Ganesh and Aengals 2018; Ganesh et al. 2021; Pratyush Mohapatra pers. comm).

Paratypes. Two unsexed specimens in ZSI (museum numbers unavailable), same data and status as holotype.

Neotype. (designated herein) NRC-AA-1291 (AK-R 2222). Adult female, from Sitteri Hills (11.90208°N, 78.51800°E; elevation ca. 880 m asl.), Dharmapuri District, Tamil Nadu State, India, collected by Akshay Khandekar, Ishan Agarwal, Swapnil Pawar and team on 29th May 2022.

Additional material (n = 9). NRC-AA-1292 (AK 803), NRC-AA-1293 (AK 804), and NRC-AA-1294 (AK 805), subadults, from Forest Department campus, Sitteri Hills (11.89152°N, 78.50747°E; elevation ca. 950 m asl.), Dharmapuri District, collected by Akshay Khandekar, Ishan Agarwal, Swapnil Pawar, Tejas Thackeray and team on 1st June 2019; BNHS 2525 (AK-R 2197), BNHS 2557 (AK-R 2198), BNHS 2558 (AK-R 2200), adult males, from Palamalai Hills (11.70744°N, 77.73598°E; elevation ca. 1000 m asl.); ZSI-R-28600 (AK-R 2201), subadult, from Palamalai Hills (11.73335°N, 77.73156°E; elevation ca. 600 m asl.), Salem District, same collectors as neotype, collected on 28th May 2022; ZSI-R-28601 (AK-R 2716), adult male, from Vanavasi Reserve Forest (11.75203°N, 77.84129°E; elevation ca. 520 m asl.), Salem District, same collectors as neotype, collected on 11th October 2022; ZSI-R-28602 (AK-R 2750), adult female, from north of Yercaud (11.90822°N, 78.18878°E; elevation ca. 650 m asl.), in Shevaroy Hills, Salem District, same collectors as neotype, collected on 15th October 2022.

Referred material (n = 1). AK-R-2213, from Sitteri Hills (11.92978°N, 78.51765°E), Dharmapuri District, Tamil Nadu.

Etymology. Named for the collector of the holotype, H.S. Pruthi.

Suggested common name. Pruthi's leaf-litter skink.

Diagnosis. A medium-sized skink, snout to vent length up to 56 mm (n = 10). Seven supralabials and six (rarely seven, n = 1/10) infralabials up to angle of mouth; fifth supralabial elongate and below eye; a single post-supralabial; 6–8 supraciliaries; a single slightly elongated nuchal on either side, separated by two or three scales behind parietal; 64–69 scales in paravertebral rows; 30 scales around mid-body; 64–70 ventral scales (rarely 76, n = 1/10); 10 enlarged precloacal scales; scales on lateral sides of tail base smooth, 21–23 scales around the tail. Subdigital lamellae unpaired, smooth to weakly keeled; five or six lamellae under digit I of manus and 4–7 under digit I of pes; 10 or 11 lamellae under digit IV of manus; and 14–17 under digit IV of pes (rarely 18, n = 1/10). Dorsum dull sand; thick grey stripe from rostrum to tail speckled with light spots; supralabials with a white streak; males with yellow on lower parts of forebody and flanks; venter glossy grey-white with some darker markings.

Comparisons. *Dravidoseps pruthi* **comb. nov.** is diagnosed against *D. goaensis* **comb. nov.**, *D. nilgiriensis* **comb. nov.** and the new species described below as part of their respective descriptions.

Description of the neotype. Adult female (SVL 54.9 mm) in good state of preservation except body slightly bent towards right at forearm insertion, tail towards left posterior to base, a 3.4 mm long incision in the sternal re-

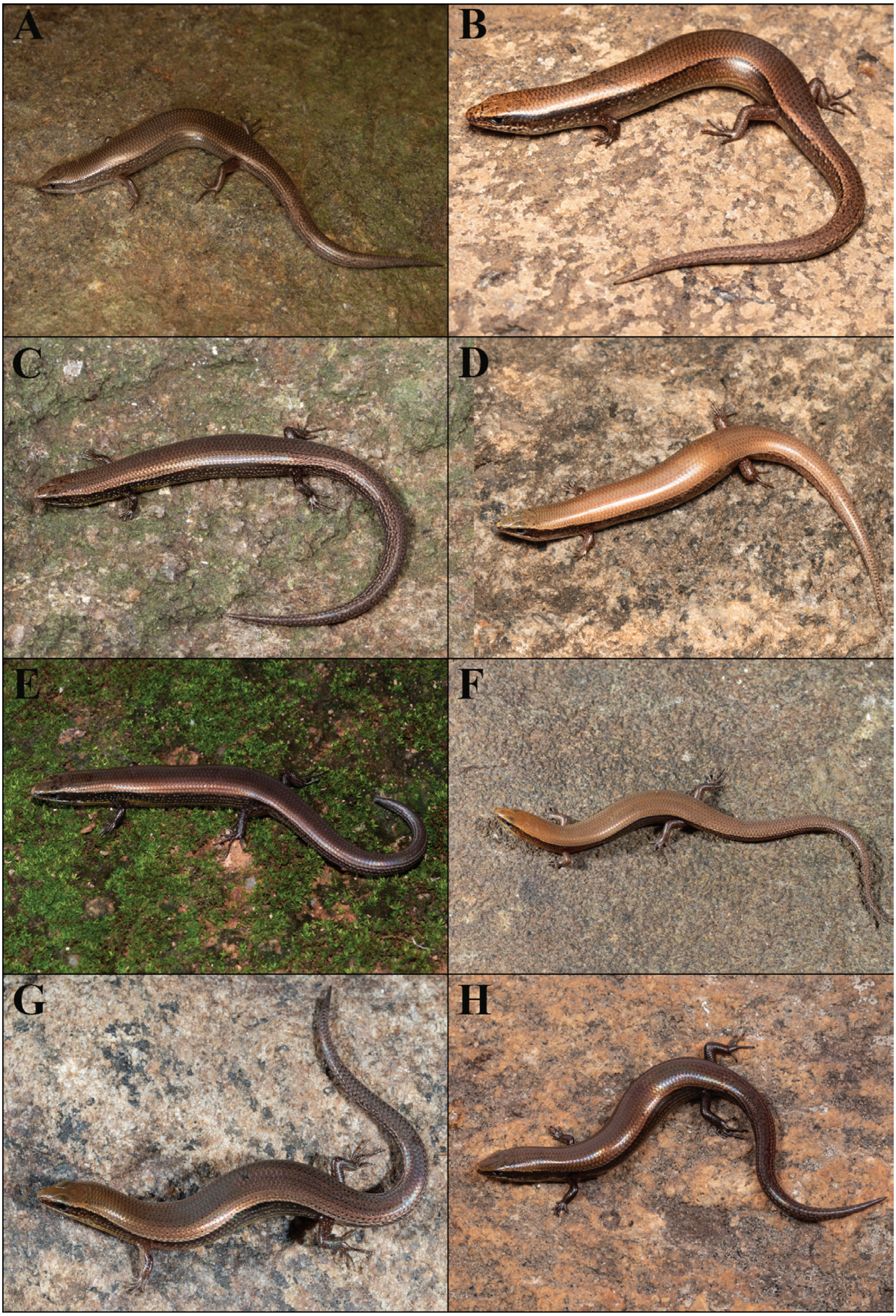

Figure 9. *Dravidoseps* **gen. nov.** species in life: **A** *D. pruthi* **comb. nov.** (neotype, NRC-AA-1291); **B** *D. goaensis* **comb. nov.** (neotype, BNHS 2567); **C** *D. nilgiriensis* **comb. nov.** (ZSI-R-28604); **D** *D. gingeeensis* **sp. nov.** (holotype, NRC-AA-8273); **E** *D. jawadhuensis* **sp. nov.** (holotype, NRC-AA-8274); **F** *D. kalakadensis* **sp. nov.** (holotype, NRC-AA-8275); **G** *D. srivilliputhurensis* **sp. nov.** (holotype, NRC-AA-8279); and **H** *D. tamilnaduensis* **sp. nov.** (holotype, NRC-AA-8286). Photos by Akshay Khandekar (B–D, F–H) and Ishan Agarwal (A, E).

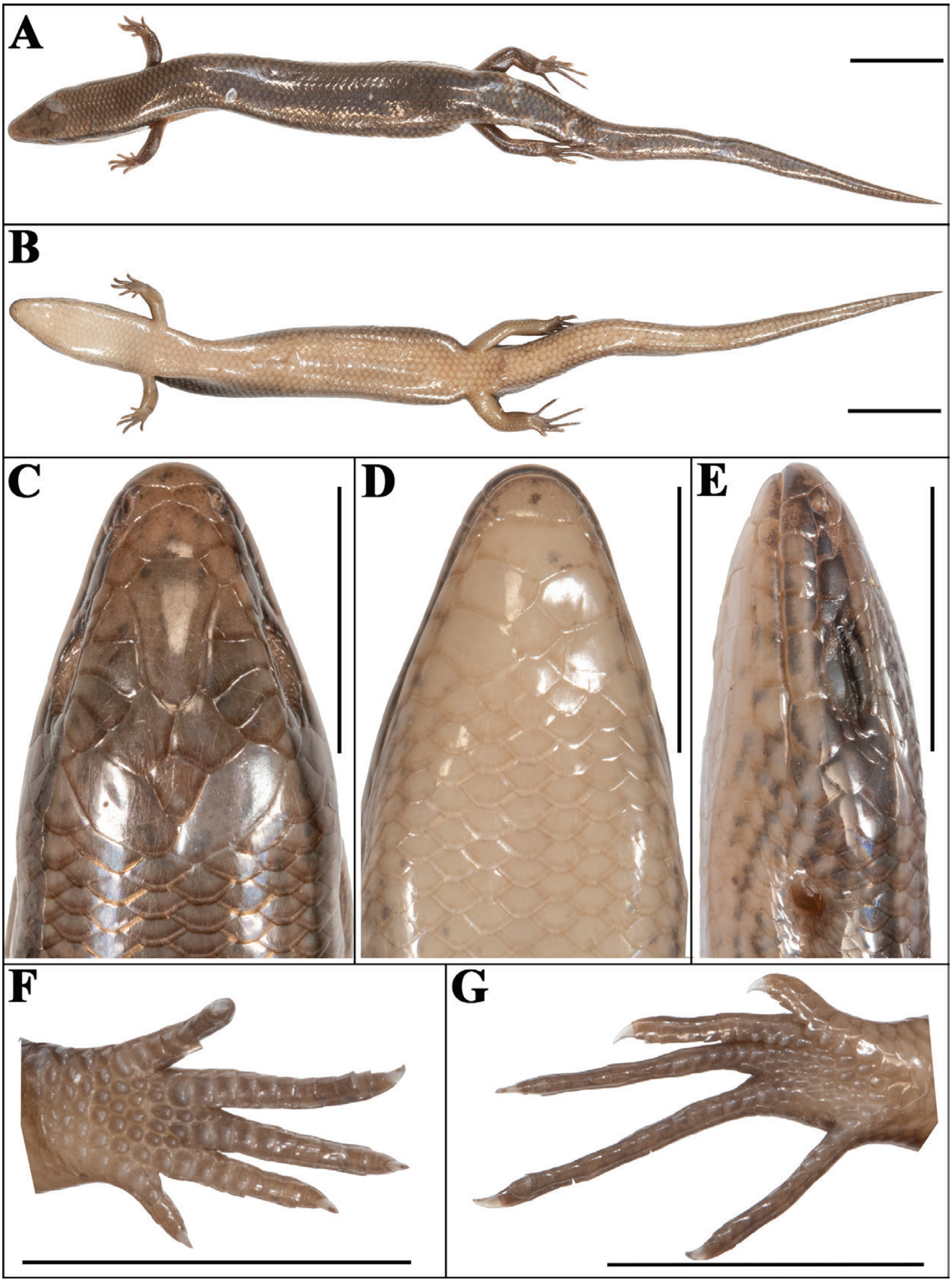

Figure 10. *Dravidoseps pruthi* **comb. nov.** (neotype, NRC-AA-1291): **A** dorsal view of body, **B** ventral view of body, **C** dorsal view of head, **D** ventral view of head, **E** lateral left side view of head, **F** ventral view of left manus, and **G** ventral view of left pes. Scale bars: A, B = 10 mm; C–E, G = 5 mm; F = 3 mm. Photos by Akshay Khandekar.

gion for liver tissue collection, and 15.5 mm long incision (made after taking morphological data and photos) at ventral mid-body to check for eggs/ embryos (Fig. 10A, B). Head short (HL/SVL 0.14), wide (HW/HL 0.71), not strongly depressed (HH/HL 0.52), indistinct from neck. Loreal region not inflated, canthus rostralis indistinct. Snout almost half head length (ES/HL 0.46), more than twice eye diameter (ES/ED 2.23). Rostral almost twice as wide (1.5 mm) as long (0.8 mm), in broad contact with supranasals posteriorly and supralabial I and nasals on either side; supranasals in contact with each other medially, frontonasal posteriorly, nasals and anterior loreals laterally; frontonasal much wider (1.8 mm) than long (1.1 mm), in contact with supranasals anteriorly, prefrontals and frontal posteriorly, anterior loreals laterally; prefrontals relatively small, widely separated on midline, anteriorly in contact with frontonasal, posteriorly with frontal, first supraocular and first supraciliary, laterally with anterior and posterior loreals. Frontal elongate, roughly bell-shaped, widest anteriorly at the point where prefrontals and first supraciliary connect; in contact with frontonasal anteriorly, frontoparietals posteriorly, prefrontals and first two supraoculars on either side; four supraoculars and one small post-supraocular and postocular on either side; frontoparietals in medial contact posterior to frontal, in contact with second, third, and fourth supraoculars anterolaterally and parietals and interparietal posteriorly. Interparietal large, roughly diamond-shaped, slightly projecting posteriorly, eyespot in posterior projection; postinterparietal absent; parietals large, in medial contact posterior to interparietal, in contact with frontoparietals, fourth supraocular, and post-supraocular anteriorly, two nuchal scales and three dorsal scales posteriorly, first secondary temporal laterally; a single enlarged nuchal scale on either side separated from each other by three dorsal scales (Fig. 10C). Nasals small, trapezoidal, widely separated, in contact with rostral anteriorly, supranasal dorsally, anterior loreal posteriorly, first supralabial ventrally; nostril in center of nasal; anterior loreal marginally taller (0.7 mm) than wide (0.6 mm); posterior loreal slightly larger than anterior loreal and slightly wider (0.8 mm) than tall (0.6 mm); a single small supra-preocular, an upper and lower preocular, and a single sub-preocular present on either side (Fig. 10E). Eye small (ED/ HL 0.20) with round pupil; lower eyelid with enlarged, transparent central window; eight supraciliaries on left and seven on right, anterior supraciliary largest, bordered by prefrontal anteriorly, first supraocular dorsally, and pre-supraocular, upper preocular and posterior loreal laterally; posterior superciliary elongate and projecting dorsomedially, bordered by fourth supraocular dorsally, post-supraocular posteriorly, and first post-subocular laterally; four post-suboculars on either side; a single primary temporal, two secondary temporals, and three tertiary temporals on either side; seven supralabials, fifth and sixth below eye; fifth supralabial elongate, in broad contact with four or five small scales on lower eyelid below eye on either side; a single post-supralabial on either side; six infralabials on either side; two scales separating post-supralabial and external ear opening; external ear opening small (EL/HL 0.07), oval, bearing two anterior lobules on either side; tympanum deep (Fig. 10E). Mental almost twice as wide (1.8 mm) as long (1.0 mm); a single large postmental in contact with first and second infralabials on either side; three enlarged pairs of chin shields posterior to postmental; anterior pair large (1.4 mm), roughly rectangular, in medial contact with each other below postmental and bordered by second and third infralabials, middle pair of chin shields, and by a single median gular scale on either side; middle pair largest (1.7 mm), roughly rectangular, separated from each other by two longitudinally arranged gular scales, bordered by third and fourth infralabials, posterior pair of chin shields, and four gular scales on either side; posterior pair smallest (0.8 mm), roughly square, separated from each other by five transversely arranged gular scales, bordered by fourth and fifth infralabials and three gular scales on either side; rest of the gular scales much smaller than postmentals, cycloid and imbricate, two or three rows bordering infralabials slightly smaller and elongate (Fig. 10D).

Body relatively slender (BW/AGL 0.23), elongate (AGL/SVL = 0.59); dorsal scales on body smooth, cycloid, imbricate; ventrals similar to dorsals except subequal from chest to vent, marginally larger on pectoral and precloacal region; 69 scales in paravertebral rows; 30 scales around mid-body; 69 ventral scales; 10 enlarged precloacal scales (Fig. 10A, B). Limbs, robust, short (FL/SVL = 0.06; CL/SVL = 0.08), widely separated when adpressed; dorsal scales slightly larger than ventral scales; palmar scales raised; plantar scales large, raised, coarse granules; all digits short, scales on dorsal surfaces in single row, subdigital lamellae unpaired, smooth to weakly keeled; lamellae series: 6-8-9-11-7 left manus (Fig. 10F), 6-10-14-16-11 left pes (Fig. 10G), 6-10-10-11-8 right manus, 6-11-14-15-11 right pes. Relative length of digits (measurements in mm in parentheses): IV (2.2) > III (2.1) > II (1.7) > V (1.4) > I (0.9) (left manus); IV (4.5) > III (3.7) > V (2.9) > II (2.6) > I (1.2) (left pes).

Tail original, entire, cylindrical, slightly shorter than snout-vent length (TL/SVL 0.88); dorsal and ventral scales on tail cycloid, imbricate, similar to those on body dorsum except for posterior 1/3rd on which median dorsal and subcaudal scale rows distinctly larger than surrounding scales; tail ending in a pointed scute; scales on lateral sides of tail base smooth, 21 scales around the tail (Fig. 10A, B).

Colouration in life (Fig. 9A). Dorsal ground colouration of body, head and tail dull sand with a bronze tint; head with a few dark markings; dorsal scales of body and tail outlined by dark brown, centre of scales with dark markings, more prominent on hindbody and tail; limbs darker than body dorsum and with light spots; a thick grey stripe running from rostrum through orbit and onto flank and tail with scattered white spots, flanked dorsally by an indistinct, narrow, lighter stripe; supralabials with a white streak, dark band forming reticulations on lateral aspect of tail; ventral regions glossy grey-white with fine black stripes on edges of throat, neck and tail.

Variation and additional information. Mensural and meristic data for topotypic and additional specimens are given in Table 5. There are four subadults, four adult males and a single adult female. All specimens resemble the neotype female (NRC-AA-1291) in overall morphology and head scalation except for the following variation: four SO with an additional small scale between SO I and II on left side; six SC on either side in NRC-AA-1292,

Table 5. Mensural (mm) and meristic data for *Dravidoseps pruthi* **comb. nov.**. Abbreviations are listed in Materials and Methods except for: L&R = Left & Right; M = male; F = female; Sa = Subadult; * = data incomplete; and / = data unavailable.

Museum number	NRC-AA-1291	NRC-AA-1292	NRC-AA-1293	NRC-AA-1294	BNHS 2525	BNHS 2557	BNHS 2558	ZSI-R-28600	ZSI-R-28601	ZSI-R-28602
Type	Neotype	Topotypes			Referred Material					
Sex	F	Sa	Sa	Sa	M	M	M	Sa	M	F
SVL	54.9	28.2	28.3	28.8	52.4	48.2	51.1	27.1	47.5	56.0
TL	48.8	7.3*	7.1*	31.9	42.7	42.7	41.5	21.7*	44.5	42.2
TW	4.6	2.3	2.2	2.3	4.9	4.1	4.4	2.2	4.2	5.0
FL	3.4	2.0	1.9	2.0	3.6	3.6	3.0	2.0*	3.3	3.0
CL	4.6	2.5	2.5	2.5	4.8	4.8	4.6	2.3*	4.3	4.3
AGL	32.7	14.8	15.0	15.2	30	27.7	28.4	13.6	27.7	34.4
BH	4.0	2.7	2.9	2.4	5.0	5.2	5.7	2.7	4.3	4.5
BW	7.7	4.0	4.1	4.4	8.2	7.6	8.1	4.2	7.7	8.7
HL	8.2	5.8	5.5	5.8	9.3	8.7	9.6	5.6	8.0	8.2
HW	5.9	3.7	4.0	3.9	6.3	6.2	6.1	3.5	5.4	5.8
HH	4.3	2.8	2.6	2.5	5.1	4.0	4.6	2.5	4.2	4.5
ED	1.7	1.3	1.3	1.4	1.9	1.8	1.8	1.3	1.7	1.8
TWD	0.8	0.8	0.7	0.7	1.0	0.9	0.8	0.7	0.9	0.9
EE	3.4	2.2	2.4	2.3	3.3	3.1	3.4	2.1	3.2	3.1
EL	0.6	0.4	0.4	0.3	0.5	0.5	0.8	0.5	0.5	0.5
ES	3.8	2.3	2.3	2.2	3.7	3.4	3.6	2.3	3.3	3.2
EN	2.2	1.6	1.4	1.2	2.6	2.3	2.5	1.5	2.0	2.1
IN	1.5	1.1	1.1	1.1	1.7	1.4	1.6	1.0	1.4	1.5
IO	3.0	2.2	2.3	2.4	3.3	3.0	3.1	2.2	3.0	3.2
Nu	1&1	1&1	1&1	1&1	1&1	1&1	1&1	1&1	1&1	1&1
Sb Nu	3	2	2	2	3	2	2	2	3	3
SL L&R	7&7	7&7	7&7	7&7	7&7	7&7	7&7	7&7	7&7	7&7
IL L&R	6&6	6&6	6&6	6&6	6&6	6&6	6&6	6&6	6&7	6&6
PoSL L&R	1&1	1&1	1&1	1&1	1&1	1&1	1&1	1&1	1&1	1&1
Elo L&R	2&2	3&2	2&2	2&2	2&2	2&2	2&3	3&3	3&2	2&2
PVS	69	69	69	67	64	64	65	66	68	66
RBS	30	30	30	30	30	30	30	30	30	30
VS	69	69	76	68	66	65	64	65	67	70
SPCLR	10	10	10	10	10	10	10	10	10	10
RTS	21	/	/	/	21	21	21	/	23	/
LamF1 L&R	6&6	6&6	5&5	5&6	6&6	5&5	6&6	6&6	6&6	5&6
LamF4 L&R	11&11	11&10	10&10	11&11	11&11	11&12	11&11	11&11	11&11	11&11
LamT1 L&R	6&6	5&5	5&6	5&5	7&6	6&6	3*&6	4&4	6&6	6&6
LamT4 L&R	16&15	14&16	15&16	16&16	17&14*	17&16	17&12*	16&16	18&16*	10*&15
Elongate supra-labial below eye, fourth (1) or fifth (0) L&R	0&0	0&0	0&0	0&0	0&0	0&0	0&0	0&0	0&0	0&0

seven in BNHS 2557, six on left and seven on right side in ZSI-R-28602, and eight on either side in BNHS 2525, BNHS 2558, ZSI-R-28600, ZSI-R-28601; a single PrSbO on either side in NRC-AA-1292, NRC-AA-1293, BNHS 2525, BNHS 2558, ZSI-R-28600, ZSI-R-28601, ZSI-R-28602, and PrSbO absent on either side in BNHS 2557; 2.8 mm and 3.9 mm skin injury on right side of head between posterior postmental till ear opening in ZSI-R-28601 and ZSI-R-28602, respectively. More than half the tail of NRC-AA-1292 and NRC-AA-1293 collected as tissue for DNA sampling; ZSI-R-28601 with entire and original tail; BNHS 2525, BNHS 2557 and, BNHS 2558 with entire but partially regenerated tails; NRC-AA-1294, ZSI-R-28600, and ZSI-R-28602 with entire but partially regenerated tails which are detached from the body. BNHS 2557 with partial everted hemipenis on either side, BNHS 2525 with partially everted hemipenis only on right, and BNHS 2558 with only on left side. After collection of morphological data, ZSI-R-28601 (adult male) and ZSI-R-28602 (adult female) were dissected from the ventral region of mid-body (11.3 mm and 15.3 mm long incision respectively) to check sex and the presence of eggs/ embryos.

