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Two new species of the *Ophisops microlepis* (Squamata: Lacertidae) complex from northwestern India with a key to Indian *Ophisops*

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ABSTRACT

We describe two new species of the lacertid genus *Ophisops* based on a series of 19 specimens from semi-arid habitats in the states of Gujarat and Rajasthan in northwestern India, provide a description of *Ophisops microlepis* sensu stricto, and a key to Indian *Ophisops*. *Ophisops pushkarensis* sp. nov. and *Ophisops kutchensis* sp. nov. are allied to *Ophisops microlepis* and can be diagnosed from all other Indian *Ophisops* by the fusion of the lower and upper eyelids, their large body size (snout to vent length > 50 mm), and ≥ 50 scales around midbody. They differ from *O. microlepis* and each other in the number of scales around midbody, the number of dorsal scales, subtle colour pattern differences, as well as uncorrected mitochondrial sequence divergence (6–9%). These are some of the only known endemic reptiles in these semi-arid landscapes and indicate that many other such habitats may harbour endemic biodiversity.

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Introduction

The Old World Lacertidae includes three subfamilies, the chiefly temperate Lacertinae (124 spp.), the Canary Islands endemic Gallotiinae (18 spp.), and the most diverse subfamily, the Eremiadinae, with 185 species distributed in arid and semi-arid Africa, Saharo-Arabia and southwest and Central Asia (Arnold et al. 2007; Mayer and Pavlicev 2007; Uetz et al. 2017). India forms the southeastern distributional limit of the Eremiadinae, three genera recorded from the region – including *Acanthodactylus* Daudin, 1802 with the single species *Acanthodactylus cantoris* Günther, 1864 distributed in sandy habitats in the north and northwest; ambiguous historical records of *Mesalina watsonana* Stoliczka, 1872 from northwest India; and *Ophisops* Ménétries, 1832 distributed across much of the Indian subcontinent (Smith 1935; Agarwal and Ramakrishnan 2017).

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Ophisops, also known as snake-eyed lizards (or snake-eyes) are diurnal, terrestrial lacertids found in open, grassy habitats, with five recognized species in India and three in the Saharo-Arabian region. Basal divergences within *Ophisops* separate a small-bodied clade (snout to vent length, SVL < 45 mm) and a large-bodied clade (SVL > 50 mm; Agarwal and Ramakrishnan 2017). Mitochondrial sequence data suggest that the relatively low species diversity in *Ophisops* is an underestimate, with ~30 candidate species in India (Agarwal and Ramakrishnan 2017). Much of this diversity is within the small-bodied clade, which includes 26 candidate species in three species complexes: *Ophisops beddomei* (Jerdon, 1870), *Ophisops jerdonii* Blyth, 1853 and *Ophisops nictans* Arnold, 1989. Indian members of the large-bodied clade include the possibly widespread single species *Ophisops leschenaultii* (Milne-Edwards, 1829), and the *Ophisops microlepis* Blanford, 1870 complex, which includes three candidate species based on mitochondrial sequence divergence (Agarwal and Ramakrishnan 2017).

Ophisops microlepis was described based on a single specimen from Central India, near Korba, Chhattisgarh (Figure 1; Blanford 1870). The species was subsequently collected ~900–1300 km west and northwest of the type locality (from Ajmer, Rajasthan and Kutch, Gujarat) and ~400 km northeast of the type locality (Karharbari, Jharkhand), suggesting a disjunct range spanning ~1700 km across northern India (Figure 1; Stoliczka 1872; Boulenger 1887, 1921). This conception of *O. microlepis* as a single, widely distributed species has persisted, and subsequent records of the species in the literature are mainly in regional and Indian checklists (e.g. Vyas 2000; Venugopal