Distribution and natural history. *Dravidoseps pruthi* **comb. nov.** is known from Sitteri Hills in Dharmapuri District (type locality), and the northern slopes of Yercaud in Shevaroy Hills, Vanavasi Reserve Forest, and

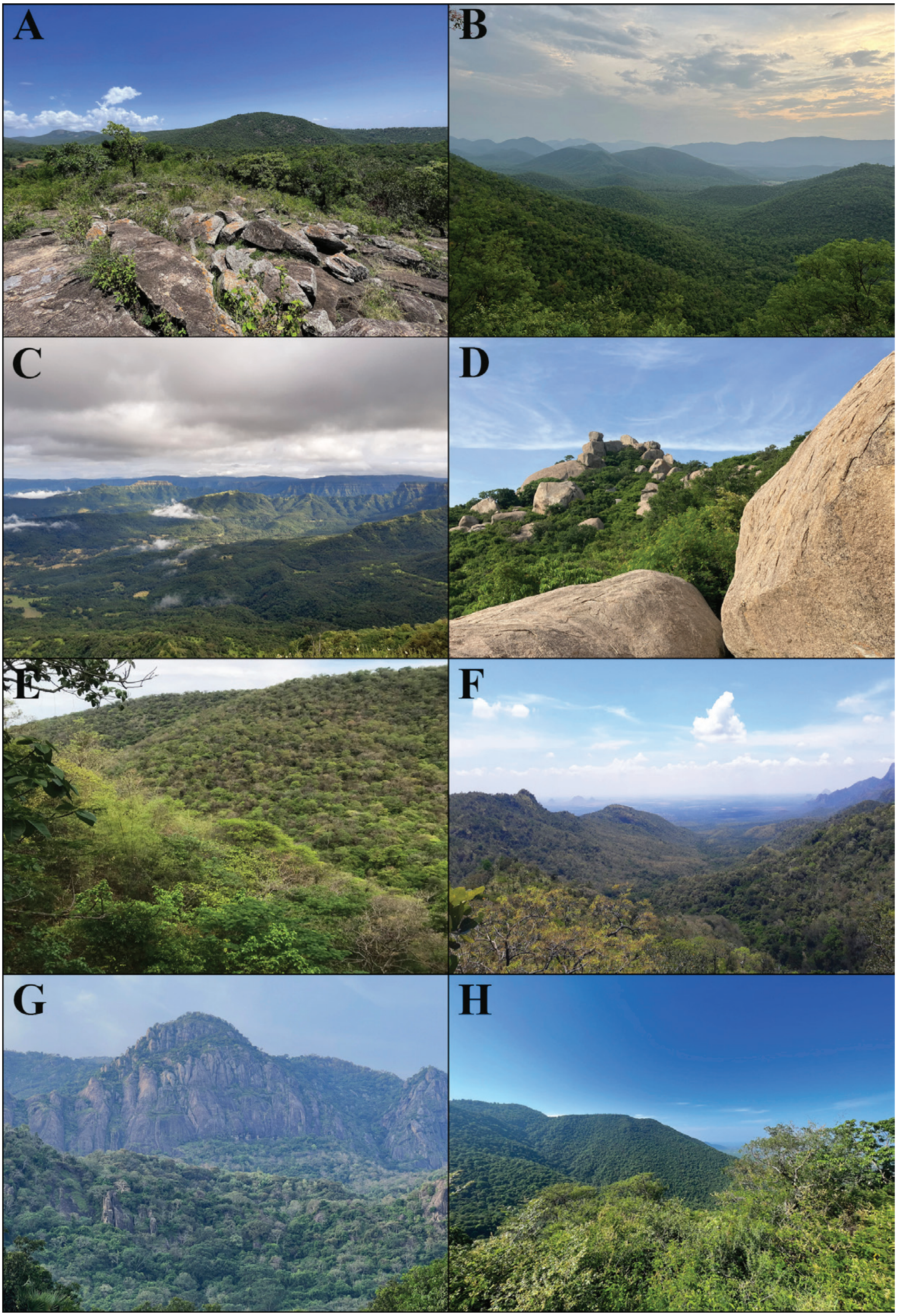

Figure 11. General habitats of all species of *Dravidoseps* **sp. nov.**: **A** type locality of *D. pruthi* **comb. nov.**; **B** neotype locality of *D. goaensis* **comb. nov.**; **C** habitat photo of *D. nilgiriensis* **comb. nov.**, from Thamarakarai; **D** type locality of *D. gingeeensis* **sp. nov.**; **E** type locality of *D. jawadhuensis* **sp. nov.**; **F** type locality of *D. kalakadensis* **sp. nov.**; **G** paratype locality of *D. srivilliputhurensis* **sp. nov.**, near Atthi Kovil Falls; and **H** type locality of *D. tamilnaduensis* **sp. nov.**. Photos by Akshay Khandekar (A–C, F–H), Ishan Agarwal (D), and Vinod (E).

Palamalai, all in Salem District, Tamil Nadu India. The two most distant localities (Palamalai and Sitteri Hills) are >85 km apart in aerial distance (Fig. 1). The locality, Teerthamalai, reported by Ganesh and Aengals (2018) is likely to represent an additional locality for *D. pruthi* as it is just 20 km north of the type locality and falls within the same hill complex. However, genetic and morphological data are needed to confirm this.

Diurnal, found in the day either moving in leaf litter, in soil or under rocks. The four localities we recorded the species from are at elevations of 500–1000 m asl. with a mix of scrub, deciduous and dry evergreen to semi-evergreen forest with scattered sheet rocks (Fig. 11A). At Sitteri, three subadults were collected in the Forest Department Guesthouse campus from under rocks surrounded by dry leaf-litter during the day (1430 hrs). The adult female neotype was found < 2 km from the first locality during the day (1030 hrs); sympatric lizards found at the first locality include *Cyrtodactylus* (*Geckoella*) cf. *collegalensis*; *Hemidactylus frenatus* Duméril & Bibron; *H. leschenaultii* Duméril & Bibron; *H. whitakeri* Mirza, Gowande, Patil, Ambekar & Patel; *Hemiphyllodactylus* cf. *jnana*, and *Calotes versicolor* (Daudin); and at the second locality include *Eutropis carinata* (Schneider); *E. macularia* (Blyth); *E. beddomei* (Jerdon); *Riopa albopunctata* Gray; and *Psammophilus dorsalis* (Gray). At Yercaud, the species was found buried inside loose soil under a rock in a shaded area within a small open patch during the morning (0830 hrs). Sympatric lizards encountered were *Riopa albopunctata* and *Calotes versicolor*. At Vanavasi Reserve Forest, the species were found under a rock in an open area along the path during the day time (1030 hrs); the sympatric lizards seen were *Cnemaspis* cf. *agarwali*, *Eutropis carinata*, and *Calotes versicolor*. At Palamalai Hills, individuals were found buried in loose, moist soil under or around rocks in a large sheet rock patch surrounded by dry evergreen forest during the early evening (1530–1730 hrs). Sympatric lizards were *Hemidactylus sankariensis* Agarwal, Bauer Giri & Khandekar; *Eutropis beddomei*; *E. macularia*; *Riopa albopunctata*; *Ophisops leschenaultii* (Milne-Edwards); and *Psammophilus dorsalis*.

Reproduction. Unknown. No gravid female in the additional material examined (two non-gravid females dissected: ZSI-R-28602 and neotype, NRC-AA-1291).

Note. Our topotypical and genetically assigned specimens match the original description provided by Sharma (1977) except for SVL (up to 56 mm, n = 10, versus 67 mm in original description); TL (up to 49 mm, n = 7; versus 72 mm); the number of nuchals (a single nuchal on either side separated by two or three scales versus two pairs of nuchals); the number of Elo (two or three on either side versus six); RBS (30 versus 32–34); and PVS (64–69 versus 50). We could not verify the counts as the type specimens are lost (Das et al. 1998; Ganesh and Aengals 2018; Ganesh et al. 2021; Pratyush Mohapatra pers. comm.). The values for SVL and TL, and paravertebral scale count in original description are likely to be incorrect as none of the species in the genus have such high values. The RBS (32–34) count is also likely to be incorrect as all topotypical and other specimens assigned to the species have 30 RBS (n = 10). The nuchal scale count was most likely defined and counted differently and includes two paravertebral scales between a single elongated nuchal on either side instead of two pairs as can be seen in the line drawing from Sharma (1977); and Elo is most likely a combined count of left and right (three each). Subsequently, Ganesh et al. (2021) used morphological data (from Ganesh and Aengals 2018) and morphological + genetic data from a single specimen of *Dravidoseps* **gen. nov.** each from Pachaimalai Hills and Jawadhu Hills respectively to establish taxonomic and genetic conscription of *D. pruthi* **comb. nov.** in the absence of the type or topotypic specimens of the species, based on similarities in taxonomic characters and geography. However, our sampling from the type locality of *D. pruthi* **comb. nov.**, the Pachaimalai Hills, and Jawadhu Hills show that topotypic samples of *D. pruthi* **comb. nov.** are morphologically and genetically divergent from samples from both other localities given by Ganesh et al. (2021), which we describe as new species below. Comments on discrepancies in certain morphological characters based on our data and that provided by Ganesh and Aengals (2018) and Ganesh et al. (2021) are listed as part of the respective descriptions of the new species.

Dravidoseps goaensis Sharma, 1976 comb. nov.

Figures 8A, 9B, 12, Table 6

Chresonymy.

Riopa goaensis – Sharma (1976), Freitas et al. (2019)

Lygosoma goaensis – Das (1996)

Holotype. ZSI 22032, unsexed adult, "ca. 5 km N.E. of Forest Rest House, Molem" [South Goa District, Goa State, India], collected by Zoological Survey of India during 1966–1969 (Sharma 1976). Not in the specimen jar at ZSI, Kolkata (Pratyush Mohapatra pers. comm).

Neotype. (designated herein) BNHS 2567 (AK 1345), adult female, from the vicinity of Hotel Whistling Woods (15.96006°N, 73.99736°E; elevation ca. 720 m asl.), Amboli, Sindhudurg District, Maharashtra State, India, collected by Akshay Khandekar on 18th February 2021.

Additional material (n = 6). ZSI-R-28612 (AK-R 847), adult male same data as neotype except collected on 3rd January 2022; NRC-AA-1303 (AK 1052), subadult, from near Ugwai temple (16.37237°N, 73.86344°E; elevation ca. 650 m asl.), Dajipur; NRC-AA-1304 (AK 1192), subadult, from Talaye (16.65794°N, 73.91782°E; elevation ca. 600 m asl.); NRC-AA-1305 (AK 1300), adult male, from near Pandivare (16.36671°N, 74.09036°E; elevation ca. 820 m asl.); and BNHS 2566 (AK 1303), adult female, from near Kapurkada Falls, Washi (16.72807°N, 73.87645°E; elevation ca. 700 m asl.); all in Kolhapur District, Maharashtra State, India, same collectors as neotype, collected March–July 2019. NRC-AA-1302 (AK-R 2808), subadult, from Ustam (15.55983°N, 74.18788°E; elevation ca. 150 m asl.), South Goa District, Goa State, India, collected by Akshay Khandekar, Satpal Gangalmale, and Swapnil Pawar on 20 June 2023.

Etymology. Named for its type locality, Goa.

Suggested common name. Goan leaf-litter skink.

Diagnosis. A medium-sized skink snout to vent length up to 56 mm (n = 7). Six or seven supralabials and six (rarely seven, n = 1/7) infralabials up to angle of mouth; fifth supralabial elongate and below eye (rarely fifth on one side, n = 2/7); one or two post-supralabials; seven supraciliaries (rarely six on one side, n = 1/7); a single slightly elongated nuchal on either side (rarely two on one side n = 1/7), in contact with each other behind parietal or separated by one or two scales; 62–67 scales in paravertebral rows; 28–30 scales around mid-body; 64–66 ventral scales (rarely 73, n = 1/7); eight enlarged precloacal scales (rarely 10, n = 1/7); scales on lateral sides of tail base smooth, 18 or 19 scales around the tail. Subdigital lamellae unpaired, smooth; five or six lamellae under digit I of manus and pes (rarely four on one side on manus, n = 1/7); 10 or 11 lamellae under digit IV of manus; and 13–15 under digit IV of pes (rarely 12 on one side, n = 1/7). Dorsum coconut brown; thick stripe from rostrum to tail speckled with light spots; supralabials with white streak; males with yellow on lower parts of forebody and flanks; venter glossy grey-white with darker markings.

Comparisons. *Dravidoseps goaensis* **comb. nov.** can be diagnosed from *D. pruthi* **comb. nov.** (data in parentheses) based on the following characters: keeled scales on tail base (versus unkeeled scales on tail base); 29.0 ± 1.00 (28–30) RBS (versus 30.0 ± 0.00 (30)); 13.4 ± 0.79 (13–15) Lam4T (versus 16.1 ± 1.20 (14–18)); 18 or 19 RTS (versus 21–23 in *D. pruthi* **comb. nov.**). *Dravidoseps goaensis* **comb. nov.** is diagnosed against *D. nilgiriensis* **comb. nov.** and the new species described below as part of their respective descriptions.

Description of the neotype. Adult female (SVL 54.9 mm) in good state of preservation except tail damaged at three places along its length, a 4.0 mm long incision in the sternal region for liver tissue collection, and 14.1 mm long incision at ventral mid-body (made after taking morphological data and photos) to check for eggs/embryos (Fig. 12A, B). Head short (HL/SVL 0.15), wide (HW/HL 0.73), not strongly depressed (HH/HL 0.51), indistinct from neck. Loreal region not inflated, canthus rostralis indistinct. Snout almost half head length (ES/HL 0.40), twice eye diameter (ES/ED 2.00). Rostral twice as wide (1.8 mm) as long (0.9 mm), in broad contact with supranasals posteriorly and supralabial I and nasals on either side; supranasals in contact with each other medially, frontonasal posteriorly, nasals and anterior loreals laterally; frontonasal much wider (1.8 mm) than long (1.2 mm), in contact with supranasals anteriorly, prefrontals and frontal posteriorly, anterior loreals laterally; prefrontals relatively small, widely separated on midline, in contact anteriorly with frontonasal, posteriorly with frontal, first supraocular and first supraciliary, laterally with anterior and posterior loreals. Frontal elongate, roughly bell-shaped, widest anteriorly at the point where prefrontals and first supraocular connect; in contact with frontonasal anteriorly, frontoparietals posteriorly, prefrontals and first two supraoculars on either side; four supraoculars and one small post-supraocular and postocular on either side; frontoparietals in medial contact posterior to frontal, in contact with second, third and fourth supraoculars anterolaterally and parietals and interparietal posteriorly. Interparietal large, roughly diamond-shaped, slightly projecting posteriorly, eyespot in posterior projection; postinterparietal absent; parietals large, in medial contact posterior to interparietal, in contact anteriorly with frontoparietals, fourth supraocular, and post-supraocular, posteriorly with three nuchal scales and a single dorsal scale, laterally with first secondary temporal; two slightly enlarged nuchal scales on left and a single on right separated from each other by a single dorsal scale (Fig. 12C). Nasals small, trapezoidal, widely separated, in contact with rostral anteriorly, supranasal dorsally, anterior loreal posteriorly, first supralabial ventrally; nostril in center of nasal; anterior loreal marginally taller (0.6 mm) than wide (0.5 mm); posterior loreal slightly larger than anterior loreal and slightly wider (1.0 mm) than tall (0.7 mm); a single small supra-preocular, an upper and lower preocular, and a single sub-preocular present on either side (Fig. 12E). Eye small (ED/ HL 0.21) with round pupil; lower eyelid with enlarged, transparent central window; seven supraciliaries on either side, anterior supraciliary largest, bordered by prefrontal anteriorly, first supraocular dorsally, and pre-supraocular, upper preocular and posterior loreal laterally; posterior superciliary elongate and projecting dorsomedially, bordered by fourth supraocular dorsally, post-supraocular posteriorly, and first post-subocular laterally; four post-suboculars on either side; a single primary temporal, two secondary temporals, and three tertiary temporals on either side; seven supralabials, fifth below eye, elongate and in broad contact with four small scales on lower eyelid below eye on either side; a single post-supralabial on either side; six infralabials on either side; two scales separating post-supralabial and external ear opening; external ear opening small (EL/HL 0.07), oval, bearing a single anterior lobule on either side; tympanum deep (Fig. 12E). Mental twice as wide (1.8 mm) as long (0.9 mm); a single large postmental in contact with first and second infralabials on either side; three enlarged pairs of chin shields posterior to postmental; anterior pair large (1.6 mm), roughly rectangular, in medial contact with each other below postmental and bordered by second and third infralabials, middle pair of chin shields, and by a single median gular scale on either side; middle pair largest (1.8 mm), roughly rectangular, sepa-

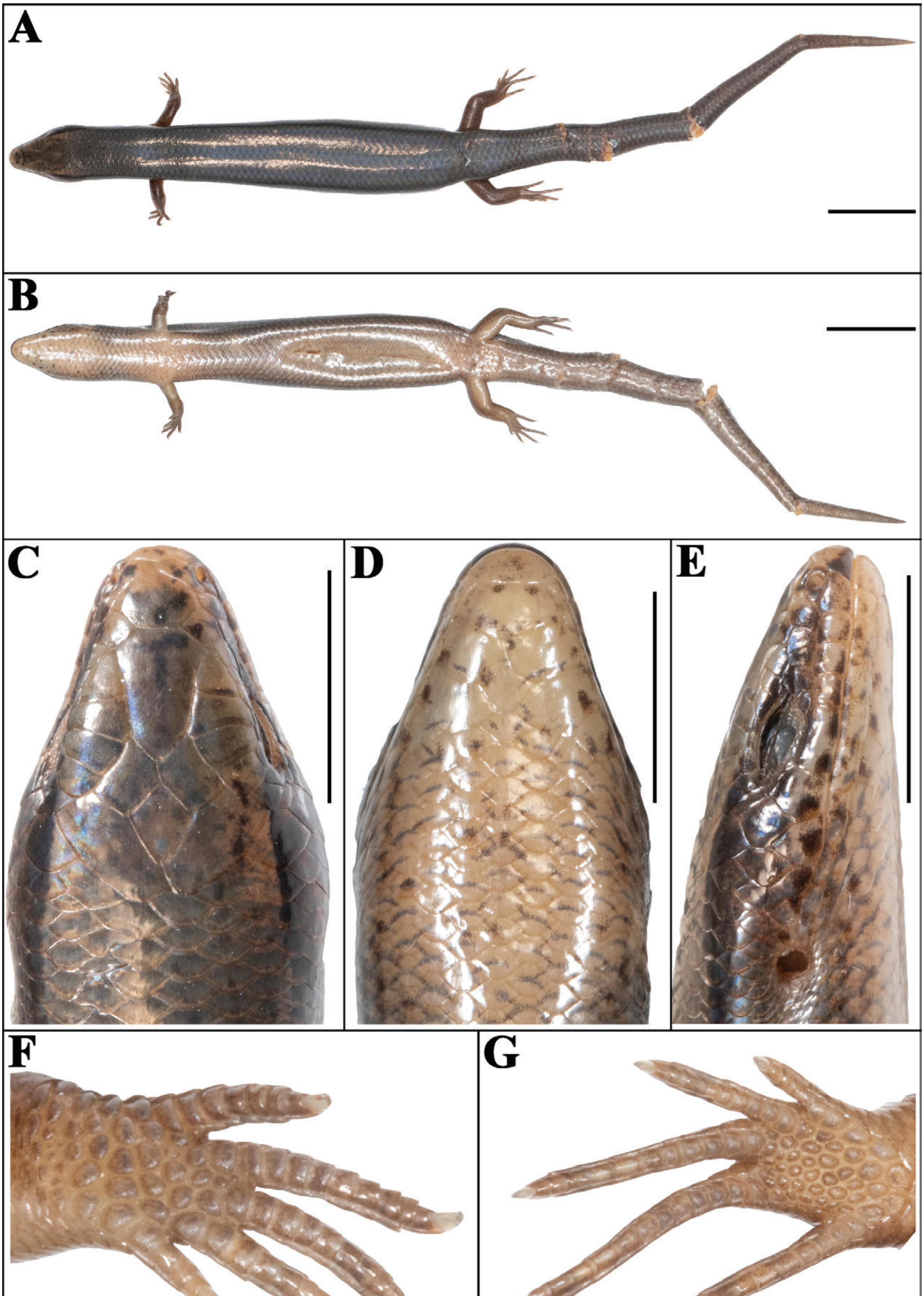

Figure 12. *Dravidoseps goaensis* **comb. nov.** (neotype, BNHS 2567): **A** dorsal view of body, **B** ventral view of body, **C** dorsal view of head, **D** ventral view of head, **E** lateral right side view of head, **F** ventral view of right manus, and **G** ventral view of right pes. Scale bars: A, B = 10 mm; C–E, G = 5 mm; F = 3 mm; photos by Akshay Khandekar.

rated from each other by two longitudinally arranged gular scales, bordered by third and fourth infralabials, posterior pair of chin shields, and three gular scales on either side; posterior pair smallest (0.9 mm), roughly square, separated from each other by five transversely arranged gular scales, bordered by fourth and fifth infralabials and three gular scales on either side; rest of the gular scales much smaller than postmentals, cycloid and imbricate, two or three rows bordering infralabials slightly smaller and elongate (Fig. 12D).

Body relatively slender (BW/AGL 0.14), elongate (AGL/SVL = 0.62); dorsal scales on body smooth, cycloid, imbricate; ventrals similar to dorsals except subequal from chest to vent, marginally larger on pectoral and precloacal region; 64 scales in paravertebral rows; 30 scales around mid-body; 66 ventral scales; eight enlarged precloacal scales (Fig. 12A, B). Limbs, robust, short (FL/SVL = 0.05; CL/SVL = 0.07), widely separated when adpressed; dorsal scales slight larger than ventral scales; palmar scales raised; plantar scales large, raised, coarse granules; all digits short, scales on dorsal surfaces in single row, subdigital lamellae unpaired, smooth; lamellae series: 5-8-10-10-7 left manus, 6-9-12-13-9 left pes, 5-7-9-10-7 right manus (Fig. 12F), 5-10-11-13-10 right pes (Fig. 12G). Relative length of digits (measurements in mm in parentheses): IV (2.1) > III (2.0) > V (1.6) > II (1.5) > I (1.0) (left manus); IV (4.8) > III (3.2) > V (2.4) > II (2.1) > I (1.1) (left pes).

Tail original, entire, cylindrical, marginally shorter than snout-vent length (TL/SVL 0.94); damaged at three places at its length; dorsal and ventral scales on tail cycloid, imbricate, similar to those on body dorsum except for posterior 1/3rd on which median dorsal and subcaudal scale rows distinctly larger than surrounding scales; tail ending in a pointed scute; scales on lateral sides of tail base keeled, tricarinate; 19 scales around the tail (Fig. 12A, B).

Colouration in life (Fig. 9B). Dorsal ground colouration of body, head and tail coconut brown with a bronze tint; head with scattered dark markings; dorsal scales of body and tail finely outlined by dark brown, centre of scales with dark markings forming indistinct stripes; limbs darker than body dorsum and with light spots; a thick stripe with a fine black dorsolateral border running from rostrum through orbit and onto flank and tail with scattered light spots, some scales with orange; supralabials with a white streak; ventral regions glossy, off-white with scattered black markings.

Variation and additional information. Mensural and meristic data for the topotypic and additional specimens are given in Table 6. There are three subadults, two adult males and a single adult female. All specimens resemble the neotype female (BNHS 2567) in overall morphology and head scalation except for the following variation: six SC on left and seven on right side in ZSI-R-28612; PoO absent on left side in NRC-AA-1303; NRC-AA-1302 and NRC-AA-1303 with entire and original tail, tail marginally longer than body (TL/SVL = 1.09 and 1.11 respectively); NRC-AA-1304 with entire but regenerated tail, much shorter than body (TL/SVL = 0.59); remaining three specimens with tail either completely or partially broken and missing. ZSI-R-28612 with partial everted hemipenis on either side.

Distribution and natural history. Apart from the type locality (“ca. 5 kms NE of Forest Rest House, Molem [Goa]; Sharma, 1976), *Dravidoseps goaensis* **comb. nov.** has been recorded by us from Ustam and Mhadei Wildlife Sanctuary, South Goa District in Goa State (< 25 km south of the type locality) and from Amboli in Sindhudurg District, four localities (Dajipur, Talaye, Padivare, and Washi) Kolhapur District of Maharashtra State, India; all from the northern Western Ghats. The farthest two reported localities (Washi in north and Mhadei Wildlife Sanctuary in south) are ~140 km apart from each other in aerial distance.

The four localities we recorded the species from are at elevations of 150–820 m and habitats vary from moist deciduous to semi evergreen and evergreen forest (Fig. 11B). At Ustam in South Goa, a single subadult was spotted moving in leaf-litter in the early afternoon (1240 hr) inside a private property; a single individual (not collected) was also observed moving in the leaf-litter in the afternoon (1400 hr) on outskirts of Mhadei Wildlife Sanctuary (WLS), South Goa. At Amboli, both individuals were spotted moving in leaf-litter in the morning to afternoon (0930–1300 hrs). We recorded this species from multiple localities in similar habitats at Amboli. At other four localities (Dajipur, Talaye, Padivare, and Washi) in Kolhapur District, individuals were seen moving in the leaf-litter and also found in soil or under rocks during the day time. Sympatric lizards recorded at these localities were *Cnemaspis goaensis* Sharma (Ustam and Mhadei WLS); *Cn. amboliensis* Sayyed, Pyron & Dileepkumar, (Amboli); *Cn. flaviventralis* Sayyed, Pyron & Dahanukar (Ustam, Mhadei WLS, and Amboli); *Cn. limayei* Sayyed, Pyron & Dileepkumar (Dajipur and Talaye); *Cyrtodactylus* (*Geckoella*) *albofasciatus* (Boulenger) (Ustam, Mhadei wls, Amboli); *Cyrtodactylus* (*Geckoella*) *deccanensis* (Günther) (Dajipur, Talaye, Pandivare, and Washi); *Hemidactylus frenatus*; *Eutropis carinata*; *E. macularia*; *E.* cf. *allapallensis* (Ustam and Mhadei WLS); *Riopa guentheri* (Peters); *Calotes versicolor*; and *Monilesaurus rouxii* (Duméril & Bibron).

Reproduction. Viviparous, four embryos in early stages of development in holotype, ZSI 22032 (Fig 8A).

Note. Article 75.3.6 of The Code (Anonymous 1999) states that a neotype should be “nearly as practicable from the original type locality”, however we chose a non-topotypic, adult female as the neotype as the single specimen from closest to the type locality is a subadult, and these were shown to belong to the same lineage genetically. Our neotype and other specimens match the original description provided by Sharma (1976) except for the following mensural and meristic characters: IO (2.6–3.5 mm versus 5 mm in original description); BW

Table 6. Mensural (mm) and meristic data for *Dravidoseps goaensis* **comb. nov.**. Abbreviations are listed in Materials and Methods except for: L&R = Left & Right; M = male; F = female; Sa = Subadult; * = tail incomplete; and / = data unavailable.

Museum number	BNHS 2567	NRC-AA-1302	NRC-AA-1303	NRC-AA-1304	NRC-AA-1305	BNHS 2566	ZSI-R-28612
	Neotype	Topotype	Referred Material				
Sex	F	Sa	Sa	Sa	M	F	M
SVL	55.2	41.1	35.2	38.2	48.3	42.3	43.7
TL	51.9	44.8	39.1	22.6	5.9*	28.1*	15.5*
TW	5.1	3.2	2.9	3.4	4.4	3.9	4.3
FL	3.2	2.8	2.7	2.7	3.0	2.8	3.0
CL	4.1	3.8	3.1	3.2	3.9	3.6	4.0
AGL	34.3	24.2	18.3	21.1	28.6	23.4	25.2
BH	5.1	4.1	2.3	2.9	4.0	4.3	5.3
BW	8.2	6.1	5.6	6.1	6.9	7.0	7.5
HL	8.8	7.1	7.0	7.0	8.6	8.4	8.7
HW	6.5	5.1	4.8	5.5	5.9	5.6	5.8
HH	4.5	3.2	3.1	3.2	4.2	3.6	4.6
ED	1.8	1.5	1.4	1.4	1.8	1.6	1.7
TWD	0.8	0.7	0.7	0.7	0.8	0.8	0.7
EE	3.5	2.8	2.8	3.1	3.4	3.1	3.8
EL	0.7	0.8	0.5	0.5	0.7	0.6	0.6
ES	3.6	2.9	2.7	2.9	3.4	3.3	3.7
EN	2.4	1.9	1.8	1.8	2.2	2.2	2.4
IN	1.5	1.2	1.3	1.2	1.4	1.5	1.5
IO	3.5	2.6	2.6	2.8	3.2	3.1	3.1
Nu	2&1	1&1	1&1	1&1	1&1	1&1	1&1
Sb Nu	1	0	0	1	0	1	2
SL L&R	7&7	7&6	6&7	7&7	7&7	7&7	6&7
IL L&R	6&6	6&6	6&6	6&6	6&7	6&6	6&6
PoSL L&R	1&1	2&2	2&2	2&2	1&1	2&2	2&1
Elo L&R	1&1	3&3	2&2	2&2	1&1	2&2	1&1
PVS	64	66	62	65	67	63	62
RBS	30	29	28	28	30	28	30
VS	66	73	64	66	/	64	64
SPCLR	8	10	8	8	8	8	8
RTS	19	19	18	19	/	18	19
LamF1 L&R	5&5	6&6	6&6	6&6	4&5	5&5	5&5
LamF4 L&R	10&10	11&11	11&11	10&10	10&11	10&10	11&11
LamT1 L&R	6&5	5&6	6&6	6&6	5&5	6&6	6&6
LamT4 L&R	13&13	13&12	15&15	14&13	13&13	13&14	13&13
Elongate supralabial below eye, fourth (1) or fifth (0) L&R	0&0	0&1	1&0	0&0	0&0	0&0	0&0

(5.6–8.2 mm versus 20 mm in original description); Elo (one or two on either side versus five). We could not verify the counts as the type specimens are lost (Pratyush Mohapatra pers. comm.). The measurements of IO and BW in original description are likely to be incorrect as none of the species in the genus have such high numbers, and the number of Elo most likely include left and right combined.

Dravidoseps nilgiriensis Ganesh et al., 2021 comb. nov.

Figure 9C, Table 7

Chresonymy.

Subdoluseps nilgiriensis – Ganesh et al. (2021)

Holotype. BNHS 2642, unsexed adult, Anaikatti hills (11.110˚N, 76.769˚E; 600 m asl.) Coimbatore District, Tamil Nadu State, India, collected by Avrajjal Ghosh, SR Ganesh and NS Achyuthan on September 2019.

Paratypes (n = 2). BNHS 2643 and BNHS 2644, unsexed adults, same collection information as the holotype.

Additional material (n = 22). NRC-AA-1295 (AK R 1854), adult male from near Mangalamkombu (10.31831°N, 77.65654°E; elevation ca. 1400 m asl.) and NRC-AA-1296 (AK-R 1877), adult male from near

Mangalamkombu (10.303667°N, 77.640251°E; elevation ca. 1400 m asl.), Palani Hills, Dindigul District, Tamil Nadu, India, collected by Akshay Khandekar, Ishan Agarwal, Swapnil Pawar and team on 13th May 2022; NRC-AA-1297 (AK-R 2022), NRC-AA-1298 (AK-R 2023), subadults, from Aliyar Reserve Forest (10.48438°N, 76.92303°E; elevation ca. 400 m asl.), Anaimalai Tiger Reserve, Coimbatore District, same collectors as above except collected on 20th May 2022; NRC-AA-1299 (AK-R 2080), adult female, NRC-AA-1300 (AK-R 2081), subadult, from near Kattanchi view point (11.19985°N, 76.90867°E; elevation ca. 520 m asl.), close to Mettupalayam, Coimbatore District, same collectors as above except collected on 23th May 2022; NRC-AA-1301 (AK-R 2172), subadult, from Thamarakarai Forest Guesthouse campus (11.76779°N, 77.55715°E; elevation ca. 1000 m asl.), Erode District, same collectors as above except collected on 26th May 2022; BNHS 2559 (AK-R 2539), BNHS 2561 (AK-R 2541), adult females, BNHS 2560 (AK-R 2540), adult male, from near Kutladampatti Falls (10.12995°N, 78.01784°E; elevation ca. 280 m asl.), and BNHS 2562 (AK-R 2542), BNHS 2563 (AK-R 2543), subadults, from near Viralipatti (10.11638°N, 77.98282°E; elevation ca. 240 m asl.), Sirumalai Hills, Madurai District, same collectors as above except collected on 29th September 2022; BNHS 2564 (AK-R 2585), BNHS 2565 (AK-R 2586), ZSI-R-28603 (AK-R 2587), adult females, from Karanthamalai Hills (10.33737°N, 78.15939°E; elevation ca. 420 m asl.), Dindigul District, same collectors as above except collected on 3rd October 2022; ZSI-R-28604 (AK-R 2667), ZSI-R-28605 (AK-R 2668), adult males, ZSI-R-28606 (AK-R 2669), subadult, from Perunguntru trekking route (10.43080°N, 76.88132°E; elevation ca. 900 m asl.), and ZSI-R-28607 (AK-R 2671), ZSI-R-28608 (AK-R 2672), ZSI-R-28609 (AK-R 2673) subadults, from near Varagaliyar elephant camp (10.41913°N, 76.86747°E; elevation ca. 620 m asl.), Anaimalai Tiger Reserve, Coimbatore District, same collectors as above except collected on 9rd October 2022; ZSI-R-28694 (AK-R 2726), subadult, from Selur Reserve Forest, Kolli Hills (11.19463°N, 78.37537°E; elevation ca. 390 m asl.), Namakkal District, same collection data as above except on 12th October 2022.

Referred material (n = 1). AK-R-2173, same collection data as NRC-AA-1301 (AK-R 2172).

Etymology. Named for its type locality, the Nilgiri Hills.

Suggested common name. Nilgiri leaf-litter skink.

Diagnosis. A medium-sized skink snout to vent length up to 58 mm (n = 22). Seven supralabials and six (rarely seven, n = 4/22) infralabials up to angle of mouth; fifth supralabial elongate and below eye; two post-supralabials; seven or eight supraciliaries (rarely nine on one side, n = 1/19); a single slightly elongated nuchal on either side (rarely two on one side, n = 1/22), in contact with each other behind parietal (rarely separated by a single scale, n = 5/22); 62–70 scales in paravertebral rows; 26–30 scales around mid-body; 61–71 ventral scales; 8–10 enlarged precloacal scales; scales on lateral sides of tail base smooth, 19–21 scales around the tail. Subdigital lamellae unpaired, smooth on manus and smooth to weakly keeled on pes; five or six lamellae under digit I of manus (rarely four and seven, n = 1/22), and 5–7 under digit I of pes; 9–11 lamellae under digit IV of manus (rarely 12, n = 1/22); and 13–15 under digit IV of pes (rarely 16, n = 1/22). Dorsum brown with black markings; thick black stripe from rostrum to tail speckled with light spots, males with yellow on lower parts of forebody and flanks extending onto belly; supralabials with white streak; venter glossy grey-white with some darker markings.

Comparisons. *Dravidoseps nilgiriensis* **comb. nov.** can be diagnosed from known congeners based on the following characters: 28.1 ± 0.86 (26–30) RBS (versus 30.0 ± 0.00 (30) in *D. pruthi* **comb. nov.**, and 29.0 ± 1.00 (28–30 in *D. goaensis* **comb. nov.**); an average of 14.4 ± 0.76 (13–16) (versus 16.1 ± 1.20 (14–18) Lam4T in *D. pruthi* **comb. nov.**, and 13.4 ± 0.79 (13–15) in *D. goaensis* **comb. nov.**); two PoSL on each side (versus a single PoSL on each side in *D. pruthi* **comb. nov.**); a single NU on either side and Sb NU either absent or rarely only a single present (versus a single Nu on either side and two or three Sb Nu present in *D. pruthi* **comb. nov.**); unkeeled scales on tail base (versus keeled scales on tail base in *D. goaensis* **comb. nov.**). *Dravidoseps nilgiriensis* **comb. nov.** is diagnosed against the new species described below as part of their respective descriptions.

Distribution and natural history. *Dravidoseps nilgiriensis* **comb. nov.** is the most widely distributed member of the genus, known from the Western Ghats (north and south of Palghat gap) and hills outside the Western Ghats, between an elevation range of 200–1400 m asl.; in Tamil Nadu State, India (Fig. 1). In the Western Ghats, the species is known from Anaikatti (type locality) and Mettupalayam in the Nilgiri, multiple localities in Anaimalai Tiger Reserve, and Palani Hills; and outside the Western Ghats, from Thamarakarai, Kolli Hills, Sirumalai Hills, and two localities north of Sirumalai. The aerial distance between two farthest localities is > 185 km north-west (from Thamarakarai to Sirumalai Hills) and > 180 km east-west (from Anaimalai Tiger Reserve to Kolli Hills).

At Palani Hills, individuals were collected/ observed sheltering under rocks in the afternoon (1230–1330 hrs) in a small open patch surrounded by wet evergreen forest at high elevation (1400 m asl.). Sympatric lizards recorded were *Cnemaspis* cf. *palanica*, *Cyrtodactylus* (*Geckoella*) cf. *collegalensis*, *Dravidogecko* sp., *Eutropis* cf. *carinata*, *Kaestlea* sp. *Riopa albopunctata*, *Ristella* sp., and *Monilesaurus* cf. *rouxii*. At Anaimalai Tiger Reserve, the species was observed in a relatively open area surrounded by evergreen forest located along the Perunguntru trekking route, near Varagaliyar Elephant Camp, and also in moist deciduous to semievergreen forest at Aliyar Reserve Forest. Specimens were observed either buried in loose soil under rocks or moving in the leaf-litter during morning hours (0930–1200 hrs). Sympatric lizards recorded were *Cnemaspis* cf. *monticola*, *Cn.* cf. *littoralis*, *Eutropis carinata*, *E. macularia*, *Ristella* sp., *Sphenomorphus dussumieri* (Duméril & Bibron), *Calotes calotes* (Linnaeus), and *Monilesaurus* cf. *rouxii*. Near Mettupalayam, individuals were found under rocks in the morning (0930 hr) in thorny dry deciduous forests dominated by granite sheet rocks. Other sympatric skinks were *Eutropis bibronii* (Gray), and *Riopa albopunctata*. At Thamarakarai, a single juvenile was collected from under a rock in

Table 7 – part 1. Mensural (mm) and meristic data for *Dravidoseps nilgiriensis* **comb. nov.**. Abbreviations are listed in Materials and Methods except for: L&R = Left & Right; M = male; F= female; Sa = Subadult; * = data incomplete; / = data unavailable, # indicates discrepancy with original description (Ganesh et al. 2021).

Museum number	**BNHS 2642**	**BNHS 2643**	**BNHS 2644**	**NRC-AA-1295**	**NRC-AA-1296**	**NRC-AA-1297**	**NRC-AA-1298**	**NRC-AA-1299**	**NRC-AA-1300**	**NRC-AA-1301**	**BNHS 2559**	**BNHS 2560**	**BNHS 2561**
Type	**Holotype**	**Paratypes**		**Referred Material**									
Sex	F?	F?	F?	M	M	Sa	Sa	F	Sa	Sa	F	M	F?
SVL	57.1#	43.4#	43.7#	45.7	50.2	28.1	32.2	46.0	28.4	24.9	52.6	50.2	42.7
TL	48.2#	49.8#	38.3*#	41.3	43.9	7.2*	16.9*	44.9	7.6*	4.7*	43.2	34.7	31.2*
TW	3.9	3.5	3.6	4.7	5.2	2.2	2.4	3.6	2.2	2.0	4.7	5.1	3.6
FL	2.1*	2.6	2.8	3.1	2.9	2.0*	1.9*	2.5	1.8*	1.8	2.9	3.1	2.4
CL	4.1#	3.6	3.9	4.0	4.1	2.1*	2.5	3.5	2.0*	2.1	3.9	4.1	3.7
AGL	36.4#	25.5	25.9	25.8	28.5	16.2	18.8	29.6	15.4	14.2	31.7	30.4	25.8
BH	4.9	3.1	4.1	4.9	4.5	2.3	3.3	4.3	3.1	2.3	5.0	5.1	4.6
BW	6.2	5.3	5.8	7.3	7.7	4.2	5.0	6.7	3.8	4.0	8.4	7.4	6.7
HL	8.2	7.7#	8.0#	8.4	8.8	5.4	6.1	7.7	5.6	4.9	8.4	8.1	7.1
HW	5.8	4.7	5.0	6.2	6.0	3.4	3.9	4.5	2.4	3.0	5.6	6.0	4.9
HH	4.1	3.0	3.4	4.4	4.2	2.6	2.6	3.7	2.5	2.2	3.7	9.2	3.8
ED	1.7	1.4	1.7	1.7	1.8	1.2	1.4	1.6	1.3	1.2	1.5	1.7	1.4
TWD	/	/	/	0.6	0.7	0.6	0.6	0.7	0.5	0.5	0.8	0.8	0.7
EE	3.7#	3.1#	3.3#	3.3	3.6	2.2	2.5	3.0	2.2	2.1	3.1	3.2	2.9
EL	0.6	0.6	0.6	0.6	0.6	0.3	0.5	0.4	0.3	0.5	0.5	0.5	0.6
ES	3.4	3.0	3.3	3.3	3.6	2.1	2.5	3.0	2.2	2.1	3.2	3.5	2.8
EN	2.1	1.8	1.9	2.3	2.4	1.4	1.6	1.9	1.4	1.4	2.1	2.4	1.6
IN	1.3	1.3	1.3	1.4	1.6	0.9	1.0	1.4	1.1	0.8	1.5	1.5	1.3
IO	3.1	2.4	2.7	2.9	3.1	2.0	2.2	2.7	2.0	2.0	2.9	3.2	2.7
Nu	1&1	1&1	1&1	1&1	1&1	1&1	1&1	1&1	1&1	1&1	1&1	1&1	1&1
Sb Nu	1	0	0	0	0	0	0	1	0	0	1	0	0
SL L&R	7&7	7&7	7&7	7&7	7&7	7&7	7&7	7&7	7&7	7&7	7&7	7&7	7&7
IL L&R	6&6	7&6	7&7	7&6	6&7	6&6	6&6	6&6	6&6	6&6	6&6	6&6	6&6
PoSL L&R	2&2	2&2	2&2	2&2	2&2	2&2	2&2	2&2	2&2	2&2	2&2	2&2	2&2
Elo L&R	/	/	/	1&1	2&1	1&1	1&1	1&/	1&1	2&1	1&1	1&1	1&1
PVS	68	70#	67	63	63	67	66	67	67	67	66	64	63
RBS	28#	28	28	28	26	28	28	30	29	28	30	28	28
VS	66#	71	67#	64	63	68	67	65	63*	63	68	64	61
SPCLR	/	/	/	9	10	/	8	9	9	9	10	9	9
RTS	/	/	/	20	19	/	/	/	/	/	21	22	21
LamF1 L&R	5&5	4&5	6&6	6&7	*&6	5&5	5&5	6&6	5&5	5&5	6&6	6&6	5&5
LamF4 L&R	9&9	11&1	11&11	11&11	*&10	11&10	12&11	10&9	11&10	9&11	10&11	11&11	10&10

Museum number	BNHS 2642	BNHS 2643	BNHS 2644	NRC-AA-1295	NRC-AA-1296	NRC-AA-1297	NRC-AA-1298	NRC-AA-1299	NRC-AA-1300	NRC-AA-1301	BNHS 2559	BNHS 2560	BNHS 2561
Type	**Holotype**	**Paratypes**		**Referred Material**									
LamT1 L&R	5&5	5&5	7&6	6&6	6&6	6&6	6&5	6&5	6&6	5&5	5&5	6&6	5&5
LamT4 L&R	14&14	15&15	14&15	16&15	14&13	13&14	15&14	15&15	15&15	14&13	14&14	15&15	13&14
Elongate supralabial below eye, fourth (1) or fifth (0) L&R	/	/	/	0&0	0&0	0&0	0&0	0&0	0&0	0&0	0&0	0&0	0&0

Table 7 – part 2. Mensural (mm) and meristic data for *Dravidoseps nilgiriensis* **comb. nov.**. Abbreviations are listed in Materials and Methods except for: L&R = Left & Right; M = male; F= female; Sa = Subadult; * = data incomplete; / = data unavailable, # indicates discrepancy with original description (Ganesh et al. 2021).

Museum number	BNHS 2562	BNHS 2563	BNHS 2564	BNHS 2565	ZSI-R-28603	ZSI-R-28604	ZSI-R-28605	ZSI-R-28606	ZSI-R-28607	ZSI-R-28608	ZSI-R-28609	ZSI-R-28694
Type	**Nontypes**											
Sex	Sa	Sa	F	F	F	M	M	Sa	Sa	Sa	Sa	Sa
SVL	39.4	35.9	49.9	50.1	43.6	49.6	45.9	38.7	38.8	39.6	37.4	39.6
TL	5.9*	40	50.2	33.4	49.5	62.4	53.7	12.2*	44.6	47.4	12.4*	34.8
TW	3.5	3.1	5.0	4.7	4.2	4.4	4.4	3.3	3.7	3.7	3.4	3.1
FL	2.4	1.6*	2.8	3.1	2.8	3.2	2.8	2.0*	2.0	2.1	2.3	2.3
CL	3.5	3.1	4.3	4.1	3.7	4.3	3.7	3.1	3.1	3.2	3.3	3.3
AGL	21.8	20.4	30.1	29.3	24.9	28.4	25.7	23.5	24.1	25.2	22.1	22.9
BH	3.8	3.2	5.0	5.3	4.5	4.7	3.8	4.7	3.7	4.2	4.4	3.5
BW	5.4	5.5	8.4	8.1	7.4	7.1	6.8	6.4	5.9	5.4	5.4	5.7
HL	6.7	6.5	8.4	8.0	7.0	8.1	7.4	6.8	6.8	7.2	6.8	6.6
HW	4.4	4.3	6.4	5.7	5.4	5.6	5.4	4.5	4.8	5.1	4.3	4.5
HH	3.1	2.9	4.7	4.2	4.0	4.2	4.2	3.8	3.5	3.7	3.5	3.0
ED	1.4	1.4	1.7	1.7	1.6	1.7	1.6	1.3	1.5	1.4	1.5	1.4
TWD	0.6	0.6	0.6	0.8	0.6	0.7	0.5	/	0.7	0.6	0.6	0.7
EE	2.6	2.6	3.1	3.2	2.9	3.3	3.0	2.9	2.7	2.8	2.8	2.8
EL	0.5	0.5	0.7	0.6	0.5	0.7	0.6	0.6	0.5	0.5	0.5	0.6
ES	2.7	2.5	3.2	3.2	3.1	3.4	3.1	3.0	2.8	2.9	2.9	2.6
EN	1.7	1.5	2.2	2.0	2.1	2.3	2.2	1.9	1.7	1.8	1.7	1.6
IN	1.3	1.1	1.5	1.5	1.4	1.5	1.6	1.4	1.2	1.2	1.3	1.2
IO	2.4	2.3	3.0	3.0	2.7	3.0	2.9	2.8	2.3	2.4	2.7	2.4
Nu	1&2	1&1	1&1	1&1	1&1	1&1	1&1	1&1	1&1	1&1	1&1	1&1
Sb Nu	1	0	1	0	0	0	0	0	0	0	0	0

Museum number	BNHS 2562	BNHS 2563	BNHS 2564	BNHS 2565	ZSI-R-28603	ZSI-R-28604	ZSI-R-28605	ZSI-R-28606	ZSI-R-28607	ZSI-R-28608	ZSI-R-28609	ZSI-R-28694
Type	Nontypes											
SL L&R	7&7	7&7	7&7	7&7	7&7	7&7	7&7	7&7	7&7	7&7	7&7	7&7
IL L&R	6&6	6&6	6&6	6&6	6&6	6&6	6&6	6&6	6&6	6&6	6&6	6&6
PoSL L&R	2&2	2&2	2&2	2&2	2&2	2&2	2&2	2&2	2&2	2&2	2&2	2&2
Elo L&R	1&1	1&1	1&1	1&1	1&1	1&1	1&1	1&1	1&1	1&1	1&1	2&2
PVS	64	65	65	63	65	63	64	62	65	66	62	64
RBS	28	28	28	29	28	28	27	28	27	27	28	29
VS	66	61*	66	62	62	63	69	64	67	68	67	70
SPCLR	9	9	9	10	9	10	9	9	9	8	10	10
RTS	21	/	21	20	/	19	19	19	19	19	/	21
LamF1 L&R	5&6	6&6	5&6	5&5	6&6	7&7	6&6	6&6	6&6	6&6	5&6	5&5
LamF4 L&R	10&9	10&10	11&11	10&10	10&11	10&10	11&11	11&11	11&11	10&11	11&10	10&9
LamT1 L&R	6&6	6&6	6&6	5&6	6&6	6&5	6&6	7&6	6&6	5&6	7&6	5&5
LamT4 L&R	14&15	14&14	14&14	15&15	14&14	15&14	14&15	15&15	15&16	14&14	15&15	13&14
Elongate supra-labial below eye, fourth (1) or fifth (0) L&R	0&0	0&0	0&0	0&0	0&0	0&0	0&0	0&0	0&0	0&0	0&0	0&0

the forest guest house campus surrounded by deciduous forests (Fig. 11C). At Sirumalai Hills, Karanthamalai Hills and Kolli Hills, individuals were found under rocks or in leaf-litter during morning hours (0830–1100 hrs) in dry deciduous forest patches. Sympatric lizards recorded were *Cnemaspis* cf. *gracilis*, *Eutropis carinata*, *E. macularia*, *Riopa albopunctata*, *Calotes versicolor*, and *Psammophilus* cf. *blanfordanus*.

Reproduction. Unknown. No gravid female in the additional material examined (non-gravid females dissected: NRC-AA-1299, BNHS 2559, BNHS 2561, BNHS 2564, BNHS 2565 ranging in SVL from 42.7–52.6 mm).

Note. We examined the type series (holotype and two paratypes) of this species housed at BNHS and found discrepancies in some mensural (SVL, TL, AGL, CL, HL, EE) and meristic (PVS, RBS, VS) characters provided in the original description by Ganesh et al. (2021) and our data (Table 7). Additionally, the original description has two different SVL values for the holotype in the holotype description (63.23 mm) and 'table 4 (67.23 mm)' (Ganesh et al. 2021) versus our measurement of 57.1 mm.

Dravidoseps gingeeensis sp. nov.

https://zoobank.org/0284690E-ED9D-4930-926A-51A36370E9F6

Figures 8B, 9D, 13, Table 8

Chresonymy.
Lygosoma pruthi – Ganesh et al. (2018)

Holotype. NRC-AA-8273 (AK-R 147), adult female, from Pakkamalai Reserve Forest (12.17224°N, 79.31907°E; elevation ca. 400 m asl.), Gingee Hills, Viluppuram District, Tamil Nadu State, India, collected by Akshay Khandekar, Swapnil Pawar and team, on 3rd April 2021.

Paratype. BNHS 2568 (AK-R 192), adult female, from near Arulmigu Sri Pachaiamman Temple, Vedal (12.37095°N, 79.47239°E; elevation ca. 140 m asl.), Tiruvannamalai

District, Tamil Nadu State, India, same data as holotype except collected on 4th April 2021.

Etymology. The specific epithet is a toponym for the Gingee Hills in Villupuram District of Tamil Nadu State, the type locality of the new species.