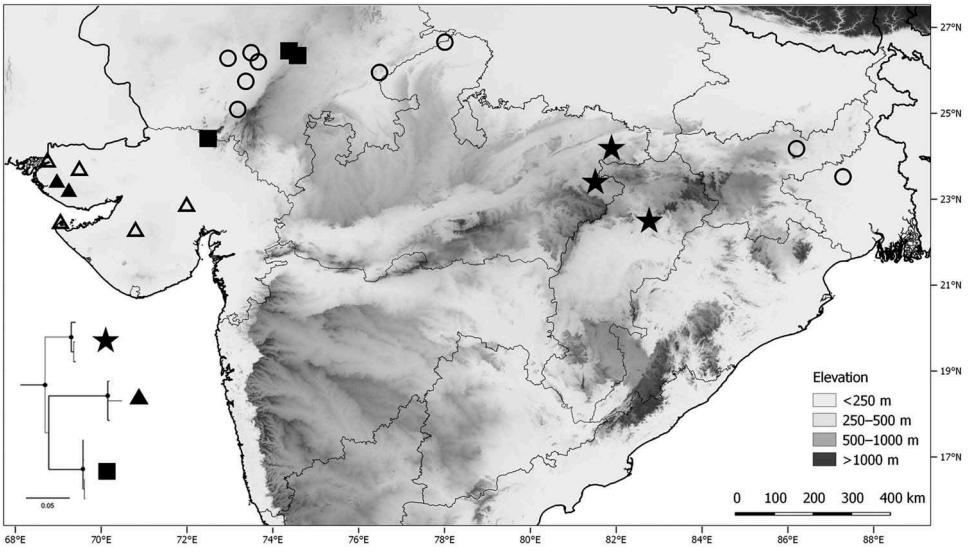

Figure 1. Relief map of India showing the known distribution of the *Ophisops microlepis* complex. Bold lines designate international borders, fine lines show Indian state borders. Solid symbols indicate sampled localities (numbers referenced in Table 1) and white-filled symbols previously published localities or visual records; stars indicate the distribution of *Ophisops microlepis*, squares *Ophisops pushkarensis* sp. nov., triangles *Ophisops kutchensis* sp. nov.; hollow circles represent literature records of members of the *O. microlepis* complex not assigned to a species. Inset left, maximum likelihood phylogeny of the *O. microlepis* complex (cytochrome *b*, bootstrap support > 75% depicted by solid circles at nodes; outgroups not shown).

2010; Nair and Krishna 2013), besides in two publications on feeding behaviour (Sharma and Vazirani 1977; Sharma et al. 2015). From literature that cites specific localities, *O. microlepis* has additionally been reported from western Gujarat (Rajkot: Sharma 1982; John et al. 1991; Nal Sarovar: Kumar 2009; Narayan Sarovar: Vyas 2002), and western Rajasthan (Jodhpur and Pali Districts, Sharma and Vazirani 1977; Sawai Madhopur District, Kumar et al. 2010). Agarwal and Ramakrishnan (2017) sampled *Ophisops microlepis* from its type locality and two previously reported western localities (Ajmer and Kutch), samples from the three localities representing deeply divergent mitochondrial lineages. We expand the sampling of Agarwal and Ramakrishnan (2017) with recent collections from western India for > 2000 nucleotides of sequence data from one mitochondrial and one nuclear marker. Examination of topotypical material allows us to present the first detailed morphological descriptions of *Ophisops microlepis* sensu stricto and describe the two genetically divergent lineages as new species.

Material and methods

Molecular data

We augmented the data set of Agarwal and Ramakrishnan (2017) for the *O. microlepis* complex, which included six cytochrome *b* (cyt *b*) and two RAG1 sequences from six individuals and localities, with sequence data for eight individuals that include an additional two localities (Figure 1). We used representatives of the large-bodied clade of *Ophisops* in our analyses, rooting the tree with the small-bodied clade (Table 1; Agarwal and Ramakrishnan 2017). We used Qiagen DNeasy® extraction kits and sent DNA extracts out for commercial polymerase chain reaction (PCR) and sequencing at Medauxin, Bangalore India, using the primers LgluLK and NTheH to amplify and sequence 1104 nucleotides of the mitochondrial gene cyt *b* and RAG-f0 and RAG-R1 for PCR amplification and sequencing along with RAG587-H to sequence a partial fragment of the nuclear marker RAG1 (1005 nucleotides; Mayer and Pavlicev 2007). Sequences were aligned in ClustalW (Thompson et al. 1994), translated to check for stop codons or errors in the reading frame, and pairwise uncorrected genetic distances were calculated in Mega 5.2 (Tamura et al. 2011).

We conducted single locus analyses, partitioning ND2 by codon position and using a single partition for RAG1, reconstructing evolutionary relationships using maximum likelihood in RAxML HPC 8.1.2 (Stamatakis 2014) through the raxmlGUI 1.5 (Silvestro and Michalak 2012) with the GTR + G model and 10 independent maximum likelihood runs, support was assessed using 500 rapid bootstraps.