Suggested common name. Gingee leaf-litter skink.

Diagnosis. A medium-sized skink snout to vent length up to 57 mm (n = 2). Seven supralabials and six or seven infralabials up to angle of mouth; fifth supralabial elongate and below eye; two post-supralabials; eight supraciliaries; a single slightly elongated nuchal on either side, separated by three scales behind parietal; 66 or 67 scales in paravertebral rows; 30–32 scales around mid-body; 67 ventral scales; 12 enlarged precloacal scales; scales on lateral sides of tail base smooth, 21 scales around the tail. Subdigital lamellae unpaired, smooth on manus and smooth to weakly keeled on pes; five or six lamellae under digit I of manus and six under digit I of pes; 11 or 12 lamellae under digit IV of manus and, 17 under digit IV of pes. Dorsum light brown with black markings; thick black stripe from rostrum to tail speckled with light spots; supralabials with white streak; venter glossy grey-white with some darker markings.

Comparisons. *Dravidoseps gingeeensis* **sp. nov.** can be diagnosed from known congeners based on the following characters: 12.0 ± 0.00 (12) SPCLR (versus 9.2 ± 0.60 (8–10) in *D. nilgiriensis* **comb. nov.**, 10.0 ± 0.00 (10) in *D. pruthi* **comb. nov.**, and 8.3 ± 0.76 (8–10) in *D. goaensis* **comb. nov.**); 17.0 ± 0.00 (17) LAM4T (versus 14.4± 0.76 (13–16) in *D. nilgiriensis* **comb. nov.**, 16.1 ± 1.20 (14–18) in *D. pruthi* **comb. nov.,** and 13.4 ± 0.79 (13–15) in *D. goaensis* **comb. nov.**); a single Nu on either side and three Sb Nu (versus a single NU on either side and Sb NU either absent or one or two presents in *D. goaensis* **comb. nov.**, and a single NU on either side and Sb NU either absent or rarely only a single present in *D. nilgiriensis* **comb. nov.**); presence of unkeeled scales on tail base (versus keeled scales on tail base in *D. goaensis* **comb. nov.**); 21 RTS (versus 18 or 19 RTS in *D. goaensis* **comb. nov.**). *Dravidoseps gingeeensis* **sp. nov.** is diagnosed against the new species described below as part of their respective descriptions.

Description of the holotype. Adult female (SVL 56.6 mm) in good state of preservation except head and tail tip slightly bent towards left side, and a 3.6 mm long incision at sternum region for liver tissue collection (Fig. 13A, B), and 15.5 mm long ventral incision at mid-body (made after taking morphological data and photos) to confirm eggs/developing embryos. Head short (HL/SVL 0.15), wide (HW/HL 0.72), not strongly depressed (HH/HL 0.58), indistinct from neck. Loreal region not inflated, canthus rostralis indistinct. Snout almost half head length (ES/HL 0.43), marginally more than twice eye diameter (ES/ED 2.03). Rostral twice as wide (1.8 mm) as long (0.9 mm), frontonasal much wider (1.9 mm) than long (1.3 mm), in contact with supranasals anteriorly, prefrontals and frontal posteriorly, anterior loreals laterally; prefrontals relatively small, widely separated on midline, in contact anteriorly with frontonasal, posteriorly with frontal, first supraocular and first supraciliary, anterior and laterally with posterior loreals. Frontal elongate, roughly bell-shaped, widest anteriorly at the point where prefrontals and first supraciliary connect; in contact with frontonasal anteriorly, frontoparietals posteriorly, prefrontals and first two supraoculars on either side; four supraoculars and one small post-supraocular and postocular on either side; frontoparietals in medial contact posterior to frontal, in contact with second, third, and fourth supraoculars anterolaterally and parietals and interparietal posteriorly. Interparietal large, roughly diamond-shaped, slightly projecting posteriorly, eyespot in posterior projection; postinterparietal absent; parietals large, in medial contact posterior to interparietal, in contact with frontoparietals, fourth supraocular, and post-supraocular anteriorly, two nuchal scales and three dorsal scales posteriorly, first secondary temporal laterally; a single enlarged nuchal scale on either side separated from each other by three dorsal scales (Fig. 13C). Nasals small, trapezoidal, widely separated, in contact with rostral anteriorly, supranasal dorsally, anterior loreal posteriorly, first supralabial ventrally; nostril in center of nasal; anterior loreal marginally taller (0.7 mm) than wide (0.6 mm); posterior loreal slightly larger than anterior loreal and slightly wider (1.0 mm) than tall (0.7 mm); a single small supra-preocular, an upper and lower preocular, and a single sub-preocular present only on right side (Fig. 13E). Eye small (ED/HL 0.21) with round pupil; lower eyelid with enlarged, transparent central window; eight supraciliaries on either side, anterior supraciliary largest, bordered by prefrontal anteriorly, first supraocular dorsally, and pre-supraocular, upper preocular and posterior loreal laterally; posterior superciliary elongate and projecting dorsomedially, bordered by fourth supraocular dorsally, post-supraocular posteriorly, and first post-subocular laterally; four post-suboculars on either side; a single primary temporal, two secondary temporals, and three tertiary temporals on either side; seven supralabials, fifth and sixth below eye; fifth supralabial elongate, in broad contact with pre-subocular and six small scales on lower eyelid below eye on either side; two post-supralabials on either side; six infralabials on either side; two scales separating post-supralabial and external ear opening; external ear opening small (EL/HL 0.07), oval, bearing two anterior lobules on either side; tympanum deep (Fig. 13E). Mental twice as wide (2.0 mm) as long (1.0 mm); a single large postmental in contact with first and second infralabials on either side; three enlarged pairs of chin shields posterior to postmental; anterior pair large (1.6 mm), roughly rectangular, in medial contact with each other below postmental and bordered by second and third infralabials, middle pair of chin shields, and by a single median gular scale on either side; middle pair largest (1.8 mm), roughly rectangular, separated from each other by two longitudinally arranged gular scales, bordered by third and fourth infralabials, posterior pair of chin shields, and four gular scales on either side; posterior pair smallest (1.0 mm), roughly square, separated from each other by five transversely arranged gular scales, bordered by fourth and fifth infralabials and three gular scales on either side; rest of the gular scales much smaller than postmentals, cycloid and imbricate, two or three rows bordering infralabials slightly smaller and elongate (Fig. 13D).

Body relatively slender (BW/AGL 0.27), elongate (AGL/SVL = 0.58); dorsal scales on body smooth, cycloid, imbricate; ventrals similar to dorsals except subequal from chest to vent, marginally larger on pectoral and precloacal region; 67 scales in paravertebral rows; 32 scales around mid-body; 67 ventral scales; 12 enlarged precloacal scales (Fig. 13A, B). Limbs, robust, short (FL/

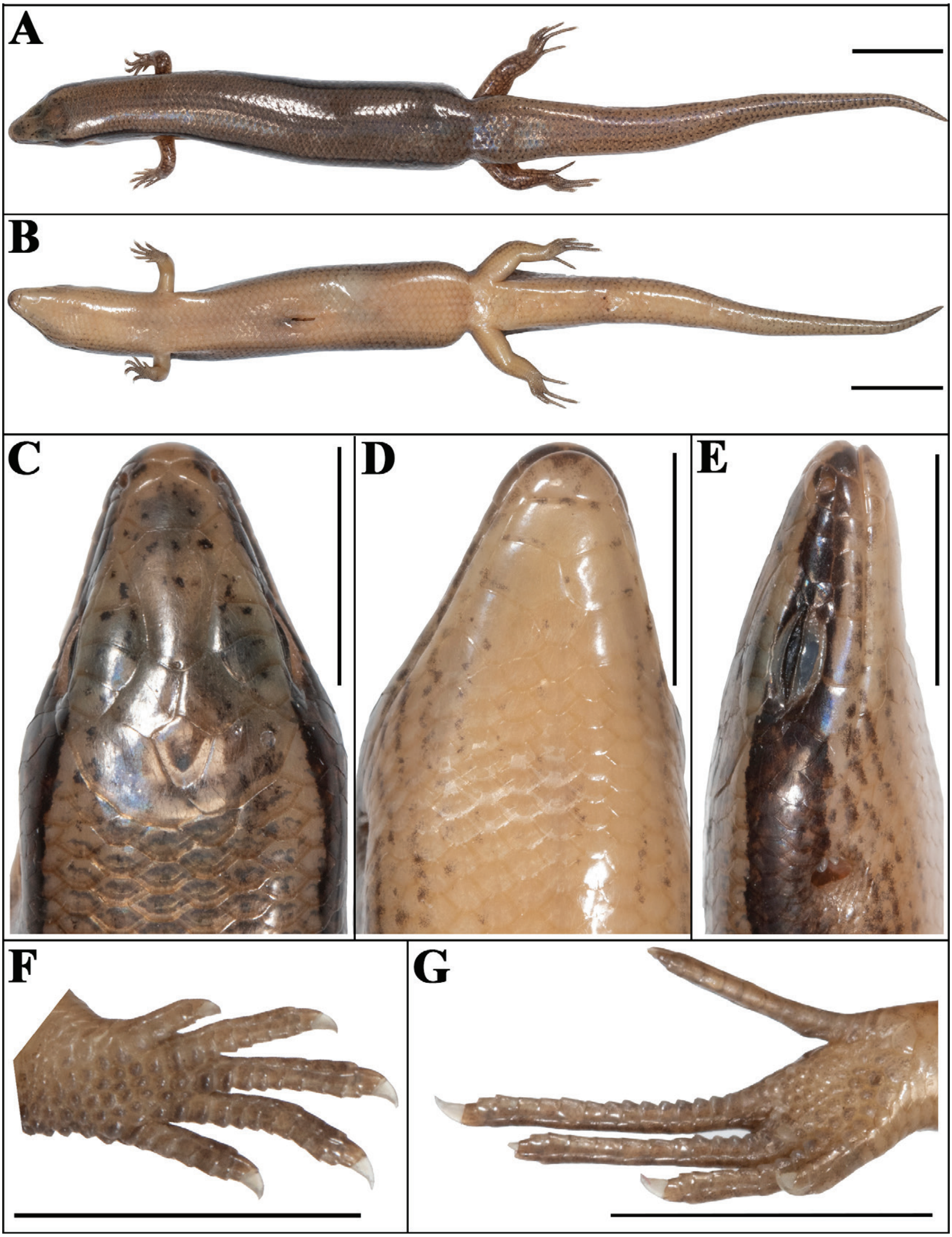

Figure 13. *Dravidoseps gingeeensis* **sp. nov.** (holotype, NRC-AA-8273): **A** dorsal view of body, **B** ventral view of body, **C** dorsal view of head, **D** ventral view of head, **E** lateral right side view of head, **F** ventral view of left manus, and **G** ventral view of left pes. Scale bars: A, B = 10 mm; C–E, G = 5 mm; F = 3 mm; photos by Akshay Khandekar.

SVL = 0.06; CL/SVL = 0.08), widely separated when adpressed; dorsal scales wider and slightly larger than ventral scales; palmar scales raised; plantar scales large, raised, coarse granules; all digits short, scales on dorsal surfaces in single row, subdigital lamellae unpaired, smooth on manus and smooth to weakly keeled on pes; lamellae series: 6-10-10-11-7 left manus (Fig. 13F), 6-10-14-17-13 left pes (Fig. 13G), 6-10-9-11-7 right manus,

Table 8. Mensural (mm) and meristic data for *Dravidoseps gingeeensis* **sp. nov.** and *Dravidoseps jawadhuensis* **sp. nov.**. Abbreviations are listed in Materials and Methods except for: L&R = Left & Right; M = male; F = female; Sa = Subadult; * = tail incomplete.

Museum number	**NRC-AA-8273**	**BNHS 2568**	**NRC-AA-8274**	**BNHS 2569**
	***D. gingeeensis* sp. nov.**		***D. jawadhuensis* sp. nov.**	
Type	Holotype	Paratype	Holotype	Paratype
Sex	F	F	M	Sa
SVL	56.6	53.6	46.6	32.5
TL	50.1	21.8*	13.6*	24.9*
TW	5.9	5.1	4.3	2.6
FL	3.5	3.6	3.3	2.5
CL	4.8	4.4	4.4	3.0
AGL	33.2	30.2	27.7	17
BH	5.8	4.6	4.6	3.2
BW	9.1	8.8	7.6	5.4
HL	9.0	9.0	7.6	6.3
HW	6.5	6.3	5.9	4.4
HH	5.3	4.2	4.2	3.1
ED	1.9	1.9	1.7	1.4
TWD	0.9	0.8	0.8	0.7
EE	3.4	3.4	3.0	2.6
EL	0.7	0.7	0.6	0.5
ES	3.9	3.6	3.4	2.7
EN	2.6	2.3	2.2	1.7
IN	1.4	1.5	1.4	1.2
IO	3.5	3.3	3.3	2.6
Nu	1&1	1&1	1&1	2&2
Sb Nu	3	3	0	0
SL L&R	7&7	7&7	7&7	7&7
IL L&R	6&6	7&7	6&6	6&6
PoSL L&R	2&2	2&2	2&2	2&2
Elo L&R	2&2	2&2	3&3	2&2
PVS	67	66	65	66
RBS	32	30	30	32
VS	67	67	68	66
SPCLR	12	12	13	12
RTS	21	21	22	23
LamF1 L&R	6&6	5&5	6&6	7&6
LamF4 L&R	11&11	11&12	11&11	11&11
LamT1 L&R	6&6	6&6	6&5	6&6
LamT4 L&R	17&17	17&17	17&17	16&16
Elongate supralabial below eye, fourth (1) or fifth (0) L&R	0&0	0&0	0&0	0&0

6-11-15-17-13 right pes. Relative length of digits (measurements in mm in parentheses): IV (2.4) > III (2.3) > II (1.9) > V (1.7) > I (1.1) (left manus); IV (4.5) > III (3.7) > V (2.8) > II (2.5) > I (1.3) (left pes).

Tail half original half regenerated, cylindrical, slightly shorter than snout-vent length (TL/SVL 0.88); dorsal and ventral scales on original tail cycloid, imbricate, similar to those on body dorsum; scales on lateral sides of tail base smooth, 21 scales around the tail; dorsal and ventral scales on regenerated tail similar to those on original tail except for median dorsal and subcaudal scale rows distinctly rectangular and larger than surrounding scales (Fig. 13A, B).

Colouration in life (Fig. 9D). Dorsal ground colouration of body, head and tail light brown with a bronze tint; head with scattered dark markings; dorsal scales of body and tail finely outlined by dark brown, centre of some scales with dark markings forming indistinct stripes; limbs darker than body dorsum and with light spots; a thick dark brown stripe running from rostrum through orbit and onto flank and tail with scattered light spots; supralabials with a white streak; ventral regions glossy, off-white with scattered black and grey markings.

Variation and additional information. Mensural and meristic data for the adult (SVL 53.6 mm) female paratype (BNHS 2568) are given in Table 8. It resemble the holotype female (NRC-AA-8273) in overall morphology, head scalation, and colouration except for the following variation: a single PrSbO on either side; three PoSbO on either side; and more than half of its tail is detached and missing.

Distribution and natural history. *Dravidoseps gingeeensis* **sp. nov.** is known from its type locality (Pakkamalai Reserve Forest in Viluppuram District; 400 m asl.) and paratype locality (Arulmigu Sri Pachaiamman Temple, near Vedal, Tiruvannamalai District; 140 m asl.), both in north-eastern Tamil Nadu, < 30 km apart from each other in aerial distance (Fig. 1). Both localities have sparse, dry tropical evergreen forests dominated by granite boulders (Fig. 8D). *Dravidoseps gingeeensis* **sp. nov.** was encountered during a single day of fieldwork at each locality. At Pakkamalai, the female holotype was collected from under a rock in leaf-litter inside a forested patch during the day (1130 hrs). At Vedal, the female paratype was observed feeding on cockroach in the morning (0915 hrs) in dry leaf-litter among granite boulders. Sympatric species at both localities recorded were *Calodactylodes aureus* (Beddome), *Hemidactylus frenatus* Duméril & Bibron; *Hemidactylus pakkamalaiensis* Narayanan et al., 2023, *Hemidactylus whitakeri*, *Eutropis carinata*, and *Psammophilus dorsalis*.

Reproduction. Viviparous, litter size four (two pairs of embryos in early stages of development in holotype NRC-AA-8273 (Fig. 8B).

Dravidoseps jawadhuensis sp. nov.

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Figures 9E, 14, Table 8

Chresonymy.
Lygosoma cf. *pruthi* – Ganesh and Arumugam (2016)
Lygosoma pruthi – Ganesh and Aengals (2018)
Subdoluseps pruthi – Ganesh et al. (2021).

Holotype. NRC-AA-8274 (CES 09/930), adult male, from near Beeman falls (12.60174°N, 78.84590°E; elevation ca. 450 m asl.), Jawadhu Hills, Vellore District, Tamil Nadu State, India, collected by Ishan Agarwal and team on 12th July 2009.

Paratype. BNHS 2569 (AK 850), subadult, from Beeman falls car parking (12.60513°N, 78.86947°E; elevation ca. 580 m asl.), same data as holotype except collected by Akshay Khandekar, Ishan Agarwal, Swapnil Pawar, Tejas Thackeray and team on 4th June 2019.

Etymology. The specific epithet is a toponym for the Jawadhu Hills in Vellore District of Tamil Nadu State, the type and currently only known locality for the new species.

Suggested common name. Jawadhu leaf-litter skink.

Diagnosis. A medium-sized skink snout to vent length up to 47 mm (n = 2). Seven supralabials and six infralabials up to angle of mouth; fifth supralabial elongate and below eye; two post-supralabials; seven or eight supraciliaries; one or two elongated nuchals on either side, in contact with each other behind parietal; 65 or 66 scales in paravertebral rows; 30–32 scales around mid-body; 66–68 ventral scales; 12 or 13 enlarged precloacal scales; scales on lateral sides of tail base smooth, 22 or 23 scales around the tail. Subdigital lamellae unpaired, smooth on manus and smooth to weakly keeled on pes; six or seven lamellae under digit I of manus and five or six under digit I of pes; 11 lamellae under digit IV of manus and, 16 or 17 under digit IV of pes. Dorsum dark brown with black markings; thick black stripe from rostrum to tail speckled with light spots; males with yellow on lower parts of forebody and flanks; supralabials with white streak; venter glossy off-white with some darker markings.

Comparisons. *Dravidoseps jawadhuensis* **sp. nov.** can be diagnosed from known congeners based on the following characters: five PoSbO on each side (versus three or four in *Dravidoseps gingeeensis* **sp. nov.**, four (rarely three or five on one side) in *D. nilgiriensis* **comb. nov.**, four on each side in *D. goaensis* **comb. nov.** and in *D. pruthi* **comb. nov.**); 12.5 ± 0.71 (12–13) SPCLR (versus 9.2 ± 0.60 (8–10) in *D. nilgiriensis* **comb. nov.**, 10.0 ± 0.00 (10) in *D. pruthi* **comb. nov.**, and 8.3 ± 0.76 (8–10) in *D. goaensis* **comb. nov.**); presence of unkeeled scales on tail base (versus keeled scales on tail base in *D. goaensis* **comb. nov.**); two PoSL on either side (versus single on either in *D. pruthi* **comb. nov.**); one or two Nu on either side and Sb Nu absent (versus a single Nu on either side and three Sb Nu in *D. gingeeensis* **sp. nov.**); 22 or 23 RTS (versus 21 RTS in *D. gingeeensis* **sp. nov.**). *Dravidoseps jawadhuensis* **sp. nov.** is diagnosed against the new species described below as part of their respective descriptions.

Description of the holotype. Adult male (SVL 45.7 mm) in good state of preservation except more than half of the tail missing (Fig. 14A, B). Head short (HL/SVL 0.16), wide (HW/HL 0.77), not strongly depressed (HH/HL 0.55), indistinct from neck. Loreal region not inflated, canthus rostralis indistinct. Snout almost half head length (ES/HL 0.44), two times eye diameter (ES/ED 2.00). Rostral almost twice as wide (1.7 mm) as long (0.9 mm), in broad contact with supranasals posteriorly and supralabial I and nasals on either side; supranasals marginally separated from each other below rostral by frontonasal, in contact with frontonasal posteriorly, nasals and anterior loreals laterally; frontonasal much wider (1.7 mm) than long (1.2 mm), in contact with supranasals anteriorly, prefrontals and frontal posteriorly, anterior loreals laterally; prefrontals relatively small, widely separated on midline, in contact with frontonasal anteriorly, frontal, first supraocular and first supraciliary posteriorly, anterior and posterior loreals laterally. Frontal elongate, roughly bell-shaped, widest anteriorly at the point where prefrontals and first supraocular connect; in contact with frontonasal anteriorly, frontoparietals posteriorly, prefrontals and first two supraoculars on either side; four supraoculars and one small post-supraocular and postocular on either side; frontoparietals in medial contact posterior to frontal, in contact with second, third, and fourth supraoculars anterolaterally and parietals and interparietal posteriorly. Interparietal large, roughly diamond-shaped, slightly projecting posteriorly, eyespot in posterior projection; postinterparietal absent; parietals large, in medial contact posterior to interparietal, in contact anteriorly with frontoparietals, fourth supraocular, and post-supraocular, two nuchal scales posteriorly, first secondary temporal laterally; a single enlarged, elongate, nuchal scale on either side in median contact posterior to parietals (Fig. 14C). Nasals small, trapezoidal, widely separated, in contact with rostral anteriorly, supranasal dorsally, anterior loreal posteriorly, first supralabial ventrally; nostril in center of nasal; anterior loreal slightly taller (0.8 mm) than wide (0.5 mm); posterior loreal larger than anterior loreal and slightly wider (0.9 mm) than tall (0.7 mm); a single small supra-preocular, an upper and lower preocular, and a single sub-preocular present on either sides (Fig. 14E). Eye small (ED/ HL 0.22) with round pupil; lower eyelid with enlarged, transparent central window; eight supraciliaries on left and seven on right, anterior supraciliary largest, bordered by prefrontal anteriorly, first supraocular dorsally, and pre-supraocular, upper preocular and posterior loreal laterally; posterior superciliary elongate and projecting dorsomedially, bordered by fourth supraocular dorsally, post-supraocular posteriorly, and first post-subocular laterally; five post-suboculars on either side; a single primary temporal, two secondary temporals, and three tertiary temporals on either side; seven supralabials, fifth elongate and in broad contact with pre-subocular, last post-subocular and five small scales on lower eyelid below eye on left and four on right side; two post-supralabials on either side; six infralabials on either side; two scales separating post-supralabial and external ear opening; external ear opening small (EL/HL 0.07), oval, bearing three anterior lobules on either side; tympanum deep (Fig. 14E). Mental twice wide (2.0 mm) as long (1.0 mm); a single large postmental in contact with first and second infralabials on either side; three enlarged pairs of chin shields posterior to postmental; anterior pair large (1.4 mm), roughly rectangular, in medial contact with each other below postmental and bordered by second and third infralabials, middle pair of chin shields, and by a single median gular scale on either side; middle pair largest (1.7 mm), roughly rectangular, separated from each other by two longitudinally arranged gular scales, bordered by third and fourth infralabials, posterior pair, and four gular scales on either side; posterior pair smallest (0.9 mm), roughly square, separated from each other by five transversely arranged gular scales, bordered by fourth and fifth infralabials and three gular scales on either side; rest of the gular scales much smaller than postmentals, cycloid and imbricate, two or three rows bordering infralabials slightly smaller and elongate (Fig. 14D).

Body relatively slender (BW/AGL 0.27), elongate (AGL/SVL = 0.59); dorsal scales on body smooth, cycloid, imbricate; ventrals similar to dorsals except subequal from chest to vent, marginally larger on pectoral and precloacal region; 65 scales in paravertebral rows; 30 scales around mid-body; 68 ventral scales; 13 enlarged precloacal scales (Fig. 14A, B). Limbs, robust, short (FL/SVL = 0.07; CL/SVL = 0.09), widely separated when adpressed; dorsal scales wider and slightly larger than ventral scales; palmar scales raised; plantar scales large, raised, coarse granules; all digits short, scales on dorsal surfaces in single row, subdigital lamellae unpaired, smooth on manus and smooth to weakly keeled on pes; lamellae series: 6-8-11-11-8 left manus (Fig. 14F), 6-10-15-17-12 left pes (Fig. 14G), 6-8-10-11-8 right manus, 5-11-14-17-12 right pes. Relative length of digits (measurements in mm in parentheses): IV (2.3) > III (2.2) > II (1.6) > V (1.4) > I (0.7) (left manus); IV (4.9) > III (4.1) > V (3.1) > II (2.4) > I (1.5) (left pes).

Tail original, cylindrical, more than half broken and lost; dorsal and ventral scales smooth, cycloid, imbricate, similar to those on body dorsum; scales on lateral tail base smooth, 22 scales around the tail (Fig. 14A, B).

Colouration in life (Fig. 9E). Dorsal ground colouration of body, head and tail dark brown; head with a few dark blotches on and between supraoculars; dorsal scales of body and tail finely outlined by dark brown, centre of scales with dark markings forming indistinct stripes; limbs darker than body dorsum and with light spots; a thick dark black stripe running from rostrum through orbit and onto flank and tail with scattered light spots; supralabials with a white streak; two or three rows of scales below the dark band between ear opening and mid-body yellow; ventral regions glossy cream with fine dark stripes.