Morphology

Morphological data were recorded from a total of 32 preserved specimens of the *O. microlepis* complex and 15 specimens of other Indian *Ophisops* spp. in the collections of the Bombay Natural History Society, Mumbai (BNHS), Centre for Ecological Sciences, Bangalore (ESV), and the National Centre for Biological Sciences, Bangalore (NCBS/ Ishan Agarwal field series: IAL/ Varad Giri field series: VG) (Table 2). Data on other species of *Ophisops* were taken from Smith (1935) and confirmed on additional specimens listed in the material examined (Appendix 1). As we could not examine the holotype of

Table 1. Species, voucher number, locality and GenBank accession numbers used in this study.

Species	Field no.	Voucher no.	Locality	GenBank Accession numbers	
				Cytochrome *b*	RAG1
Ophisops microlepis	IAL099	NCBS AU739	India; Chattisgarh, Korba District, Nr. Chuhiya	KX753534	MG885737
Ophisops microlepis	IAL101	NCBS AU741	India; Madhya Pradesh, Shahdol District, Ksheer Sagar	KX753533	MG885738
Ophisops microlepis	IAL105	NCBS AU744	India; Madhya Pradesh, Shahdol District, nr. Tikri	KX753532	MG885739
Ophisops pushkarensis sp. nov.	IAL006	BNHS 2031	India; Rajasthan, Ajmer District, nr. Pushkar	KX753530	KX753618
Ophisops pushkarensis sp. nov.	IAL038	NCBS AU749	India; Rajasthan, Ajmer District, hill Nr. Ajmer city	KX753531	MG885742
Ophisops pushkarensis sp. nov.	VG0335	NCBS AU750	India; Rajasthan, Ajmer District, 9 km from Ajmer	MG885733	MG885743
Ophisops pushkarensis sp. nov.	VG0336	NCBS AU751	India; Rajasthan, Ajmer District, 9 km from Ajmer	MG885734	MG885744
Ophisops kutchensis sp. nov.	IAL002	BNHS 2024	India; Gujarat, Kacchh District, Yellowstone	KX753529	KX753617
Ophisops kutchensis sp. nov.	VG0299	NCBS AU755	India; Gujarat, Kacchh District, 50 km from Bhuj	MG885735	MG885740
Ophisops kutchensis sp. nov.	VG0300	NCBS AU756	India; Gujarat, Kacchh District, 50 km from Bhuj	MG885736	MG885741
Ophisops elegans	-		Armenia; Khosrov	AF206532	–
Ophisops elegans	IPMB 40627		Iran, Tehran Province	FJ416172	KJ486178
Ophisops elegans	NHM Vienna		Greece; Evros, Gianuli	GQ142116	EF632235
Ophisops leschenaulti	IAL072	IAL072	India; Karnataka, Tumkur District, Devarayanadurga	KX753517	KX753609
Ophisops leschenaulti	IAL080	IAL080	India; Karnataka, Bellary District, Shupra RF	KX753512	KX753607
Ophisops leschenaulti	IAL232	IAL232	India; Tamil Nadu, Krishnagiri	KX753517	KX753609
Ophisops occidentalis	NHMC 80.3.101.3		Tunisia; Quled Maeur	EU081680	–
Ophisops beddomei	IAL042	IAL042	India; Karnataka, Kodagu District, Munnikal Caves	KX753447	KX753573
Ophisops jerdoni	IAL005	IAL005	India; Gujarat, Kacchh District, Lakhpat	KX753450	KX753576

IAL, Ishan Agarwal field series; VG, Varad Giri field series (all tissues at NCBS, National Centre for Biological Sciences, Bangalore); NHMC, Natural History Museum of Crete; NHMV; Natural History Museum of Vienna; IPMB, Institute of Pharmacy and Molecular Biotechnology, Germany.

Table 2. Morphological and selected meristic data for members of the *Ophisops microlepis* complex (measurements in mm).

Species	*Ophisops microlepis*										*Ophisops pushkarensis* sp. nov.									
	Referred Material										Holotype	Paratypes							Referred Material	
Voucher No.	NCBS AU739	NCBS AU740	NCBS AU741	NCBS AU742	NCBS AU743	NCBS AU744	NCBS AU745	NCBS AU746	NCBS AU747	NCBS AU748	BNHS 2031	NCBS AU749	NCBS AU750	NCBS AU751	NCBS AU752	NCBS AU753	NCBS AU754	NCBS AU701	BNHS 1726	BNHS 1727
Field No.	IAL 099	IAL 100	IAL 101	IAL 102	IAL 103	IAL 105	IAL 107	IAL 108	IAL 109	IAL 110	CES G30	CES G458	VG 0335	VG 0336	VG 0337	VG 0338	VG 0339			
Sex	M	M	M	M	F	F	F	M	M	M	F	F	M	F	F	F	M	F	F	F
SVL	60.2	61.3	61.5	54.5	56.7	49.06	51	53.5	54.5	58.8	62.7	54.3	57.5	54.5	55.4	55.8	59.6	48.5	59.1	40.7
TL	139.7	135.3	126.7	115.4	115.3	95.0	100.7	36.0*	101.9	128.3	70.1*	120.2	14.1*	21.5*	117	102	136.3	29.7*	101.8	11.1*
TW	7.2	7.4	7.1	6.3	6.1	4.09	5.3	6.2	6.2	6.9	6.8	6	6.4*	6.3	5.8	6	7.1	4.3	5.4	3.5
UAL	7.7	8.4	8	5.3	6.4	5.06	6.7	7.1	6.9	7.7	7.3	6.2	7.1	7.5	6.9	6.3	7.3	6.4	6.1	4.5
LAL	8.2	8.5	8.3	7.2	7.8	6	6.4	8	7.4	8.1	8.3	7.4	8.5	7.8	7.7	7	8.2	6.6	6.9	5
F1	2.8	3	3.5	3.4	2.8	2.05	2.5	2.9	3.1	2.5	2.3	3.1	3	1.7*	2.9	2.8	2.7	2.5	-	-
F2	4.1	4.1	4.9	5.3	4.6	3.08	4	4.7	4.7	5.2	3.9*	4.7	5.3	4.8	4.7	4.9	5.3	3.4	-	-
F3	6.6	5.7	7	7.1	6.8	6	5.7	6.9	6.7	6.8	6.4	6.7	6.5	6.3	6.3	6	6.7	5.8	-	-
F4	6.9	5.9	7.7	7.3	6.8	6.04	6.1	7.3	6.7	7.3	6.8	6.9	7.2	7.1	7.2	7.1	7.8	6.2	-	-
F5	4	3.8	3.8	4.7	4	3.08	3.2	4.3	3.8	4.2	4.1	4	4.6	4.2	4.5	4.1	4.5	3.7	-	-
FEL	11.5	11.7	11.2	10.4	9.7	8.08	9.3	10.4	10.3	11.3	11.9	10.3	10.5	10.1	9.6	10.6	11.2	8.7	9.2	7.1
CL	12.2	12.3	12.2	10.9	10.8	9.5	9.6	10.6	11.1	11.8	12.1	11.2	12.1	11.9	11	11.1	12.2	10	11.2	7.2
HFL	18.9	20.1	19.4	21.1	18.1	16.8	12.2	18.5	18.2	19.4	18.9	20.4	21.5	20.2	21	19.9	21.4	13.4	19.3	16.7
T1	3.8	5.1	5.6	5	4.2	3.5	3.7	4.7	4.7	4.2	3.7	3.9	5	3.7	5	4.6	5.7	4.1	-	-