Variation and additional information. Mensural and meristic data for the subadult paratype (SVL = 32.5 mm) is given in Table 8. It resembles the holotype male (NRC-AA-8274) in overall morphology and head scalation except for the following variation: supranasals in contact with each other behind rostral; seven SC present on either side; anterior pair of CS separated from each other below postmental; and tail tip collected in molecular grade ethanol for DNA extraction.

Distribution and natural history. *Dravidoseps jawadhuensis* **sp. nov.** is known only from the type locality (in and around Beeman falls), Jawadhu Hills in Vellore District, Tamil Nadu, India (Fig. 1). The new species was collected between elevations of 450–580 m from moist deciduous forests with scattered open rocky patches (Fig. 11E). The holotype was observed active at ~ 1130 hrs at the mouth of an ant burrow in a patch of deciduous forest with leaf litter. The subadult paratype was collected during the day time (1130 hrs) and was found under a rock surrounded by dry leaf-litter along a path leading towards Beeman fall. Sympatric lizards recorded were *Calodactylodes aureus*, *Cnemaspis* cf. *mysoriensis*, *Cn. otai* Das & Bauer, *Cyrtodactylus* (*Geckoella*) cf. *collegalensis*, *Hemidactylus frenatus*, *H.* cf. *graniticolus*, *H.*

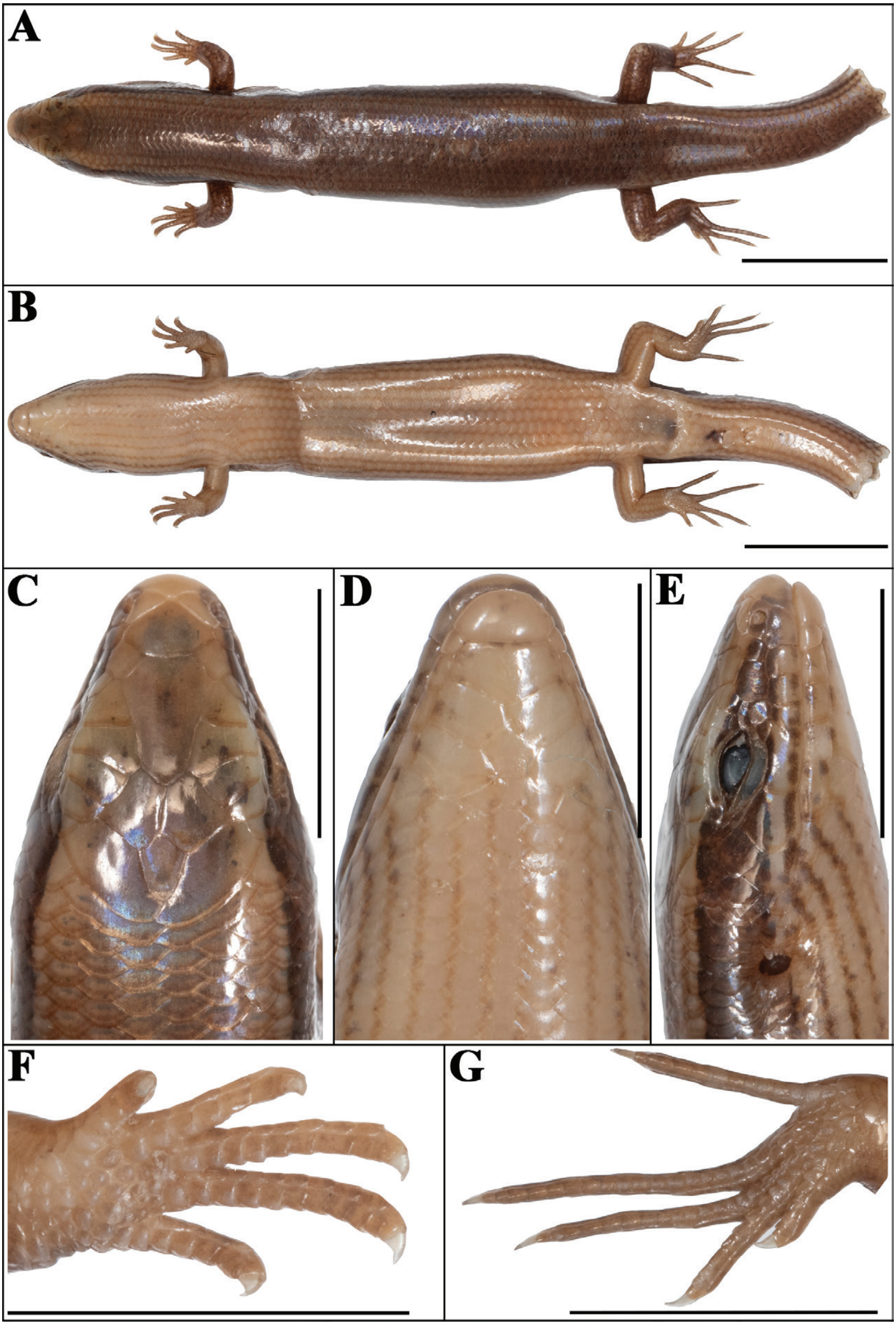

Figure 14. *Dravidoseps jawadhuensis* **sp. nov.** (holotype, NRC-AA-8274): **A** dorsal view of body, **B** ventral view of body, **C** dorsal view of head, **D** ventral view of head, **E** lateral right side view of head, **F** ventral view of left manus, and **G** ventral view of left pes. Scale bars: A, B = 10 mm; C–E, G = 5 mm; F = 3 mm; photos by Akshay Khandekar.

leschenaultii, *Eutropis carinata*, *E. macularia*, *Calotes versicolor*, and *Psammophilus dorsalis*.

Reproduction. Unknown, there are no females in the type series.

Note. We found the following discrepancies in mensural and meristic characters of specimen CES 09/930 as against the data provided by Ganesh et al. (2021) as *Subdoluseps pruthi*: TL (13.6* mm versus 31.22 mm; * = tail incomplete), HL (7.6 mm versus 6.27 mm), PVS (65 versus 62), RBS (30 versus 34) VS (68 versus 69), and LamT4 (17 versus 16) (Table 8).

Dravidoseps kalakadensis sp. nov.

https://zoobank.org/A27644AB-35E1-4D4E-8C73-E971BA1304A0

Figures 8C–E, 9F, 15, Table 9

Holotype. NRC-AA-8275 (AK-R 984), adult male, from near Wood House, Talayanai road, (8.52200°N, 77.50403°E; elevation ca. 200 m asl.), Kalakadu Reserve Forest, Kalakad-Mundanthurai Tiger Reserve (KMTR), Tirunelveli District, Tamil Nadu State, India, collected by Akshay Khandekar, Ishan Agarwal, Swapnil Pawar and team, on 30th March 2022.

Paratypes (n = 9). ZSI-R-28614 (AK-R 982), adult male, ZSI-R-28615 (AK-R 983) adult female, same data as holotype; NRC-AA-8278 (AK-R 666), adult male, BNHS 2829 (AK-R 667), ZSI-R-28613 (AK-R 981), adult females, from below Sengaltheri (8.52824°N, 77.47968°E; elevation ca. 400 m asl.), collected by Akshay Khandekar, Swapnil Pawar and team on 4th May 2021; NRC-AA-8276 (AK-R 605), adult male, NRC-AA-8277 (AK-R 606), subadult, from Therku Viravallanur Reserve Forest (8.57553°N, 77.53916°E; elevation ca. 400 m asl.) collected by Akshay Khandekar, Swapnil Pawar and team on 5th May 2021; BNHS 2830 (AK-R 700), BNHS 2831 (AK-R 701), adult males from near Kodumudiyaru dam (8.43122°N, 77.52425°E; elevation ca. 400 m asl.), Thirukkurungudi Reserve Forest, collected by Akshay Khandekar, Swapnil Pawar and team on 8th May 2021; all from KMTR, Tirunelveli District, Tamil Nadu State, India.

Etymology. The specific epithet is a toponym for Kalakad in Kalakad-Mundanthurai Tiger Reserve (KMTR), Tirunelveli District of Tamil Nadu State, the type locality of the new species.

Suggested common name. KMTR leaf-litter skink.

Diagnosis. A medium-sized skink snout to vent length up to 55.7 mm (n = 10). Six or seven supralabials and six infralabials up to angle of mouth; fourth supralabial elongate and below eye (rarely fifth on both sides, n = 1/10 or and fifth only on one side, n = 3/10); two post-supralabials (rarely single on one side, n = 2/10); seven supraciliaries; one elongated nuchal on either side (rarely two on one side, n = 2/10), in contact with each other behind parietal; 63–66 scales in paravertebral rows; 28 scales around mid-body; 64–71 ventral scales; eight enlarged precloacal scales; scales on lateral sides of tail base smooth, 18 or 19 scales around the tail. Subdigital lamellae unpaired, smooth on manus and smooth to weakly keeled on pes; five lamellae under digit I of manus (rarely four on one of the side, n = 1/10); five or six under digit I of pes; 10 or 11 lamellae under digit IV of manus (rarely nine on one of the side, n = 1/10); and 14–16 under digit IV of pes. Dorsum coconut brown with black markings; thick brown stripe from rostrum to tail speckled with light spots; supralabials with white streak; males with yellow on lower parts of forebody and flanks extending onto belly; venter glossy grey-white without darker markings.

Comparisons. *Dravidoseps kalakadensis* **sp. nov.** can be diagnosed from known congeners based on the following characters: 28.0 ± 0.00 (28) RBS (versus 30.0 ± 0.00 (30) in *D. pruthi* **comb. nov.**, and 31.0 ± 1.41 (30–32) in *D. gingeeensis* **sp. nov.** and in *S. jawadhuensis* **sp. nov.**); 8.0 ± 0.00 (8) SPCLR (versus 12.0 ± 0.00 (12) in *D. gingeeensis* **sp. nov.**, 12.5 ± 0.71 (12–13) in *D. jawadhuensis* **sp. nov.**, 9.2 ± 0.60 (8–10) in *D. nilgiriensis* **comb. nov.**, 10.0 ± 0.00 (10) SPCLR in *D. pruthi* **comb. nov.**, and 8.3 ± 0.76 (8–10) in *D. goaensis* **comb. nov.**); 18.7 ± 0.52 (18–19) RTS (versus 21.0 ± 0.00 (21) in *D. gingeeensis* **sp. nov.**, 22.5 ± 0.71 (22–23) in *D. jawadhuensis* **sp. nov.**, 20.1 ± 1.07 (19–22) in *D. nilgiriensis* **comb. nov.**, and 21.4 ± 0.89 (21–23) in *D. pruthi* **comb. nov.**); six SL (rarely seven on just one specimen on both sides and on three specimens on one side) (versus seven SL in *D. pruthi* **comb. nov.**, *D. nilgiriensis* **comb. nov.**, *D. gingeeensis* **sp. nov.**, and *D. jawadhuensis* **sp. nov.**); SL IV elongate and below eye (rarely SL V elongate and below eye, on just one specimen on either side and on three specimens on one side) (versus SL V elongate and below eye in *D. pruthi* **comb. nov.**, *D. nilgiriensis* **comb. nov.**, *D. gingeeensis* **sp. nov.**, *D. jawadhuensis* **sp. nov.**, and in *D. goaensis* **comb. nov.** (SL IV elongate and below eye only on two specimens on one side)); a single (rarely two on one side) Nu on either side and Sb Nu absent (versus a single Nu on either side and two or three Sb Nu present in *D. pruthi* **comb. nov.**, and a single Nu on either side and three Sb Nu in *D. gingeeensis* **sp. nov.**); presence of unkeeled scales on tail base (versus keeled scales on tail base in *D. goaensis* **comb. nov.**). *Dravidoseps kalakadensis* **sp. nov.** is diagnosed against the new species described below as part of their respective descriptions.

Description of the holotype. Adult male (SVL 45.7 mm) in good state of preservation except body and tail tip slightly bent towards left side, tail slightly detached at its half-length from ventral side, and hemipenis everted partially on left and entirely on right (Fig. 15A, B). Head short (HL/SVL 0.16), wide (HW/HL 0.72), not strongly depressed (HH/HL 0.53), indistinct from neck. Lore-

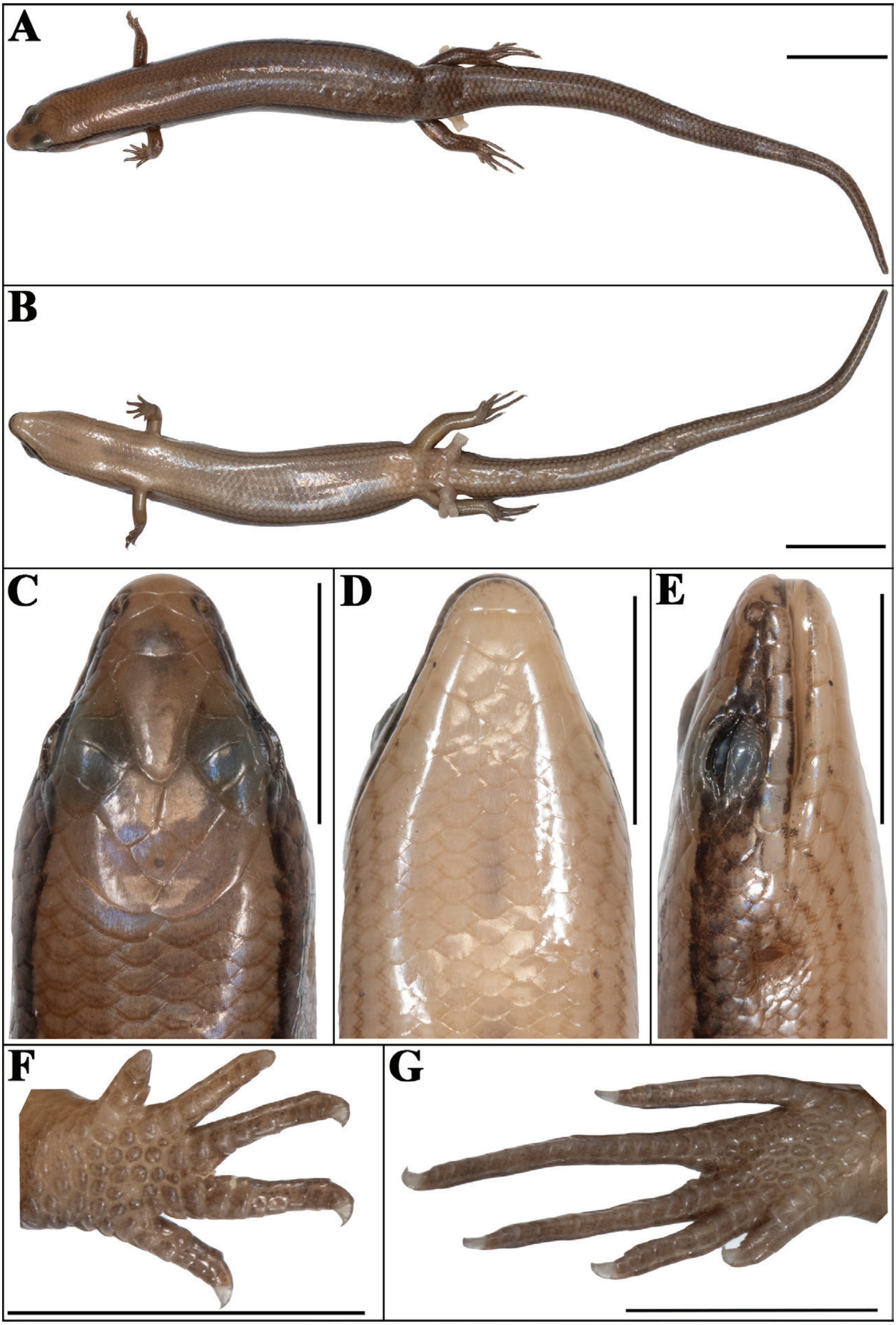

Figure 15. *Dravidoseps kalakadensis* **sp. nov.** (holotype, NRC-AA-8275): **A** dorsal view of body, **B** ventral view of body, **C** dorsal view of head, **D** ventral view of head, **E** lateral right side view of head, **F** ventral view of left manus, and **G** ventral view of left pes. Scale bars: A, B = 10 mm; C–E, G = 5 mm; F = 3 mm; photos by Akshay Khandekar.

al region not inflated, canthus rostralis indistinct. Snout almost half head length (ES/HL 0.41), slightly less than twice eye diameter (ES/ED 1.88). Rostral more than twice as wide (1.7 mm) as long (0.8 mm), in broad contact with supranasals posteriorly and supralabial I and nasals on either side; supranasals in contact with each other medially, frontonasal posteriorly, nasals and anterior loreals laterally; frontonasal much wider (1.8 mm) than long (1.1 mm), in contact with supranasals anteriorly, prefrontals and frontal posteriorly, anterior loreals laterally; prefrontals relatively small, widely separated on midline, in contact with frontonasal anteriorly, frontal, first supraocular and first supraciliary posteriorly, anterior and posterior loreals laterally. Frontal elongate, roughly bell-shaped, widest anteriorly at the point where prefrontals and first supraciliary connect; in contact with frontonasal anteriorly, frontoparietals posteriorly, prefrontals and first two supraoculars on either side; four supraoculars and one small post-supraocular and postocular on either side; frontoparietals in medial contact posterior to frontal, in contact with second, third, and fourth supraoculars anterolaterally and parietals and interparietal posteriorly. Interparietal large, roughly diamond-shaped, slightly projecting posteriorly, eyespot in posterior projection; postinterparietal absent; parietals large, in medial contact posterior to interparietal, in contact with frontoparietals, fourth supraocular, and post-supraocular anteriorly, two nuchal scales posteriorly, first secondary temporal laterally; a single enlarged, elongate, nuchal scale on either side in median contact posterior to parietals (Fig. 15C). Nasals small, trapezoidal, widely separated, in contact with rostral anteriorly, supranasal dorsally, anterior loreal posteriorly, first supralabial ventrally; nostril in center of nasal; anterior loreal marginally taller (0.6 mm) than wide (0.5 mm); posterior loreal slightly larger than anterior loreal and slightly wider (0.8 mm) than tall (0.7 mm); a single small supra-preocular, an upper and lower preocular, and a single sub-preocular present only on either side (Fig. 15E). Eye small (ED/ HL 0.22) with round pupil; lower eyelid with enlarged, transparent central window; seven supraciliaries on either side, anterior supraciliary largest, bordered by prefrontal anteriorly, first supraocular dorsally, and pre-supraocular, upper preocular and posterior loreal laterally; posterior superciliary elongate and projecting dorsomedially, bordered by fourth supraocular dorsally, post-supraocular posteriorly, and first post-subocular laterally; four post-suboculars on either side; a single primary temporal, two secondary temporals, and three tertiary temporals on either side; six supralabials, fourth and fifth below eye; fourth supralabial elongate, in broad contact with pre-subocular, last post-subocular and four small scales on lower eyelid below eye on either side; two post-supralabials on either side; six infralabials on either side; two scales separating post-supralabial and external ear opening; external ear opening small (EL/HL 0.09), oval, bearing a single anterior lobule on either side; tympanum deep (Fig. 15E). Mental slightly more than twice as wide (1.9 mm) as long (0.8 mm); a single large postmental in contact with first and second infralabials on either side; three enlarged pairs of chin shields posterior to postmental; anterior pair large (1.4 mm), roughly rectangular, in medial contact with each other below postmental and bordered by second and third infralabials, middle pair of chin shields, and by a single median gular scale on either side; middle pair largest (1.7 mm), roughly rectangular, separated from each other by two longitudinally arranged gular scales, bordered by posterior pair of chin shields, four gular scales on either side, and third and fourth infralabials on left and only third infralabial on right side; posterior pair smallest (0.9 mm), roughly square, separated from each other by five transversely arranged gular scales, bordered by fourth and fifth infralabials and three gular scales on either side; rest of the gular scales much smaller than postmentals, cycloid and imbricate, two or three rows bordering infralabials slightly smaller and elongate (Fig. 15D).

Body relatively slender (BW/AGL 0.26), elongate (AGL/SVL = 0.57); dorsal scales on body smooth, cycloid, imbricate; ventrals similar to dorsals except subequal from chest to vent, marginally larger on pectoral and precloacal region; 63 scales in paravertebral rows; 28 scales around mid-body; 66 ventral scales; eight enlarged precloacal scales (Fig. 15A, B). Limbs, robust, short (FL/SVL = 0.05; CL/SVL = 0.08), widely separated when adpressed; dorsal scales wider and slightly larger than ventral scales; palmar scales raised; plantar scales large, raised, coarse granules; all digits short, scales on dorsal surfaces in single row, subdigital lamellae unpaired, smooth on manus and smooth to weakly keeled on pes; lamellae series: 4-6-9-10-7 left manus (Fig. 15F), 6-9-14-16-10 left pes (Fig. 15G), 5-8-9-10-7 right manus, 6-9-16-16-11 right pes. Relative length of digits (measurements in mm in parentheses): IV (1.7) > III (1.6) > II (1.3) > V (1.0) > I (0.9) (left manus); IV (4.9) > III (3.1) > V (2.5) > II (2.1) > I (1.0) (left pes).

Tail original, entire, cylindrical, slightly longer than snout-vent length (TL/SVL 1.14); dorsal and ventral scales cycloid, imbricate, similar to those on body dorsum except for median dorsal and median subcaudal scale rows somewhat larger than surrounding scales on tail; scales on lateral sides of the base tail base smooth, 19 scales around the tail counted (Fig. 15A, B)).

Colouration in life (Fig. 9F). Dorsal ground colouration of body, head and tail dull coconut brown; head with scattered dark markings; head with a large dark blotch on the frontonasal; dorsal scales of body and tail finely outlined by dark brown, centre of scales with dark markings forming indistinct stripes, more prominent on tail; limbs darker than body dorsum and with light spots; a thick dark brown stripe running from rostrum through orbit and onto flank and tail with scattered light spots; supralabials with a white streak; yellow markings below dark stripe from throat to hindlimb insertions extending onto belly; ventral regions glossy grey-white.

Variation and additional information. Mensural and meristic data for the paratype series are given in Table 9. There are six adult males, three adult females and a single subadult. All specimens resemble the holotype male

Table 9. Mensural (mm) and meristic data for *Dravidoseps kalakadensis* **sp. nov.**. Abbreviations are listed in Materials and Methods except for: L&R = Left & Right; M = male; F = female; Sa = Subadult; * = tail and lamellae incomplete; and / = data unavailable.

Museum number	**NRC-AA-8275**	**NRC-AA-8276**	**NRC-AA-8277**	**NRC-AA-8278**	**BNHS 2829**	**BNHS 2830**	**BNHS 2831**	**ZSI-R-28613**	**ZSI-R-28614**	**ZSI-R-28615**
Type	Holotype	Paratypes								
Sex	M	M	Sa	M	F	M	M	F	M	F
SVL	45.7	46.5	38.3	46.6	49.4	50.8	43.6	56.0	50.5	50.0
TL	52.1	52.8	43.8	32.9	41.4	40.9	30.7	29.9	39.7	7.8*
TW	4.5	3.7	3.5	4.6	4.6	5.2	3.6	5.2	4.4	4.7
FL	2.7	3.2	2.5	2.9	2.9	3.1	2.9	3.5	2.9	2.9
CL	3.9	4.0	3.3	3.9	3.9	4.2	3.6	4.1	4.6	3.6
AGL	26.5	26.9	21.1	26.9	29.0	30.7	25.5	36.4	30	30
BH	5.5	3.6	2.7	5.0	5.5	4.4	3.2	7.2	5.7	5.1
BW	7.0	6.8	5.8	6.6	6.7	7.9	5.9	10.1	7.9	8.0
HL	7.7	7.6	7.1	8.4	7.5	8.8	7.6	8.4	9.0	7.5
HW	5.6	5.5	4.6	5.8	5.8	6.4	5.1	6.1	6.2	4.9
HH	4.1	3.5	3.3	4.2	3.5	4.3	3.5	4.4	4.1	3.5
ED	1.7	1.6	1.5	1.6	1.5	1.7	1.6	1.7	1.7	1.6
TWD	0.7	0.7	0.7	0.7	0.7	0.7	0.7	0.7	0.8	0.7
EE	3.3	2.7	2.7	3.3	2.8	3.5	2.9	3.5	3.6	3.1
EL	0.7	0.7	0.4	0.5	0.6	0.6	0.7	0.5	0.7	0.6
ES	3.2	3.0	2.7	3.3	3.1	3.6	3.1	3.3	3.4	3.1
EN	2.0	1.9	1.6	2.3	1.9	2.2	1.9	2.2	2.0	1.9
IN	1.5	1.3	1.3	1.5	1.3	1.5	1.3	1.4	1.6	1.3
IO	2.8	3.0	2.7	3.1	3.0	3.3	2.9	3.2	3.1	2.7
Nu	1&1	1&1	2&1	1&1	1&1	1&1	1&1	1&2	1&1	1&1
Sb Nu	0	0	0	0	0	0	0	0	0	0
SL L&R	6&6	6&6	7&6	6&7	6&6	6&6	6&6	7&7	6&6	7&6
IL L&R	6&6	6&6	6&6	6&6	6&6	6&6	6&6	6&6	6&6	6&6
PoSL L&R	2&2	2&2	2&2	2&2	2&2	2&1	2&1	2&2	2&2	2&2
Elo L&R	1&1	1&1	2&2	1&1	1&1	1&1	1&2	1&1	1&1	1&1
PVS	63	65	66	64	64	65	64	64	66	65
RBS	28	28	28	28	28	28	28	28	28	28
VS	66	68	68	64	71	67	65	70	68	68
SPCLR	8	8	8	8	8	8	8	8	8	8
RTS	19	18	/	19	19	18	/	/	19	/
LamF1 L&R	4&5	5&5	5&5	4*&5	5&5	5&5	5&5	5&5	5&5	5&5
LamF4 L&R	10&10	10&10	10&11	8*&9*	10&11	10&5*	10&10	9&10	10&10	10&10
LamT1 L&R	6&6	5&5	6&5	5&5	5&5	6&5	6&6	5&6	6&6	6&6
LamT4 L&R	16&16	14&15	15&15	15&15	15&15	15&15	15&14	15&14	15&15	14&15
Elongate supra-labial below eye, fourth (1) or fifth (0) L&R	1&1	1&1	0&1	1&0	1&1	1&1	1&1	0&0	1&1	0&1

(NRC-AA-8275) in overall morphology and head scalation except for the following variation: three PoSbO on either side in ZSI-R-28613, three on left and four on right side in BNHS 2830 and ZSI-R-28615, four on left and three on right side in NRC-AA-8278; middle postmental bordered by IL III and IV, posterior pair of CS, and four gular scales on either side in all paratypes. NRC-AA-8276 with complete and original tail, slightly longer than body (TL/SVL 1.13 mm); ZSI-R-28615 without tail; rest of the paratypes with either fully or partially regenerated tails, shorter than body. BNHS 2830 and ZSI-R-28614 with partial or fully everted hemipenis on either side. NRC-AA-8276–8278 and BNHS 2829–2831 with small incision in sternum region for liver tissue collection. Three gravid females – BNHS 2829, ZSI-R-28613, and ZSI-R-28615 with longitudinal incision on ventral midbody (17.5, 29.0, and 21.2 mm, respectively) to check for eggs/ developing embryos. NRC-AA-8278 (adult male) was dissected (12.4 mm long incision on ventral mid-body) to confirm the sex.