T2	5.4	7.5	6.8	7.2	5.8	5.6	5.9	6.9	7.1	7.1	5.8	6	5.9*	6	6.5	6.6	7.8	5.5	-	-
T3	9	10.7	8.9	9.9	8.7	7.7	8	9.6	9.6	10	9.6	9.5	10.6	9.4	10.3	10.4	10.4	8.7	-	-
T4	12.7	15.3	13.5	14.8	12.7	11.1	12.1	13	13.3	13.8	13.7	13.8	14.6	14	14.5	14.4	15	12.3	-	-
T5	8	8.5	9	8.9	7.3	6.3	6.9	8.3	7.6	8.3	7.7	8.7	8.8	8	8.3	7.8	9.5	7.3	-	-
AGL	23.2	26.9	27.8	27.3	22	23.5	24	25.8	24.8	26.5	29.7	23.5	25.6	25.5	29.4	27.8	31.3	23.3	29.8	18.3
BH	6.9	5.5	6.3	5.9	5.7	4.4	5.8	6.8	5.3	6.1	8.4	5	5.2	6.1	5.5	5.7	6.1	5.9	7.1	4.3
BW	10.3	11.9	11.4	11.3	11.5	7.8	10.6	11.2	9.7	9.8	14.7	11.5	10.2	10.3	12	10.3	11.5	8.4	10.5	6.5
HL	13.2	13.1	13	12	11.9	10.7	10.7	11.6	11.7	12.1	13.2	13	14.4	13.2	13.5	13.2	14.5	11.6	13.1	10
SL	13.5	13.5	13.5	12.5	12.3	11.3	10.9	12.5	12.5	12.6	13	12.4	13.4	12	12.3	12.6	13.3	-	12.2	9.8
HW	8	7.5	7.9	7.2	7.5	6.4	6.4	7.3	7.2	6.9	7.8	7.1	7.5	7.3	7	7.3	7.6	6.3	6.9	5.5
HD	6.8	6.3	6.5	5.6	6	4.8	5.3	6.3	5.9	6	6.7	5.8	6.3	6.2	5.6	5.6	6.4	4.8	5.5	4.3
ED	2.2	2.2	2.1	2.1	2.1	2.1	2.1	2.1	2.1	2.1	2.1	2.1	2	1.9	2	1.9	2.1	2	2.1	1.8
EE	5.2	5.2	5.1	4.6	4.7	4.1	4.3	4.6	4.8	4.7	4.7	4.3	5	4.3	4.2	4.1	4.7	3.8	3.8	3.3
ES	7.4	7.4	7.6	6.8	6.7	6.2	6.2	6.4	6.8	7	7.3	6.7	7.2	6.5	6.3	6.5	7.2	6	6.9	5.7
EN	6	6.1	6.1	5.5	5.2	4.9	5	5.4	5.6	5.5	5.9	5.5	5.8	5.4	5.6	5.4	6	5	5.5	4.2
IO	5.2	5	5	4.8	4.5	4.1	4.3	4.7	4.7	5	5.1	4.7	5.1	4.6	4.8	4.4	4.4	4.2	4.4	3.8
EL	0.7	0.9	1.1	0.9	0.7	0.8	0.6	0.8	1.1	0.9	0.7	0.8	1	0.9	0.8	0.9	1	1	1	0.8
IN	1.6	1.5	1.4	1.4	1.4	1.2	1.2	1.4	1.2	1.4	1.4	1.4	1.4	1.4	1.4	1.3	1.4	1.3	1.4	1.2
DS	122	127	131	122	136	128	135	133	128	134	135	133	135	140	148	142	141	142	119	117
ESFL	37	30	39	37	41	32	32	34	30	32	38	35	37	39	35*	35*	40	42	**	**
FP L&R	14&14	14&16	14&14	17&18	13&14	13&14	14&14	14&15	14&15	16&15	15&15	15&15	16&16	15&14	17&17	16&16	16&17	16&17	15&15	15&15
RBS	56	59	61	56	56	56	59	58	57	59	58	58	59	57	60	62	57	61	50	50