Distribution and natural history. *Dravidoseps kalakadensis* **sp. nov.** is known only from a few closely spaced localities (< 20 km in aerial distance) on the eastern slopes of the southern Western Ghats in Kalakad-Mundanthurai Tiger Reserve (Fig. 1). All localities are dry and moist deciduous forests at elevations between 200–400 m asl. (Fig. 11F). At Kalakad, *D. kalakadensis* **sp. nov.** was observed moving in dry leaf-litter at night (1900–2100 hrs) after being disturbed. *Dravidoseps kalakadensis* **sp. nov.** was observed moving in leaf-litter and also found under rocks during the day (0730–1030 hrs) at Therku Viravallanur and Thirukkurungudi Reserve forests. Sympatric lizards encountered were *Hemidactylus acanthopholis* Mirza & Sanap, *H. frenatus*, *H. leschenaultii*, *H. whitakeri*, *Cnemaspis azhagu* Khandekar, Thackeray & Agarwal, *Cn. mundanthuraiensis* Khandekar, Thackeray & Agarwal, *Eutropis carinata*, *E. macularia*, *Riopa albopunctata*, *Calotes calotes*, *Ca. versicolor*, and *Psammophilus dorsalis*.

Reproduction. Viviparous, litter size two or three. ZSI-R-28613, three embryos in late stages of development; ZSI-R-28615, two embryos in late stages of development; and BNHS 2829, two embryos in early stages of development (Fig. 8C–E).

Dravidoseps srivilliputhurensis sp. nov.

https://zoobank.org/6B09E0ED-CB46-4EBB-A003-053A910683D7

Figures 8F–N, 9G, 16, Table 10

Holotype. NRC-AA-8279 (AK-R 1344), adult male, from near Ayyanar Kovil Falls (9.51294°N, 77.45183°E; elevation ca. 340 m asl.), Srivilliputhur-Megamalai Tiger Reserve (SMTR), Virudhunagar District, Tamil Nadu State, India, collected by Akshay Khandekar, Ishan Agarwal, Swapnil Pawar and team on 16th April 2022.

Paratypes (n = 19). NRC-AA-8280 (AK-R 1343), NRC-AA-8281 (AK-R 1345), adult females, same data as holotype; NRC-AA-8283 (AK-R 1347), adult male, NRC-AA-8282 (AK-R 1346), NRC-AA-8284 (AK-R 1348), adult females, from near Sri Sastha Kovil, Settur Reserve Forest (9.40362°N, 77.37211°E; elevation ca. 340 m asl.), and NRC-AA-8285 (AK-R 1349), adult female, (9.47178°N, 77.42983°E; elevation ca. 300 m asl.), Madurai District, same collectors as holotype except collected on 17th April 2022; BNHS 2832 (AK-R 1434), BNHS 2833 (AK-R 1435), BNHS 2834 (AK-R 1436), adult females, (9.58131°N, 77.55227°E; elevation ca. 960 m asl.), and BNHS 2835 (AK-R 1455), adult female, from Shenbagathoppu (9.55173°N, 77.55445°E; elevation ca. 200 m asl.), Virudhunagar District, same collectors as holotype except collected on 20th April 2022; BNHS 2836 (AK-R 1489), BNHS 2837 (AK-R 1490), BNHS 2838 (AK-R 1491), adult females, from near Atthi Kovil (9.59990°N, 77.53374°E; elevation ca. 200 m asl.), Virudhunagar District, same collectors as holotype except collected on 25th April 2022; BNHS 2839 (AK-R 1492), ZSI-R-28616 (AK-R 1493), ZSI-R-28617 (AK-R 1516), adult females, from near Sathuragiri Falls (9.70927°N, 77.63074°E; elevation ca. 240 m asl.), Madurai District, same collectors as holotype except collected on 26th April 2022; ZSI-R-28618 (AK-R 1716), from near Chinnasurli Falls, Megamalai (9.70961°N, 77.42213°E; elevation ca. 610 m asl.), Theni District, same collectors as holotype except collected on 4th May 2022; ZSI-R-28619 (AK-R 1761), ZSI-R-28620 (AK-R 1762), subadults, from near Megamalai Viewpoint (9.72559°N, 77.41983°E; elevations ca. 1000 m asl.), Theni District, same collectors as holotype except collected on 8th May 2022; all from SMTR, Tamil Nadu State, India.

Referred material (n = 1). AK-R-1717, same collection data as ZSI-R-28618 (AK-R 1716).

Etymology. The specific epithet is a toponym for Srivilliputhur in Srivilliputhur-Megamalai Tiger Reserve (SMTR), Virudhunagar District of Tamil Nadu State, the type locality of the new species.

Suggested common name. SMTR leaf-litter skink.

Diagnosis. A medium-sized skink snout to vent length up to 56 mm (n = 20). Seven supralabials (rarely six on one of the side, n = 1/20) and six infralabials (rarely seven on one of the side, n = 1/20) up to angle of mouth; fifth supralabial elongate and below eye (rarely fourth on one of the side, n = 1/20); two post-supralabial; seven supraciliaries (rarely six or eight n = 1 each/20); one elongated nuchal on either side (rarely two, n = 3/20), in median contact behind parietal (rarely separated by one or two scales, n = 5/20); 63–66 scales in paravertebral rows; 26–28 scales around mid-body (rarely 29, n = 1/20); 62–68 ventral scales (rarely 70, n = 1/20); 8–10 enlarged precloacal scales; scales on lateral sides of tail base smooth, 19–21 scales around the tail. Subdigital lamellae unpaired, mostly smooth; five or six lamellae under digit I of manus and pes; 9–11 lamellae under digit IV of manus (rarely 12, n = 1/20); and 13–16 under digit IV of pes (rarely 12, 17; n = 1/20). Dorsum bronze-brown with black markings; thick brown stripe from rostrum to tail speckled with light spots; supralabials with white streak; males with yellow on lower parts of forebody and flanks extending onto belly; venter glossy grey-white without darker markings.

Comparisons. *Dravidoseps srivilliputhurensis* **sp. nov.** can be diagnosed from known congeners based on the following characters: 27.8 ± 0.79 (26–29) RBS (versus 31.0 ± 1.41 (30–32) in *D. gingeeensis* **sp. nov.** and *D. jawadhuensis* **sp. nov.**, 28.1 ± 0.86 (26–30) in *D. nilgiriensis* **comb. nov.**, 30.0 ± 0.00 (30) in *D. pruthi* **comb. nov.**, and 29.0 ± 1.00 (28–30) in *D. goaensis* **comb.

nov.); 14.8 ± 0.97 (13–17) Lam4T (versus 17.0 ± 0.00 (17) in *D. gingeeensis* **sp. nov.**, 16.5 ± 0.71 (16–17) in *D. jawadhuensis* **sp. nov.**, 16.1 ± 1.20 (14–18) in *D. pruthi* **comb. nov.**, and 13.4 ± 0.79 (13–15) in *D. goaensis* **comb. nov.**); 9.2 ± 0.77 (8–10) SPCLR (versus 10.0 ± 0.00 (10) SPCLR in *D. pruthi* **comb. nov.**, and 8.3 ± 0.76 (8–10) in *D. goaensis* **comb. nov.**); 20.3 ± 0.78 (19–21) RTS (versus 21.4 ± 0.89 (21–23) in *D. pruthi* **comb. nov.**); Elo two or three (rarely one, on just one individual on one side) (versus one or two Elo in *D. kalakadensis* **sp. nov.**, one Elo (rarely two in 3/22 individuals) in *D. nilgiriensis* **comb. nov.**); seven SL (rarely six on one side in 1/20 specimens) (versus six SL (seven on both sides in one specimen and on one side in three specimens) in *D. kalakadensis* **sp. nov.**); SL V elongate and below eye (rarely IV elongated and below eye, on one side in 1/ 20 individuals) (versus SL IV elongate and below eye (rarely SL V elongate and below eye, on just one specimen on either side and on three specimens on one side) in *D. kalakadensis* **sp. nov.**); presence of unkeeled scales on tail base (versus keeled scales on tail base in *D. goaensis* **comb. nov.**). *Dravidoseps srivilliputhurensis* **sp. nov.** is diagnosed against the new species described below as part of their respective descriptions.

Description of the holotype. Adult male (SVL 44.5 mm) in good state of preservation except body bent towards right and tail curved towards left side, a 3.7 mm long incision at marginally above the mid-body ventral for liver tissue collection, and hemipenis partially everted only on right side (Fig. 16A, B)). Head short (HL/SVL 0.17), wide (HW/HL 0.67), not strongly depressed (HH/HL 0.47), indistinct from neck. Loreal region not inflated, canthus rostralis indistinct. Snout almost half head length (ES/HL 0.44), slightly more than twice eye diameter (ES/ED 2.12). Rostral twice as wide (1.8 mm) as long (0.9 mm), in broad contact with supranasals posteriorly and supralabial I and nasals on either side; supranasals in contact with each other medially, frontonasal posteriorly, nasals and anterior loreals laterally; frontonasal much wider (1.7 mm) than long (1.1 mm), in contact with supranasals anteriorly, prefrontals and frontal posteriorly, anterior loreals laterally; prefrontals relatively small, widely separated on midline, in contact with frontonasal anteriorly, frontal and first supraciliary posteriorly, anterior and posterior loreals laterally. Frontal elongate, roughly bell-shaped, widest anteriorly at the point where prefrontals and first supraciliary connect; in contact with frontonasal anteriorly, frontoparietals posteriorly, prefrontals and first two supraoculars on either side; four supraoculars and one small post-supraocular and postocular on either side; frontoparietals in medial contact posterior to frontal, in contact with second, third, and fourth supraoculars anterolaterally and parietals and interparietal posteriorly. Interparietal large, roughly diamond-shaped, slightly projecting posteriorly, eyespot in posterior projection; postinterparietal absent; parietals large, in medial contact posterior to interparietal, in contact with frontoparietals, fourth supraocular, and post-supraocular anteriorly, two nuchal scales and a single dorsal scale posteriorly, first secondary temporal laterally; a single enlarged, elongate, nuchal scale on either side, separated medially by a single dorsal scale, left nuchal scale much larger than the one on the right side (Fig. 16C). Nasals small, trapezoidal, widely separated, in contact with rostral anteriorly, supranasal dorsally, anterior loreal posteriorly, first supralabial ventrally; nostril in center of nasal; anterior loreal marginally taller (0.6 mm) than wide (0.5 mm); posterior loreal slightly larger than anterior loreal and slightly wider (0.7 mm) than tall (0.5 mm); a single small supra-preocular, an upper and lower preocular, and a single sub-preocular present only on either side (Fig. 16E). Eye small (ED/ HL 0.21) with round pupil; lower eyelid with an enlarged, transparent central window; seven supraciliaries on either side, anterior supraciliary largest, bordered by prefrontal anteriorly, frontal and first supraocular dorsally, and pre-supraocular, upper preocular and posterior loreal laterally; posterior superciliary elongate and projecting dorsomedially, bordered by fourth supraocular dorsally, post-supraocular posteriorly, and first post-subocular laterally; four post-suboculars on either side; a single primary temporal, two secondary temporals, and three tertiary temporals on either side; seven supralabials, fifth and sixth below eye; fifth supralabial elongate, in broad contact with pre-subocular, last post-subocular and four small scales on lower eyelid below eye on either side; two post-supralabials on either side; six infralabials on either side; two scales separating post-supralabial and external ear opening; external ear opening small (EL/HL 0.11), oval, bearing two anterior lobules on either side; tympanum deep (Fig. 16E). Mental twice as wide (1.8 mm) as long (0.9 mm); a single large postmental in contact with first and second infralabials on either side; three enlarged pairs of chin shields posterior to postmental; anterior pair large (1.4 mm), roughly rectangular, in medial contact with each other below postmental and bordered by second and third infralabials, middle pair of chin shields, and by a single median gular scale on either side; middle pair same in size (1.4 mm) and shape as anterior pair, separated from each other by two longitudinally arranged gular scales, bordered by third and fourth infralabials, posterior pair of chin shields, and four gular scales on either side; posterior pair smallest (0.9 mm), roughly square, separated from each other by five transversely arranged gular scales, bordered by fourth and fifth infralabials and three gular scales on either side; rest of the gular scales much smaller than postmentals, cycloid and imbricate, two or three rows bordering infralabials slightly smaller and elongate (Fig. 16D).

Body relatively slender (BW/AGL 0.25), elongate (AGL/SVL = 0.60); dorsal scales on body smooth, cycloid, imbricate; ventrals similar to dorsals except subequal from chest to vent, marginally larger on pectoral and precloacal region; 64 scales in paravertebral rows; 28 scales around mid-body; 66 ventral scales; 10 enlarged precloacal scales (Fig. 16A, B)). Limbs, robust, short (FL/SVL = 0.06; CL/SVL = 0.08), widely separated when adpressed; dorsal scales wider and slightly larger than ventral scales; palmar scales raised; plantar scales large, raised, coarse granules; all digits short, scales on dor-

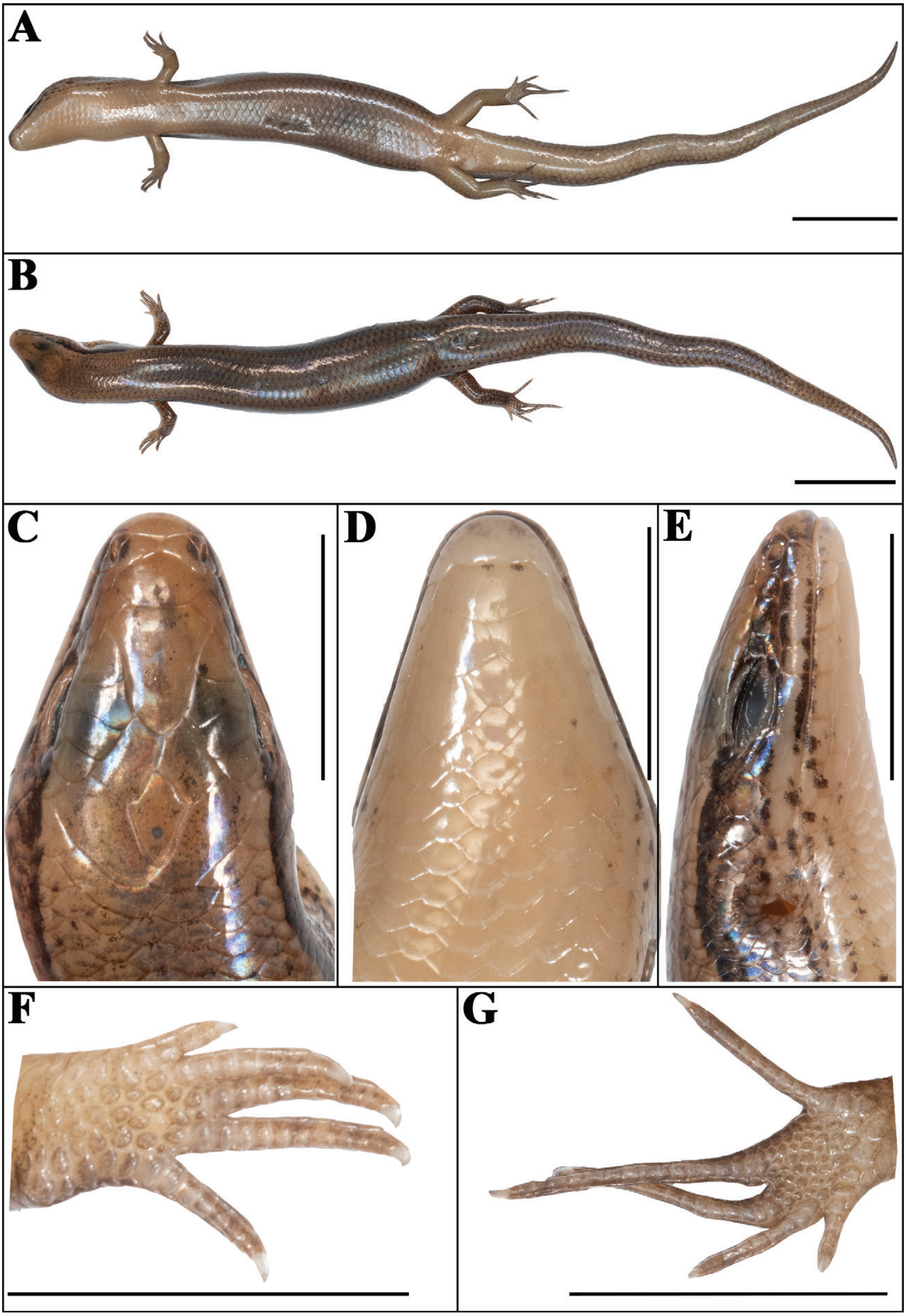

Figure 16. *Dravidoseps srivilliputhurensis* **sp. nov.** (holotype, NRC-AA-8279): **A** dorsal view of body, **B** ventral view of body, **C** dorsal view of head, **D** ventral view of head, **E** lateral right side view of head, **F** ventral view of left manus, and **G** ventral view of left pes. Scale bars: A, B = 10 mm; C–E, G = 5 mm; F = 3 mm; photos by Akshay Khandekar.

Table 10 – part 1. Mensural (mm) and meristic data for *Dravidoseps srivilliputhurensis* **sp. nov.**. Abbreviations are listed in Materials and Methods except for: L&R = Left & Right; M = male; F = female; Sa = Subadult; * = tail and lamellae incomplete; and / = data unavailable.

Museum number	**NRC-AA-8279**	**NRC-AA-8280**	**NRC-AA-8281**	**NRC-AA-8282**	**NRC-AA-8283**	**NRC-AA-8284**	**NRC-AA-8285**	**BNHS 2832**	**BNHS 2833**	**BNHS 2834**
Type	Holotype	Paratypes								
Sex	M	F	F	F	M	F	F	F	F	F
SVL	44.5	43.3	54.7	51.0	47.5	55.6	48.2	55.5	50.4	52.3
TL	45.8	47.1	41.0	55.2	42.9	36.2	37.3	33.8	6.1*	34
TW	4.1	3.7	4.6	3.9	3.9	5.0	4.4	4.9	4.4	4.4
FL	2.9	2.9	2.8	2.7	2.7	3.3	2.8	3.3	3.1	3.0
CL	4.0	4.0	4.3	3.8	4.3	4.3	3.8	4.2	4.0	3.9
AGL	26.7	23.4	34	30.7	28.0	34.8	28.8	34.2	31.6	34
BH	5.3	4.4	5.1	4.6	7.8	7.6	5.5	5.4	4.8	7.3
BW	6.8	6.4	9.3	8.1	8.3	9.8	7.6	9.3	7.7	10.4
HL	7.6	7.4	8.6	7.9	8.8	8.3	7.6	8.9	8.2	8.8
HW	5.1	5.1	5.6	5.5	5.7	5.7	5.3	5.9	5.1	5.6
HH	3.6	3.5	4.0	3.7	4.5	4.4	3.6	4.0	4.1	4.3
ED	1.6	1.6	1.6	1.7	1.6	1.6	1.6	1.7	1.6	1.7
TWD	0.7	0.7	0.8	0.8	0.8	0.8	0.8	0.7	0.7	/
EE	3.6	2.9	3.3	3.3	3.3	3.6	3.0	3.4	3.1	3.3
EL	0.9	0.6	0.5	0.6	0.7	0.6	0.7	0.6	0.7	0.6
ES	3.4	3.2	3.3	3.3	3.2	3.5	3.1	3.5	3.1	3.3
EN	2.4	2.0	2.2	2.2	2.1	2.1	2	2.2	2.0	2.2
IN	1.5	1.4	1.5	1.4	1.5	1.5	1.5	1.5	1.5	1.5
IO	2.9	2.5	3.0	2.8	3.1	2.8	2.9	3.1	2.6	3.0
Nu	1&1	1&1	1&1	1&1	1&1	1&1	1&1	1&1	1&1	2&1
Sb Nu	1	2	1	0	1	0	0	0	0	0
SL L&R	7&7	7&7	7&7	7&7	7&7	7&7	7&7	7&7	7&7	7&7
IL L&R	6&6	6&6	6&6	6&6	6&6	6&6	6&6	6&6	6&6	6&6
PoSL L&R	2&2	2&2	2&2	2&2	2&2	2&2	2&2	2&2	2&2	2&2
Elo L&R	2&2	2&3	2&2	2&3	2&2	1&2	2&2	3&3	3&2	2&3
PVS	64	66	64	65	65	66	65	64	66	64
RBS	28	28	28	28	28	26	28	28	28	26
VS	66	66	66	70	64	64	67	64	65	65
SPCLR	10	8	9	9	10	9	9	10	9	10
RTS	21	21	21	21	21	19	/	/	/	21
LamF1 L&R	5&5	5&5	6&6	5&5	5&5	5&6	6&5	6&6	6&5	5&6
LamF4 L&R	11&10	10&10	4*&11	11&10	10&10	10&10	11&11	11&11	11&9	9&9
LamT1 L&R	5&5	5&5	5&6	6&5	5&5	6&6	6&5	5&6	5&5	5&5
LamT4 L&R	16&15	16&16	16&16	14&15	14&14	15&15	17&16	14&13	14&13	14&14
Elongate supralabial below eye, fourth (1) or fifth (0) L&R	0&0	0&0	0&0	0&0	0&0	0&0	0&0	0&0	0&0	0&0

Table 10 – part 2. Mensural (mm) and meristic data for *Dravidoseps srivilliputhurensis* **sp. nov.**. Abbreviations are listed in Materials and Methods except for: L&R = Left & Right; M = male; F = female; Sa = Subadult; * = tail and lamellae incomplete; and / = data unavailable.

Museum number	**BNHS 2835**	**BNHS 2836**	**BNHS 2837**	**BNHS 2838**	**BNHS 2839**	**ZSI-R-28616**	**ZSI-R-28617**	**ZSI-R-28618**	**ZSI-R-28619**	**ZSI-R-28620**
Type	Paratypes									
Sex	F	F	F	F	F	F	F	F	Sa	Sa
SVL	53.4	44.4	48.5	43.1	52.9	43.1	46.1	46.4	32.0	31.8
TL	43.2	34.6	37	40.3	35.8	23.4	19.9*	44.7	24.4*	32.3
TW	4.4	3.4	4.0	3.5	5.0	3.6	4.0	3.8	3.3	2.5
FL	3.2	2.3	2.5	2.6	2.9	2.8	3.1	2.6	2.2	2.0*
CL	4.1	3.4	3.6	3.7	4.0	3.8	4.0	3.7	3.3	2.5

Museum number	BNHS 2835	BNHS 2836	BNHS 2837	BNHS 2838	BNHS 2839	ZSI-R-28616	ZSI-R-28617	ZSI-R-28618	ZSI-R-28619	ZSI-R-28620
Type	Paratypes									
AGL	32.9	25.1	27.6	25.2	31.5	26.4	26.9	27.5	18.0	17.2
BH	6.7	3.6	6.4	4.3	5.1	4.5	5.0	4.8	3.2	4.2
BW	8.8	5.6	8.4	6.4	9.2	6.3	7.8	6.6	5.7	4.7
HL	8.6	7.8	8.1	7.7	7.6	7.2	8.1	7.8	6.0	6.3
HW	5.8	4.8	5.5	4.7	5.6	4.8	5.2	5.0	5.0	4.1
HH	4.1	3.3	3.5	3.4	4.2	3.6	3.7	3.2	3.1	2.6
ED	1.6	1.5	1.6	1.5	1.6	1.4	1.5	1.6	1.4	1.3
TWD	0.7	0.8	0.7	0.6	0.7	0.5	0.7	0.8	0.6	0.6
EE	3.4	3.0	3.2	2.9	3.6	2.9	3.2	3.0	2.5	2.5
EL	0.8	0.6	0.5	0.6	0.5	0.5	0.6	0.5	0.6	0.3
ES	3.3	2.9	3.3	2.8	3.4	2.9	3.4	3.0	2.4	2.5
EN	2.0	1.9	2.2	1.9	2.2	1.8	2.2	1.9	1.6	1.5
IN	1.7	1.3	1.4	1.3	1.6	1.3	1.3	1.4	1.2	1.2
IO	3.1	2.7	2.7	2.7	2.8	2.7	2.8	2.6	2.3	2.2
Nu	1&1	1&1	1&1	1&1	1&1	2&2	1&1	2&2	1&1	1&1
Sb Nu	0	0	0	0	0	0	0	0	0	1
SL L&R	7&7	7&7	7&7	7&7	7&7	7&7	7&7	7&6	7&7	7&7
IL L&R	6&6	6&6	6&6	6&6	6&6	6&6	6&6	6&7	6&6	6&6
PoSL L&R	2&2	2&2	2&2	2&2	2&2	2&2	2&2	2&2	2&2	2&2
Elo L&R	2&3	2&2	3&3	2&2	2&2	3&3	2&2	2&2	2&3	3&2
PVS	64	63	64	65	65	63	66	63	64	63
RBS	28	26	29	28	28	28	28	28	28	28
VS	62	66	67	68	67	66	66	63	68	64
SPCLR	10	8	8	9	10	9	9	8	10	10
RTS	19	20	20	20	/	20	/	/	/	/
LamF1 L&R	6&6	6&6	5&5	5&5	6&6	5&5	5&5	5&5	6&6	6&6
LamF4 L&R	11&11	10&10	10&10	10&10	10&10	11&9	11&11	10&8*	11&11	12&11
LamT1 L&R	5&5	5&5	6&6	5&6	5&5	5&5	5&6	5&5	6&6	5&5
LamT4 L&R	15&15	14&15	14&14	15&14	15&15	14&14	15&14	13&12	15&16	15&15
Elongate supralabial below eye, fourth (1) or fifth (0) L&R	0&0	0&0	0&0	0&0	0&0	0&0	0&0	0&1	0&0	0&0

sal surfaces in single row, subdigital lamellae unpaired, mostly smooth; lamellae series: 5-8-9-11-8 left manus (Fig. 16F), 5-10-14-16-13 left pes (Fig. 16G), 5-9-9-10-8 right manus, 5-10-14-15-12 right pes. Relative length of digits (measurements in mm in parentheses): IV (2.0) > III (1.7) > II (1.5) > V (1.3) > I (0.9) (left manus); IV (4.1) > III (3.3) > V (2.5) > II (2.0) > I (1.0) (left pes).

Tail original except tip which is regenerated, entire, cylindrical, equal to snout-vent length (TL/SVL 1.02); dorsal and ventral scales cycloid, imbricate, similar to those on body dorsum except for median dorsal and subcaudal scale rows somewhat larger than surrounding scales on tail, ending in a pointed scute; scales on lateral sides of tail base smooth, 21 scales around the tail (Fig. 16A, B).

Colouration in life (Fig. 9G). Dorsal ground colouration of body, head and tail dull bronze-brown; head with scattered dark markings; dorsal scales of body and tail finely outlined by dark brown, centre of scales with black markings forming indistinct stripes; limbs darker than body dorsum and with light spots; a thick dark brown stripe running from rostrum through orbit and onto flank and tail with scattered light spots bordered dorsally by a fine white stripe; yellow markings below dark stripe from throat to hindlimb insertions extending onto belly; yellow markings below dark stripe from throat to hindlimb insertions extending onto belly; supralabials with a white streak; ventral regions glossy grey-white without darker markings.

Variation and additional information. Mensural and meristic data for the paratype series are given in Table 10. There are 16 adult females, an adult male and two subadults. All specimens resemble the holotype male (NRC-AA-8279) in overall morphology and head scalation except for the following variation: supranasals barely in contact with each other behind rostral in ZSI-R-28618; prefrontals in contact with frontal, first supraocular, and first supraciliary posteriorly in NRC-AA-8281–8284, BNHS 2832–2836, ZSI-R-28618 and ZSI-R-28619; two supraoculars in contact with frontoparietal on either side in NRC-AA-8284, three on left and two on right side in BNHS 2834; frontal in contact with prefrontals and first two supraoculars on either side in NRC-AA-8281–8284, BNHS 2832–2836, ZSI-R-28618 and ZSI-R-28619. Eight supraciliaries present on either side in BNHS 2834, six on left and seven on right side in ZSI-R-28617; anterior supraciliary largest, bordered by only first supraocular dorsally in NRC-AA-8281–8284, BNHS 2832–2836, ZSI-R-28618 and ZSI-R-28619; three post-suboculars present on either side in ZSI-R-28618, four on left and three on right side in BNHS 2834 and ZSI-R-28617. Five paratypes – NRC-AA-8280, NRC-AA-8282, BNHS 2838, ZSI-R-28618, and ZSI-R-28620, with complete and original tail, marginally longer or shorter than body (TL/SVL 1.08, 1.08, 0.93, 0.96, and 1.01 respectively); BNHS 2833, ZSI-R-28617, and ZSI-R-28619 are either partly or completely broken tails; rest of the paratypes with either almost fully or partially regenerated tails, shorter than body. NRC-AA-8283 with partial everted hemipenis on either side. Ten gravid females – NRC-AA-8281, NRC-AA-8284, NRC-AA-8285, BNHS 2832, BNHS 2834, BNHS 2835, BNHS 2837–2839, ZSI-R-28618 with long longitudinal incision on mid-body ventral to confirm egg/developing embryos.

Distribution and natural history. *Dravidoseps srivilliputhurensis* **sp. nov.** is known only from a few closely spaced localities (< 40 km aerial distance between two farthest localities) on the eastern slopes of the Western Ghats in Srivilliputhur-Megamalai Tiger Reserve (Fig. 1). *Dravidoseps srivilliputhurensis* **sp. nov.** was recorded in dry and moist deciduous to semievergreen forests at elevations between 200–1000 m asl. (Fig. 11G). At all localities (except for Chinnasurli Falls and Megamalai Viewpoint) *Dravidoseps srivilliputhurensis* **sp. nov.** was seen moving in dry leaf-litter during the day (0830–1400 hrs). At Chinnasurli Falls, a single individual was observed inactive at the base of rock surrounded by dry leaf-litter in the evening (1830 hr) and at Megamalai, *Dravidoseps srivilliputhurensis* **sp. nov.** was found in loose soil under rocks during late afternoon to evening time (1530–1830). Sympatric lizards encountered were *Hemidactylus frenatus*, *H. leschenaultii*, *H. vanam* Chaitanya, Lajmi & Giri, *H. whitakeri*, *Hemiphyllodactylus* sp., *Cnemaspis galaxia* Pal, Mirza, Dsouza & Shanker, *Cn.* cf. *gracilis*, *Cn.* cf. *ornata*, *Cyrtodactylus* (*Geckoella*) cf. *collegalensis*, *Eutropis carinata*, *E. macularia*, *Riopa albopunctata*, *Calotes versicolor*, and *Psammophilus dorsalis*.

Reproduction. Viviparous, litter size two or three. NRC-AA-8284, BNHS 2832, BNHS 2835, with three developing embryos; NRC-AA-8281, NRC-AA-8285, BNHS 2834, BNHS 2837, BNHS 2839, ZSI-R-28618 with two developing embryos; BNHS 2838 with two eggs with embryos in early stages of development (Fig. 8F–N).

Dravidoseps tamilnaduensis sp. nov.

https://zoobank.org/51683BB4-C907-4C2D-A501-6165FAB-CC34E

Figures 8O, 9H, 17, Table 11

Chresonymy.
Lygosoma pruthi – Ganesh and Aengals (2018)
Subdoluseps pruthi – Ganesh et al. (2021).

Holotype. NRC-AA-8286 (AK-R 2396), adult female, from near Kambur, Pachaimalai Hills (11.31677°N, 78.60183°E; elevation ca. 850 m asl.), Tiruchirappalli District, Tamil Nadu State, India, collected by Akshay Khandekar, Ishan Agarwal, Swapnil Pawar and team on 22th September 2022.

Paratypes (n = 11). ZSI-R-28691 (AK-R 2397), subadult, same details as holotype; NRC-AA-8287 (AK 739), adult male, same locality as holotype except collected by Akshay Khandekar, Ishan Agarwal, Swapnil Pawar, Tejas Thackeray and team on 29th May 2019; NRC-AA-8288 (AK 740), BNHS 2857 (AK 741), adult females, BNHS 2858 (AK 742), subadult, from near Pachaimalai Eco Tourism Centre, Pachaimalai Hills (11.31588°N, 78.58103°E; elevation ca. 780 m asl.), collected by Akshay Khandekar, Ishan Agarwal, Swapnil Pawar, Tejas Thackeray and team on 29th May 2019; BNHS 2859 (AK 743), adult female, ZSI-R-28621 (AK 745), adult male, BNHS 2860 (AK 744), subadult, from Pachaimalai Ghat road, Pachaimalai Hills (11.30229°N, 78.57332°E; elevation ca. 600 m asl.), collected by Akshay Khandekar, Ishan Agarwal, Swapnil Pawar, Tejas Thackeray and team on 29th May 2019; ZSI-R-28692 (AK-R 2724), ZSI-R-28693 (AK-R 2725), adult males, from Selur Reserve Forest, Kolli Hills (11.19463°N, 78.37537°E; elevation ca. 400 m asl.), Namakkal District, Tamil Nadu State, India, same collectors as holotype, collected on 12th October 2022; ZSI-R-28695 (AK-R 2734), adult female, from near Madu Falls, Yercaud (11.73881°N, 78.24985°E; elevation ca. 410 m asl.), Salem District, Tamil Nadu State, India, same collectors as holotype, collected on 13th October 2022.

Etymology. The specific epithet is a toponym for Tamil Nadu State to which the new species is endemic.

Suggested common name. Tamil Nadu leaf-litter skink.

Diagnosis. A medium-sized skink snout to vent length up to 56 mm (n = 12). Seven supralabials and six (rarely seven, n = 1/12) infralabials up to angle of mouth; fifth supralabial elongate and below eye; two post-supralabials; seven or eight supraciliaries; one or two elongated nuchals on either side, in median contact behind parietal (rarely separated a single scale, n = 1/12); 66–70 scales in paravertebral rows; 28–30 scales around mid-body; 64–71 ventral scales; 10 enlarged precloacal scales; scales on lateral sides of tail base smooth, 20 or 21 scales around the tail. Subdigital lamellae unpaired, smooth on manus and smooth to weakly keeled on pes; five or six lamellae under digit I of manus and pes (rarely seven on manus n = 1/12); 9–11 lamellae under digit IV of manus; and 12–15 under digit IV of pes (rarely 16, n = 1/12). Dorsum dark bronze-brown with black markings; thick black stripe from rostrum to tail speckled with light spots; supralabials with white streak; males with yellow on lower parts of forebody and flanks; venter glossy white with numerous dark reticulations.

Comparisons. *Dravidoseps tamilnaduensis* **sp. nov.** can be diagnosed from known congeners based on the following characters: 29.6 ± 0.79 (28–30) RBS (versus 31.0 ± 1.41 (30–32) in *D. gingeeensis* **sp. nov.**, and *D. jawadhuensis* **sp. nov.**, 27.8 ± 0.79 (26–29) in *D. srivilliputhurensis* **sp. nov.**); 13.7 ± 1.07 (12–15) LAM4T (versus 17.0 ± 0.00 (17) in *D. gingeeensis* **sp. nov.**, 16.5 ± 0.71 (16–17) in *D. jawadhuensis* **sp. nov.**, 16.1 ± 1.20 (14–18) in *D. pruthi* **comb. nov.**); 10.0 ± 0.00 (10) SPCLR (versus 12.0 ± 0.00 (12) in *D. gingeeensis* **sp. nov.**, 12.5 ± 0.71 (12–13) in *D. jawadhuensis* **sp. nov.**, 8.0 ± 0.00 (8) in *D. kalakadensis* **sp. nov.**, 9.2 ± 0.77 (8–10) in *D. srivilliputhurensis* **sp. nov.**); 20.8 ± 0.40 (20–21) RTS (versus 18.7 ± 0.52 (18–19) in *D. kalakadensis* **sp. nov.**, 22.5 ± 0.71 (22–23) in *D. jawadhuensis* **sp. nov.**, and 18.7 ± 0.52 (18–19) in *D. goaensis* **comb. nov.**); one or two Nu on either side and Sb Nu absent (present in only 1/12 specimens) (versus a single Nu on either side and three Sb Nu present in *D. gingeeensis* **sp. nov.**, a single Nu on either side and two or three Sb Nu present in *D. pruthi* **comb. nov.**); seven SL (versus six SL (seven on just one specimen on either side and on three specimens on one side) in *D. kalakadensis* **sp. nov.**); SL V elongate and below eye (versus SL IV elongate and below eye (rarely SL V elongate and below eye, on just one specimen on either side and on three specimens on one side) in *D. kalakadensis* **sp. nov.**); two Elo on each side (a single on one side in 1/12 specimens) (versus a single Elo (rarely two in 3/22 individuals) in *D. nilgiriensis* **comb. nov.**); 68.0 ± 1.48 (66–70) PVR (versus 64.5 ± 1.05 (63–66) in *D. srivilliputhurensis* **sp. nov.**); presence of unkeeled scales on tail base (versus keeled scales on tail base in *D. goaensis* **comb. nov.**).

Description of the holotype. Adult male (SVL 48.5 mm) in good state of preservation except body and tail marginally curved towards left side, and a 3.5 mm long incision in the sternal region for liver tissue collection (Fig. 17A, B). Head short (HL/SVL 0.17), wide (HW/HL 0.73), not strongly depressed (HH/HL 0.49), indistinct from neck. Loreal region not inflated, canthus rostralis indistinct. Snout almost half head length (ES/HL 0.40), twice eye diameter (ES/ED 2.00). Rostral almost twice as wide (1.5 mm) as long (0.9 mm), in broad contact with supranasals posteriorly and supralabial I and nasals on either side; supranasals marginally in contact with each other medially, frontonasal posteriorly, nasals and anterior loreals laterally; frontonasal much wider (1.8 mm) than long (1.2 mm), in contact with supranasals anteriorly, prefrontals and frontal posteriorly, anterior loreals laterally; prefrontals relatively small, widely separated on midline, in contact with frontonasal anteriorly, frontal, first supraocular and first supraciliary posteriorly, anterior and posterior loreals laterally. Frontal elongate, roughly bell-shaped, widest anteriorly at the point where prefrontals and first supraocular connect; in contact with frontonasal anteriorly, frontoparietals posteriorly, prefrontals and first two supraoculars on either side; four supraoculars and one small post-supraocular and postocular on either side; frontoparietals in medial contact posterior to frontal, in contact with second, third, and fourth supraoculars anterolaterally and parietals and interparietal posteriorly. Interparietal large, roughly diamond-shaped, slightly projecting posteriorly, eyespot in posterior projection; postinterparietal absent; parietals large, in medial contact posterior to interparietal, in contact with frontoparietals, fourth supraocular, and post-supraocular anteriorly, two nuchal scales posteriorly, first secondary temporal laterally; a single enlarged, elongate, nuchal scale on either side in median contact posterior to parietals (Fig. 16C). Nasals small, trapezoidal, widely separated, in contact with rostral anteriorly, supranasal dorsally, anterior loreal posteriorly, first supralabial ventrally; nostril in center of nasal; anterior loreal marginally taller (0.6 mm) than wide (0.5 mm); posterior loreal slightly larger than anterior loreal and slightly wider (0.8 mm) than tall (0.7 mm); a single small supra-preocular, an upper and lower preocular, and a single sub-preocular present only on either side (Fig. 17E). Eye small (ED/ HL 0.20) with round pupil; lower eyelid with enlarged, transparent central window; eight supraciliaries on either side, anterior supraciliary largest, bordered by prefrontal anteriorly, first supraocular dorsally, and pre-supraocular, upper preocular and posterior loreal laterally; posterior superciliary elongate and projecting dorsomedially, bordered by fourth supraocular dorsally, post-supraocular posteriorly, and first post-subocular laterally; three post-suboculars on either side; a single primary temporal, two secondary temporals, and three tertiary temporals on either side; seven supralabials, fifth and sixth below eye; fifth supralabial elongate, in broad contact with pre-subocular and seven small scales on lower eyelid below eye on either side; two post-supralabials on either side; six infralabials on either side; two scales separating post-supralabial and external ear opening; external ear opening small (EL/HL 0.07), oval, bearing two anterior lobules on either side; tympanum deep (Fig. 17E). Mental twice wide (1.6 mm) as long (0.8 mm); a single large postmental in contact with first and second infralabials on either side; three enlarged pairs of chin shields posterior to postmental; anterior pair large (1.3 mm), roughly rectangular, in medial contact with each other below postmental and bordered by second and third infralabials, middle pair of chin shields, and by a single median gular scale on either side; middle pair largest (1.5 mm), roughly rectangular, separated from each other by two longitudinally arranged gular scales, bordered by third and fourth infralabials, posterior pair of chin shields, and four gular scales on either side; posterior pair smallest (0.8 mm), roughly square, separated from each other by five transversely arranged gular scales, bordered by fourth and fifth infralabials and three gular scales on either side; rest of the gular scales much smaller than postmentals, cycloid and imbricate, two or three rows bordering infralabials slightly smaller and elongate (Fig. 17D).

Body relatively slender (BW/AGL 0.23), elongate (AGL/SVL = 0.59); dorsal scales on body smooth, cy-

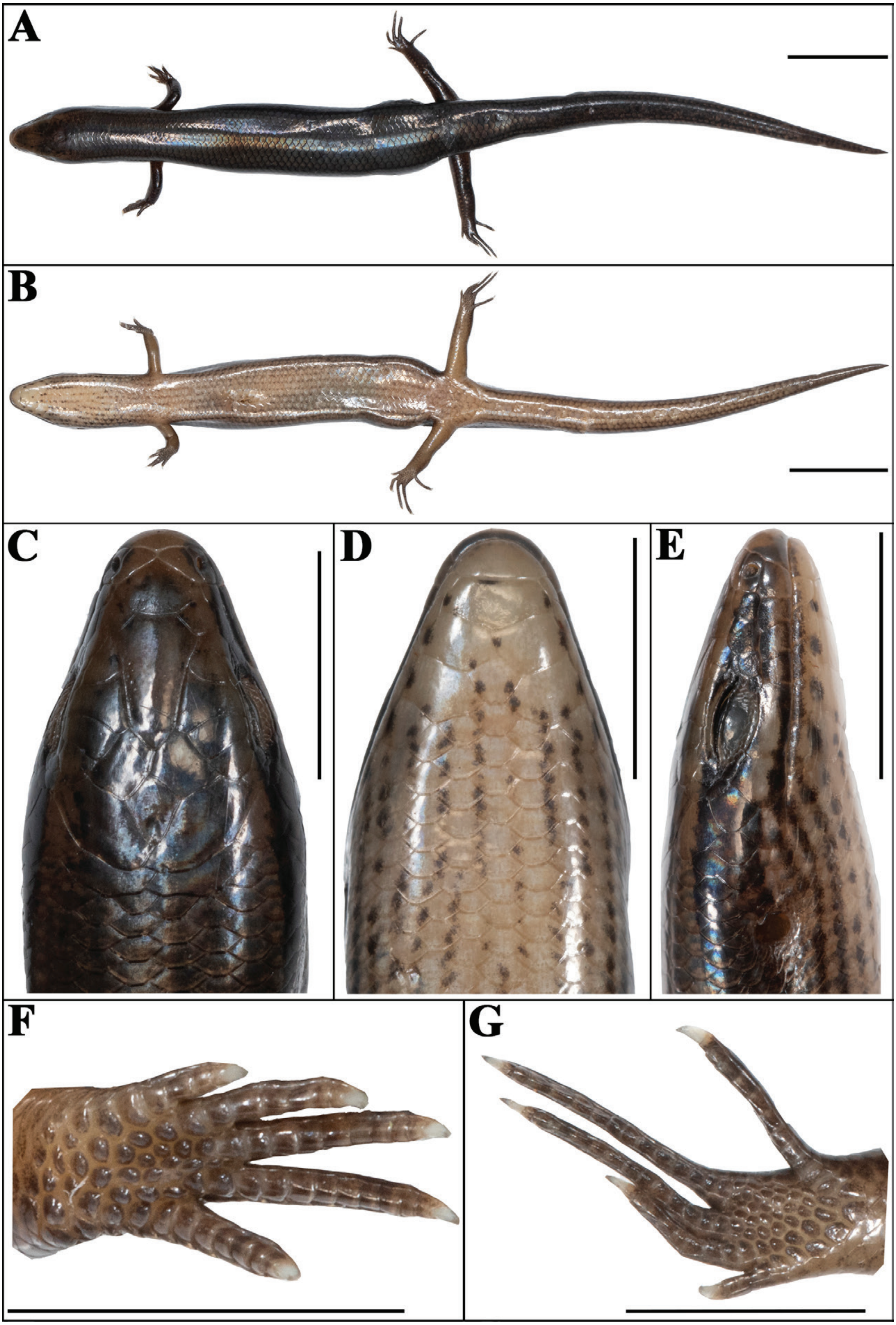

Figure 17. *Dravidoseps tamilnaduensis* **sp. nov.** (holotype, NRC-AA-8286): **A** dorsal view of body, **B** ventral view of body, **C** dorsal view of head, **D** ventral view of head, **E** lateral right side view of head, **F** ventral view of left manus, and **G** ventral view of left pes. Scale bars: A, B = 10 mm; C–E, G = 5 mm; F = 3 mm; photos by Akshay Khandekar.

cloid, imbricate; ventrals similar to dorsals except subequal from chest to vent, marginally larger on pectoral and precloacal region; 69 scales in paravertebral rows; 30 scales around mid-body; 70 ventral scales; 10 enlarged precloacal scales (Fig. 17A, B)). Limbs, robust, short (FL/SVL = 0.06; CL/SVL = 0.08), widely separated when adpressed; dorsal scales wider and slightly larger than ventral scales; palmar scales raised; plantar scales large, raised, coarse granules; all digits short, scales on dorsal surfaces in single row, subdigital lamellae unpaired, smooth on manus and smooth to weakly keeled on pes; lamellae series: 5-7-9-10-7 left manus (Fig. 17F), 5-9-13-14-11 left pes (Fig. 17G), 5-8-9-10-8 right manus, 5-9-12*-14-11 right pes. Relative length of digits (measurements in mm in parentheses): IV (2.1) > III (1.9) > II (1.6) > V (1.4) > I (1.2) (left manus); IV (3.7) > III (3.2) > V (2.5) > II (1.9) > I (1.4) (left pes).

Tail original except for tip which is regenerated, entire, cylindrical, slightly shorter than snout-vent length (TL/SVL 0.88); dorsal and ventral scales cycloid, imbricate, similar to those on body dorsum except for median dorsal and subcaudal scale rows distinctly larger than surrounding scales and roughly rectangular on regenerated tip; scales on lateral sides of tail base smooth, 20 scales around the tail (Fig. 17A, B)).

Colouration in life (Fig. 9H). Dorsal ground colouration of body, head and tail dark bronze-brown; head with scattered dark markings; dorsal scales of body and tail finely outlined by dark brown, centre of scales with black markings forming indistinct stripes, tail dark; limbs almost black, with light spots; a thick black stripe running from rostrum through orbit and onto flank and tail with scattered light spots bordered dorsally by a broken white stripe; supralabials with a white streak; ventral regions glossy white with numerous dark reticulations.

Variation and additional information. Mensural and meristic data for the paratype series are given in Table 11. There are four adult males, four adult females and three subadults. All specimens resemble the holotype male (NRC-AA-8286) in overall morphology and head scalation except for the following variation: seven SC on either side in BNHS 2860, ZSI-R-28695, seven on left and eight on right side in BNHS 2857, ZSI-R-28692; three PrO on either side in NRC-AA-8287, NRC-AA-8288, BNHS 2857, two on left and three on right side in ZSI-R-28692; three PoSbO on left and four on right side in ZSI-R-28692, rest all paratypes (except for ZSI-R-28693 which matches with holotype) have four PoSbO on either side; middle postmental separated from each other below anterior postmentals by single enlarged gular scales and bordered by three gular scales on each side in NRC-AA-8287, ZSI-R-28695. Three paratypes – BNHS 2858, BNHS 2860, and ZSI-R-28621 with complete and original tail, equal to body (TL/SVL 1.01, 1.03, and 1.00 respectively); BNHS 2857, ZSI-R-28693, and ZSI-R-28695 with tail almost completely broken and lost; rest of the paratypes with partially regenerated tails, shorter than body. Three female paratypes – BNHS 2857, BNHS 2859, and ZSI-R-28695 with long longitudinal incision on mid-body ventral to confirm egg/developing embryos; ZSI-R-28621 (adult male) was dissected (12.4 mm long incision on mid-body ventral) to confirm the sex.