(*Continued*)

Table 2. (*Continued*).

	Ophisops kutchensis sp. nov.											
Species	Holotype	Paratypes										
Voucher No.	NCBS AU760	BNHS 2024	NCBS AU755	NCBS AU756	NCBS AU757	NCBS AU758	NCBS AU759	NCBS AU761	NCBS AU762	NCBS AU763	NCBS AU764	NCBS AU765
Field No.	VG 0304	CES G10	VG 0299	VG 0300	VG 0301	VG 0302	VG 0303	VG 0305	VG 0306	VG 0307	VG 0308	VG 0309
Sex	F	M	F	M	F	F	F	F	M	M	M	F
SVL	42.6	53.4	44.8	43.4	46.2	46.1	43.5	44	45.5	41.1	47.3	43
TL	105.6	74.2*	84.3	101	23*	15.3*	102.3	103.4	12*	18.7*	115.7	90.1
TW	5	5.5	4.7	4.6	4.5	4.7	4.4	4.4	4.6	4	4.6	3.9
UAL	5.9	7.4	4.9	5.1	5.2	5.7	5.5	5.6	5.8	5	5.6	6
LAL	6.5	7.8	6.4	6.6	6.6	6.3	6	6.3	6.8	6.3	5.9	6.3
F1	2.2	3.8	2.5	2.5	2.6	2	2.4	2.3	2.7	2.6	3	2.5
F2	3.3	4.8	3.7	4	3.3	4.1	3.9	3.8	4.2	3.9	4.3	3.7
F3	5.3	7	5.5	5.6	5.1	5.6	5.4	5.6	6.1	5.6	5.9	5.5
F4	6.1	7.1	5.8	6.5	6	6	5.8	6	6.7	6.1	7.1	5.9
F5	3.1	4.2	3.4	3.6	3.1	2.9	3.5	3.3	3.4	3.1	4.7	3.5
FEL	9.3	11.6	8.4	8.6	9.3	8.1	7.7	9.2	9.2	8.1	9.2	8.1
CL	9.8	12.4	9.4	9.4	9.4	9.4	9	9.7	9.4	8.7	10.5	9.2
HFL	17.4	20.3	17.8	16.8	17.2	18.3	17	17	19.8	15.2	19.6	16.3
T1	3.7	4.6	3	3.2	4.1	3.8	3.5	4.3	4.4	4.3	4.5	4
T2	6	7.1	5.6	4.6	5.4	5.8	5.8	6.3	3*	5.04	6.5	5.8
T3	9.5	11.1	8.9	7.5	7.6	9.3	8.3	8.8	9.8	7.8	9.3	8.5
T4	13.3	15.3	12.6	11.1	12.6	12.6	12.1	13	14.5	11.9	13.8	12.6
T5	7.4	9.3	6.7	6.2	7.3	7	6.5	7.1	8.4	7.6	9.4	9.1
AGL	23.4	24.6	21.5	18.5	21.7	23.2	20.6	20.4	20.5	18.6	23.1	21.2
BH	4.3	5.8	4.1	3.4	3.6	3.5	4.2	3.7	3.4	3.8	3.6	3.1
BW	8.7	9.7	7.4	7.6	8	8.4	8	7.5	8.3	7.5	7.7	6.5
HL	11.3	13	11.3	10.6	11.5	10.4	10.4	10.1	11.2	10	10.4	9.8
SL	11.4	13.2	10.5	10.7	11	10.7	10.5	10.2	11.3	10.4	11	10.1
HW	6.6	7.3	6	6.3	6.2	6.3	6	6	6.1	6	6.1	5.4
HD	5.5	6.4	4.8	4.6	4.8	4.9	4.5	4.6	4.7	4.7	4.9	4.4
ED	1.8	2.2	1.8	1.8	1.9	1.9	1.8	1.8	1.9	1.8	1.9	1.8
EE	3.9	5.1	3.6	3.9	3.8	3.5	3.3	3.6	3.7	3.6	3.8	3.6
ES	6	7.1	5.5	5.6	5.7	5.6	5.5	5.5	6	5.5	5.9	5.2
EN	4.9	5.7	4.6	4.6	4.8	4.6	4.5	4.5	4.9	4.5	4.9	4.4
IO	4.2	5.2	4	4	4	3.9	4	3.9	4.1	3.8	4	3.9
EL	0.8	0.8	0.8	0.9	0.8	0.8	0.7	0.8	0.9	0.8	1.1	0.9
IN	1.2	1.4	1.2	1.2	1.3	1.2	1.2	1.2	1.3	1.1	1.2	1.2
DS	123	113	119	117	129	127	122	122	120	122	118	119
ESFL	30	21	28	27	27	31	29	29	27	**	**	26
FP L&R	11&12	13&15	11&11	12&13	13&13	12&13	11&12	12&13	14&13	14&14	13&13	12&12
RBS	53	52	50	50	58	53	56	53	53	52	52	50

Note: L and R indicates left and right, other abbreviations as in methods.