Distribution and natural history. *Dravidoseps tamilnaduensis* **sp. nov.** is known from three broad localities in the broader Shevaroyan landscape, from Pachaimalai Hills in Tiruchirappalli District (type locality), Kolli Hills in Namakkal District, and southern slopes of Yercaud in Salem District, Tamil Nadu India, between elevations of 400–850 m asl. (Fig. 1). The two farthest localities for the species (Yercaud in north and Kolli Hills in south) are ~60 km apart from each other in aerial distance.

At the type locality, *Dravidoseps tamilnaduensis* **sp. nov.** was observed in high abundance (n = >15 hr) in a semi-evergreen forest patch with more or less closed canopy and heavy leaf-litter on the forest floor (Fig. 11H). Individuals were found under rocks surrounded by leaf-litter or moving in the leaf-litter during the afternoon to early evening (1330–1800 hrs). At Kolli Hills and Yercaud, *Dravidoseps tamilnaduensis* **sp. nov.** was observed in dry deciduous to semi evergreen forest patches at the hill base during the morning hours (0830–1130 hrs). They were found either under rocks or in leaf-litter in well shaded areas along a stream. Sympatric lizards recorded at all three localities include *Cnemaspis yercaudensis* Das & Bauer, *Cyrtodactylus* (*Geckoella*) cf. *collegalensis*, *Hemidactylus frenatus*, *H.* cf. *graniticolus*, *H. whitakeri*, *Eutropis* cf. *allapallensis*, *E. carinata*, *E. macularia*, *Riopa albopunctata*, *Calotes versicolor*, and *Psammophilus* cf. *blanfordanus*. We found *Dravidoseps nilgiriensis* **comb. nov.** in syntopy with *D. tamilnaduensis* **sp. nov.** in Kolli Hills, the only location where two *Dravidoseps* species have been found in sympatry.

Reproduction. Viviparous, litter size two (n = 1). BNHS 2859 with two almost completely developed embryos (Fig. 8O).

Note. Mensural and meristic data of a single unsexed adult specimen (ZSI/SRS/VRL 470; from Pachaimalai) given in Ganesh and Aengals (2018) as *Lygosoma pruthi* matches the type specimens of *Dravidoseps tamilnaduensis* **sp. nov.** except for the following variation: AGL 36.2 mm of ZSI/SRS/VRL 470 (versus <33.3 mm in this work n = 13); HW 6.6 mm (versus < 5.7 mm); SO four or five (versus four); Elo five (versus two on each side); RBS 32 (versus 28–30). We couldn't examine ZSI/SRS/VRL 470 to verify the counts. The measurements of AGL and HW and counts of ABS and SO given by Ganesh and Aengals (2018) are likely to be incorrect as none of the individuals (n = 13) even with same or higher SVL in the type series have such high numbers. Elo most likely include left and right combined. We however, tentatively assign this specimen to the new species pending verification of unmatched characters mentioned here.

Table 11. Mensural (mm) and meristic data for *Dravidoseps tamilnaduensis* **sp. nov.** and *Dravidoseps* sp. Abbreviations are listed in Materials and Methods except for: L&R = Left & Right; M = male; F = female; Sa = Subadult; * = data incomplete; and / = data unavailable.

Museum number	**NRC-AA-8286**	**NRC-AA-8287**	**NRC-AA-8288**	**BNHS 2857**	**BNHS 2858**	**BNHS 2859**	**BNHS 2860**	**ZSI-R-28621**	**ZSI-R-28691**	**ZSI-R-28692**	**ZSI-R-28693**	**ZSI-R-28695**	**NRC-AA-8289**
Type	Holo-type	Paratypes											*Dravido-seps* sp.
Sex	F	M	F	F	Sa	F	Sa	M	Sa	M	M	F	Sa
SVL	48.5	45.3	55.2	49.9	25.6	45.7	24.9	53.5	37	42.4	50.6	43.1	32.4
TL	43.0	34.3	35.7	6.5*	26.0	33.9*	25.8	53.8	29.0*	24.3	12.9*	10.8*	31.1
TW	4.1	3.5	4.2	3.6	1.9	4.0	2.2	4.1	2.3	3.8	4.4	3.4	2.6
FL	3	3.0	3.2	3.0	1.6	3.0	1.7	3.1	2.4	2.9	3.3	3	2*
CL	4.0	3.9	4.3	3.9	2.2	3.9	2.4	4.2	2.7*	4.0	4.4	4.0	2.6
AGL	28.9	25.5	32.4	29.9	12.9	27.7	11.6	33.3	19.9	26.1	29.3	26.0	17.8
BH	4.0	3.5	4.1	4.1	2.1	5.3	2.4	5.0	3.0	3.3	4.1	3.9	3.6
BW	6.8	7.3	8.6	7.8	3.9	8.1	4.0	8.2	4.5	6.2	7.6	7.2	4.6
HL	8.3	7.8	8.5	8.7	5.7	7.3	5.7	8.3	6.6	7.3	8.4	7.7	5.3
HW	5.0	5.0	5.7	5.6	3.9	5.0	3.7	5.6	4.0	5.4	5.4	5.3	4.1
HH	4.1	3.3	4.1	3.7	2.6	3.7	2.7	4.4	2.8	4.1	4.0	3.4	3.3
ED	1.7	1.7	1.6	1.6	1.2	1.6	1.2	1.6	1.4	1.6	1.8	1.7	1.4
TWD	0.8	0.9	0.9	0.8	0.5	0.7	0.6	0.8	0.7	0.9	0.9	0.8	0.6
EE	3.3	2.9	3.3	3.2	2.1	3.1	2.2	3.3	2.5	3.1	3.3	2.7	2.4
EL	0.6	0.8	0.8	0.7	0.3	0.5	0.4	0.5	0.5	0.7	0.7	0.6	0.4
ES	3.4	3.0	3.5	3.4	2.1	3.3	2.3	3.6	2.6	3.0	3.4	3.0	2.3
EN	2.2	2.0	2.2	2.0	1.3	2.2	1.4	2.3	1.5	2.0	2.2	2.0	1.4
IN	1.4	1.3	1.6	1.5	1.1	1.4	1.1	1.3	1.2	1.4	1.4	1.4	1.2
IO	3.0	2.8	3.3	3.5	2.2	2.9	2.2	3.5	2.4	2.8	2.9	2.7	2.3
Nu	1&1	1&1	2&2	1&1	2&2	2&2	2&1	2&2	2&2	2&2	2&2	2&2	1&1
Sb Nu	0	0	0	0	0	0	0	0	0	1	0	0	0
SL L&R	7&7	7&7	7&7	7&7	7&7	7&7	7&7	7&7	7&7	7&7	7&7	7&7	7&7
IL L&R	6&6	6&6	6&6	7&7	6&6	6&6	6&6	7&6	6&6	6&6	6&6	6&6	6&6
PoSL L&R	2&2	2&2	2&2	2&2	2&2	2&2	2&2	2&2	2&2	2&2	2&2	2&2	2&2
Elo L&R	2&2	2&2	2&2	2&2	2&2	2&2	2&2	2&2	2&2	1&2	2&2	2&2	2&2
PVS	67	67	69	66	67	69	67	70	70	69	66	69	64
RBS	29	30	30	30	30	28	30	30	28	30	30	30	28
VS	65	65	71	69	66	68	66	69	64	68	71	70	/
SPCLR	10	10	10	10	/	10	/	10	10	10	10	10	10
RTS	20	21	21	21	21	21	/	21	20	21	21	21	21
LamF1 L&R	5&5	5&5	5&5	5&5	5&5	5&5	5&5	5&6	6&5	6&6	6&6	5&5	6&5
LamF4 L&R	10&10	10&11	6*&11	9&10	10&10	9&9	10&10	11&11	10&11	10&11	11&11	11&11	10&10
LamT1 L&R	5&5	5&6	5&5	5&5	5&5	5&5	5&5	5&6	6&6	6&6	6&7	5&5	6&6
LamT4 L&R	14&14	14&14	13&15	12&13	13&14	12&13	13&13	14&14	14&15	15&15	15&16	15&5*	13&13
Elongate supra-labial below eye, fourth (1) or fifth (0) L&R	0&0	0&0	0&0	0&0	0&0	0&0	0&0	0&0	0&0	0&0	0&0	0&0	0&0

Key to species of the genus *Dravidoseps*

1. Scales on tail base not keeled **2**
– Scales on tail base keeled .... ***D. goaensis***
2. Two postsupralabials on each side **3**
– One postsupralabial on each side .... ***D. pruthi***
3. $\geq$ 12 scales on precloacal row **4**
– $\leq$ 10 scales on precloacal row **5**
4. Five post-suboculars, one or two nuchals on each side and no scales between nuchals, 22 or 23 scales around the tail .... ***D. jawadhuensis***

– Three or four post-suboculars, one nuchal on each side and three scales between nuchals, 21 scales around the tail .... ***D. gingeeensis***
5. 3–6 (mean > 3.9) total ear lobules **6**
– 2–4 (mean < 2.3) total ear lobules **7**
6. 10 (mean 10.0) scales on precloacal row, 28–30 (mean 29.6) scales around the body, 66–70 (mean 68.0) paravertebral scales .... ***D. tamilnaduensis***
– 8–10 (mean 9.2) scales on precloacal row, 26–29 (mean 27.8) scales around the body, 63–66 (mean 64.5) paravertebral scales .... ***D. srivilliputhurensis***
7. 8 (mean 8.0) scales on precloacal row, 18–19 (18.7) scales around the tail, usually 6 supralabials .... ***D. kalakadensis***
8–10 (mean 9.2) scales on precloacal row, 19–22 (20.1) scales around the tail, 7 supralabials .... ***D. nilgiriensis***

Discussion

A cryptic radiation of skinks

This is the first fine-scale phylogeographic work on a radiation of Indian skinks, resulting in the recognition of a new genus and the description of five new species, including the first micro-endemic peninsular Indian skinks outside of the Western Ghats (Datta-Roy et al. 2012, 2014; Deuti et al. 2020). With eight species, *Dravidoseps* is the most diverse skink genus endemic to peninsular India, followed by *Kaestlea* (five species) and *Ristella* (four species) from the Western Ghats, and *Barkudia* (two species) and *Sepsophis* (one species) from the Eastern Ghats (Deuti et al. 2020). It is likely that *Dravidoseps* will be found in the Western Ghats between the Nilgiri Hills and Goa, and the Tirupati Hills, both of which have suitable habitat. Peninsular India is incredibly biodiverse and poorly studied, and the low rate of species discovery in Indian skinks is likely a sampling artefact (Khandekar and Agarwal unpubl. data).

The recognition of *Dravidoseps* meets all the priority taxon naming criteria outlined by Vences et al. (2013) – monophyly, clade stability, and phenotypic diagnosability; besides the secondary criteria of time banding, biogeography, and adaptive zone (Vences et al. 2013). *Dravidoseps* is consistently well-supported as monophyletic using five different molecular markers, different subsets of data, and alternate phylogenetic reconstruction techniques. Phenotypic characters supporting the recognition of *Dravidoseps* include the open secondary palate, the presence of a transparent window in the lower eyelid, and reproductive mode (viviparity). *Dravidoseps* and *Subdoluseps* sensu stricto occupy discrete biogeographic regions and divergent climatic niches, and diverged from each other in the Eocene, around the same time that their sister taxa, *Mochlus* and *Riopa* diverged from each other. Combining these differences in molecular data, morphology, and biogeography provides strong evidence for the separation of the two genera.

With five species and an additional unnamed, genetically divergent lineage, the greater Shevaroyan landscape appears to be the hotspot of *Dravidoseps* species diversity. This sky-island landscape includes several massifs that rise above 1000 m asl. and the smaller Gingee Hills (< 500 m asl.), all of which are separated by warmer lowlands with markedly more open vegetation. A number of geckos are endemic to massifs in this landscape including seven species of the *Cnemaspis gracilis* (Beddome) clade (Khandekar et al. 2019; Agarwal et al. 2022), two *Hemidactylus* Goldfuss (Agarwal et al. 2019a; Narayanan et al. 2023) and two *Hemiphyllodactylus* Bleeker (Agarwal et al. 2019b).

Diversification of the Lygosomini

The center of diversity of the Lygosomini is India and Southeast Asia, with three subclades distributed in each region, and the ancestral area of its MRCA reconstructed as distributed in Southeast Asia (Fig. 3; Ghosh et al. 2023). The median age of the basal split within the Lygosomini at 56 (64–48) Mya is before the India-Eurasia collision (~50 Mya) and overlaps with when the drifting Indian plate is thought to have made glancing contact with Sumatra, though the upper limit of the CI is around the time of India-Seychelles separation and the lower limit is post collision (Ali and Aitchison 2008). A number of groups dispersed between India and Southeast Asia during this time period (e.g. crabs, Klaus et al. 2010; flora, Morley 2018; rhacophorid frogs, Li et al. 2013; scorpions, Loria and Prendini 2020; reviewed in Datta-Roy and Karanth 2009; Klaus et al. 2016). Ancestral area reconstructions for the MRCA of Lygosomini excluding *Lygosoma* + *Lamprolepis* and the MRCA of *Dravidoseps* + *Subdoluseps* sensu stricto were equivocal, constraining the node to either Southeast Asia or India each require four dispersals – one to Africa and three between India and Southeast Asia (Fig. 3; Freitas 2020; Ghosh et al. 2023). Though the precise order and direction of dispersals between India and Southeast Asia are unclear, the Lygosomini have an early history in the region (Freitas 2020). Similar dispersals between India and Southeast Asia have been documented in skinks and other groups from the Eocene onward (e.g., Datta-Roy et al. 2012, 2014; Barley et al. 2015; Garg and Biju 2018) with a slowdown from the middle Miocene to present (Klaus et al. 2016).

The first indications of seasonality in India date back to the late Eocene (40 Mya; Morley 2000; Licht et al. 2014; Gower et al. 2016), around when *Dravidoseps* split from *Subdoluseps* sensu stricto (Fig. 3). Forest fragmentation and seasonality increased from then on, with marked increases at 34, 23 and from 10 Mya onward, with a brief expansion of forests during the warmth of the Mid-Miocene Climatic Optimum (MMCO) 17–15 Mya (Zachos et al. 2001; Clift et al. 2008; Morley 2000; Patnaik et al. 2012; Pound et al. 2012). Early diversification in *Dravidoseps* occurred during the late Oligocene to early Miocene followed by diversification from the MMCO onward with a slowdown towards the present (likely an artefact of the species delimitation cutoff). *Subdoluseps* sensu stricto, and both subclades of *Riopa* and *Lygosoma*, also have a similar crown age and timeline of diversification, though it is unclear what the common factors across the disparate regions these groups inhabit might be (Fig. 3; Freitas 2020).

Dravidoseps biogeography

Species of *Dravidoseps* live in cooler, more seasonal and climatically extreme habitats with lower canopy cover and rainfall than *Subdoluseps* sensu stricto in Southeast Asia (Fig. 5). *Dravidoseps* species are forest obligates, as the only open habitats without canopy we encountered them in are the two highest localities for the group (> 1,400 m) in the Palani Hills, Tamil Nadu. Limited data from thermal preference trials of *D. goaensis* and *D. srivilliputhurensis* suggest a relatively high preferred temperature for the habitats they occupy in the Western Ghats (T_{pref} 33°C, range 32–34°C, n = 3 combined for both species) versus *Kaestlea* sp. (T_{pref} 27.8°C, 23.8–30.8°C, n = 8) and *Ristella* sp. (T_{pref} 23°C, 22.4–24.2°C, n = 6) (Agarwal et al. unpubl. data). This may explain the absence of *Dravidoseps* from the cooler high elevations and west-facing slopes of the Western Ghats, and their high diversity in habitats outside the Western Ghats.

The role of lowland habitats in preventing historical gene flow within *Dravidoseps* is most pronounced in the massifs outside the Western Ghats, where the lowlands are warmer and more open with scrubby or grassland vegetation, with high diversity in the landscape and each species restricted to a single massif or a few closely grouped massifs. A few species of *Dravidoseps* have been able to recently disperse across lowland habitats separating hill ranges or massifs while some Western Ghats species are distributed relatively widely across contiguous forest habitat (Fig. 1), but the group as a whole is restricted in distribution to structurally similar habitats (seasonal forests on the eastern slopes of the Western Ghats and other isolated massifs in Tamil Nadu). The only case of sympatry is of *Dravidoseps nilgiriensis* and *D. tamilnaduensis* in the Kolli Hills – where distantly related species appear to have made secondary contact, with no evidence of hybridization based on our three marker nucDNA dataset (Fig. 4). Diversification within populations of *Dravidoseps* species, which have a maximum ND2 intra-lineage divergence of 1.0–5.1 %, was between 6–1 Mya as calculated from the ND2 rate from the divergence dating analysis. This suggests that past climatic conditions and/ or the distribution of forest habitats allowed the ancestor of *Dravidoseps nilgiriensis* to disperse across a number of lowland geographic gaps at some point since the late Miocene and early Pliocene.

Dravidoseps is another non-adaptive radiation of skinks that exhibit a decoupling between speciation and phenotypic divergence (e.g. Freitas et al. 2020; Slavenko et al. 2020). Members of *Dravidoseps* have similar habits, are restricted to structurally similar habitats, and are almost entirely allopatric in distribution. Species level diversification within the group occurred during a period of increasing aridification. The highly conserved body plan of the group (Fig. 5D) might be a consequence of niche conservatism for habitat or body plan and/ or allopatric speciation without the need for disruptive selection in morphology (Wiens and Graham 2005; Bolnick and Fitzpatrick 2007; Slavenko et al. 2020). Numerous peninsular Indian lizard radiations including *Cyrtodactylus* Gray, *Dravidogecko* Smith, and *Hemiphyllodactylus* Bleeker (Gekkonidae); *Ophisops* Ménétries (Lacertidae), *Sitana* Cuvier (Agamidae) show the same pattern as *Dravidoseps* – morphologically cryptic groups with most species diversity resulting from middle to late Miocene diversification, (Agarwal and Karanth 2015; Agarwal and Ramakrishnan 2017; Deepak et al. 2016; Agarwal et al. 2019b; Chaitanya et al. 2019). Interestingly, *Subdoluseps* sensu stricto from Southeast Asia of comparable or lower genetic divergence are more morphologically variable from one another in colouration and scalation than the Indian species are from each other (Karin et al. 2018; Freitas et al. 2019; Grismer et al. 2019; Le et al. 2021).

Viviparity in the tropics

The evolution of viviparity in squamates is strongly associated with cool temperatures, but the highest number of viviparous species are in the tropics (Feldman et al. 2015; Zimin et al. 2022). The most general explanation for this observation is the maternal manipulation hypothesis, which states that viviparity would be favoured when precise thermoregulation of embryos by the mother has a fitness advantage for the offspring (Shine 1995, 2014). It has been argued that the higher diversity of viviparous phrynosomatids lizards in tropical regions with low seasonality may result from selection along the r- and K- continuum (Pianka 1970) for smaller clutches of fitter offspring (Lambert and Wiens 2013) though there is no evidence for smaller clutch sizes in viviparous lizards (Meiri et al. 2020); while on the other hand high seasonality has been invoked to explain the evolution of viviparity in the tropics (Tinkle and Gibbons 1974; Zimin et al. 2022). This dichotomy is reflective of the complex trade-offs in fitness in the evolution of viviparity (Tinkle and Gibbons 1977; Shine 2014; Domínguez-Guerrero et al. 2022). The high number of viviparous tropical species may also be, at least in part, a consequence of the effect of overall diversification (Recknagel et al. 2021). Parity mode in squamates does not affect development time or the number and size of offspring (Meiri et al. 2020) and ~28 % of squamates have a clutch size of two (Meiri, pers. comm. 2023). Viviparity is potentially disadvantageous through a reduction in the number of clutches per season (usually a single clutch versus multiple clutches in oviparous species), an overall decline in annual fecundity, and potential locomotor impacts and increased predation risk (predation of an oviparous female is unlikely to cause a loss of her clutch as against predation of a gravid female) (Tinkle and Gibbons 1977; Shine 1995; Domínguez-Guerrero et al. 2022; Zimin et al. 2022).

Live-birth has originated >12 times within skinks with over 30 % of species being viviparous (Zimin et al. 2022). All 16 gravid *Dravidoseps* we dissected contained developing embryos, representing 5/8 species and all subclades, suggesting the genus is likely viviparous as a whole. No other peninsular Indian skinks are known to be viviparous, and *Dravidoseps* is distributed in cooler, drier habitats with greater temperature and precipitation seasonality than its oviparous sister clade *Subdoluseps* sensu stricto in Southeast Asia (Fig. 5). The four viviparous species of *Mochlus* are the only other known viviparous lygosominins, and (Greer 1977) suggested aridity may be a contributing factor to the evolution of viviparity in this clade on account of their distribution in the arid Horn of Africa, though more sampling is needed to understand patterns within African lygosominins. The long branch between the MRCA of *Dravidoseps* + *Subdoluseps* sensu stricto and MRCA of *Dravidoseps* from ~ 41–25 Mya during which time viviparity presumably evolved, closely overlaps with a time of global cooling and drying during the start of the Neogene, as well as increasing seasonality and the formation and expansion of the Indian dry zone (Zachos et al. 2001; Clift et al. 2008; Morley 2000; Patnaik et al. 2012; Pound et al. 2012). This potentially lends support to the cold-climate hypothesis as well as the influence of seasonality in the evolution of viviparity in this clade (Tinkle and Gibbons 1977; Shine 2014). *Subdoluseps* sensu stricto in Southeast Asia may have been relatively buffered during this time by factors such as (short) distance to the sea, less extreme temperatures, high humidity, aseasonality, and latitude. On the other hand, other lygosominins in peninsular India (*Riopa*) are not forest obligate and are found in more seasonal and warmer habitats (not shown) than *Dravidoseps* spp., further bolstering support for the cold-climate hypothesis.

Taxonomic utility of the lower eyelid condition

The presence or absence of a transparent window in the lower eyelid has been an important character used in higher level skink taxonomy (e.g. Mittleman 1952; Siler et al. 2011; Karin et al. 2016). Freitas et al. (2019, 2020) discussed the variability of this character within Lygosomini, concluding it was not useful based on one specimen of *Riopa albopunctata* with a transparent window on one side (Hora 1927), and the presence of both characters within species provisionally referred to *Mochlus*. Five species of *Mochlus* were described as having a transparent window in the lower eyelid, none of which have been genetically sampled, and at least two were reclassified as possessing a scaly lower eyelid (Freitas et al. 2019). A re-examination of the lower eyelid of the *R. albopunctata* specimen referred to by Hora (1927; which could not be traced in ZSI-K, P. Mohapatra pers. comm. 2023) and additional *Riopa* species is needed to understand variability of this character within *Riopa*. However, the lower eyelid condition is conserved in multiple Indian skink lineages, including *Dravidoseps* (transparent window), *Lamprolepis*, *Lygosoma*, the Indian subclade of *Riopa*, and *Subdoluseps* sensu stricto (all with a scaly lower eyelid); and, the condition is slightly variable in only two of the 13 lineages within the second subclade of *Riopa* (Fig. 3; Freitas et al. 2019, 2020). Thus, apart from a few species of *Mochlus* and *Riopa*, the presence of a transparent window in the lower eyelid separates *Dravidoseps* from most of the Tribe Lygosomini.

Conclusion

We presented genetic, morphological and ecological data to recognize a new genus of lygosomine skink endemic to peninsular India and five new species. Members of *Dravidoseps* are forest-obligate and highly conserved in morphology, making species diagnoses challenging. The Lygosomini began diversifying in the Eocene and may have had an Indian or Southeast Asian origin. Diversification within *Dravidoseps* was likely driven by paleoclimate and the distribution of forests, with a similar timeline seen in *Subdoluseps* sensu stricto, *Mochlus*, *Lygosoma* and *Riopa*. *Dravidoseps* evolved at a time of global cooling and increasing seasonality, and today inhabit cooler, drier and more seasonal habitats than *Subdoluseps* sensu stricto which are oviparous – any or all of which may have contributed to the evolution of viviparity within the group.

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Supplementary Material 1

Figures S1, S2

Authors: Agarwal I, Thackeray T, Khandekar A (2024)
Data type: .pdf
Explanation notes: Figure S1. Complete chronogram from divergence dating analyses. Bars at nodes show 95% HPD. — F**igure S2.** Maximum Likelihood phylogeny of Dravidoseps gen. nov. with posterior probability/ bootstrap support shown at nodes: **A** 16S; **B** PRLR; **C** RAG-1; **D** R35.

Link: https://doi.org/vz.74.e110674.suppl1

Supplementary Material 2

Tables S1–S4

Authors: Agarwal I, Thackeray T, Khandekar A (2024)
Data type: .xlsx
Explanation notes: Table S1. Sequences used for divergence dating analyses. — **Table S2.** Best-fit models of sequence evolution and partitioning schemes selected in PartitionFinder2 for different datasets. — **Table S3.** Indian *Dravidoseps* and southeast Asian Subdoluseps localities used in climate analyses. — **Table S4.** Diagnostic differences in nuclear sequences within *Dravidoseps*.

Link: https://doi.org/vz.74.e110674.suppl2