O. microlepis we used topotypical material represent the species besides photographs of the holotype (Figure 3). Colour pattern was recorded from photographs taken in life. We explored a range of morphological characters in the group, some of which turned out to be invariant within the *O. microlepis* complex (see Results). We used a Leica S6E™ stereomicroscope to count the following characters: supraciliary scales (SCS, flat, elongate, imbricate scales above the orbit); supraocular scales (SOS); supraciliary granules (rows of granules between the SOS and SCS); supralabials (SL) and infralabials (IL) (from rostral and mental, respectively, to posterior-most enlarged scale at angle of the jaw); loreals; temporal scales; supratemporals (enlarged scales in temporal region touching parietals); chin shields (CS, enlarged scales in gular region touching infralabials); enlarged scales on ventrum anterior to fore limb insertions (SC); gular scales (small scales in gular region between CS and SC); enlarged scales on lower arm from elbow to distal end of wrist (ESLA); enlarged scales on the femur from groin to knee (ESF); enlarged scales on the flank (ESFL); enlarged scales on crus from knee to heel (ESC); dorsal scales in longitudinal series (DS, number of scales on dorsum from behind occipital to above vent); scales across the belly (RVS, counted at midbody at ~17th ventral); scales in a transverse row around midbody (RBS, counted at midbody at ~17th ventral, excluding RVS); ventral scales (VS, from SC to anterior border of cloaca); transverse subdigital lamellae, counted from the base of the digits to the claw and including the claw sheath on the finger 1 (LAM1F), finger 4 (LAM4F), toe 1 (LAM1T), toe 4 (LAM4T), toe 5 (LAM5T); femoral pores (FP); and the number of poreless scales between femoral pores (SBFP). We also recorded the condition of the lower eyelid (fused or separated), the presence or absence of an enlarged tympanic scale, and the direction and condition (smooth or keeled) of scales of the flank. The following measurements were taken with a dial caliper to the nearest 0.1 mm on the right side of the animal where possible: snout to vent length (SVL, from tip of snout to anterior border of vent); tail length (TL, posterior border of vent to tail tip); tail width (TW, taken at the tail base); upper arm length (UAL, from the anterior insertion of fore limb to elbow); forearm length (FL, from elbow to distal end of wrist); finger lengths (F1–F5, from base of the finger to tip of claw); femur length (FEL, from groin to knee); crus length (CL, from knee to heel); hind foot length (HFL, from heel to end of fourth toe); toe length (T1–T5, from base of the toe to tip of claw); axilla to groin length (AGL, from posterior margin of fore limb insertion to anterior margin of hind limb insertion); body height at midbody (BH); body width at midbody (BW); skull length (SKL, from snout tip to posterior margin of occipital); head length (HL, from snout tip to retroarticular process of jaw); head width (HW, measured at the angle of the jaw); head depth (HD, maximum height of head); eye diameter (ED, greatest horizontal diameter of eye); eye to ear distance (EE, from anterior edge of ear opening to posterior edge of eye); eye to snout distance (ES, from anterior margin of eye to tip of snout); eye to nostril distance (EN, from anterior margin of eye to the posterior margin of nostril); interorbital distance (IO, taken at the anterior margin of orbit); ear length (EL, greatest horizontal length of ear opening); and internarial distance (IN, horizontal distance between nares).

As our collections did not include large series of adult specimens, we used ratios to bring out relative body proportions (CL/SVL, HL/SVL, FL/CL) and relative head shape (EE/EN, EE/ES, HW/HL). We conducted a Principal Components Analysis and Discriminant

Function Analysis using these ratios, and explored also concatenating variable meristic characters into a single analysis.

Results

Phylogenetic relationships

The large-bodied clade of *Ophisops* is well supported in analyses with both markers, as are each of the three constituent clades – the *O. microlepis* complex, *O. leschenaultii* and *Ophisops elegans*, though relationships between these three clades received low support in both analyses (Figure S1, S2). The *O. microlepis* complex is composed of three well-supported clades in the cytochrome *b* data (Figure 1) that are moderately to deeply divergent on cyt *b* (6.0–9.4% between clades, < 1.7% within clades; Table 3), but are not recovered in analyses with RAG1 (0.5–0.7% sequence divergence; Figure S2). The position of the three lineages relative to each other is not well resolved even with the cytochrome *b* data (Figure S1).

Morphology

Members of the *O. microlepis* complex were morphologically diagnosed as *Ophisops* based on the absence of a distinct collar, digits not fringed laterally, and the lower eyelid with a large transparent disc (Boulenger 1921; Smith 1935). Of the 30 meristic characters evaluated, 27 were identical or overlapped broadly within the three genetically divergent lineages in the *O. microlepis* complex (mean count to the nearest integer with range in parentheses are presented): 4 (3–5) supraciliary scales, 4 (4–5) supraocular scales, 15 (12–19) supraciliary granules, supraocular scales, 8 (7–9) supralabials, 7 (6–9) infralabials, 2 (2) loreals, 8 (6–10) temporals, 3 (2–5) supratemporals, 6 (6–7) chin shields, 9 (7–11) SC, 25 (21–29) gular scales, 7 (6–11) ESLA, 9 (8–10) ESF, 6 (5–7) ESC, 32 (29–35) VS, 7(6–9) LAM1F, 17 (16–19) LAM4F, 8 (7–9) LAM1T, 22 (19–26) LAM4T, 14 (13–15) LAM5T, 14 (11–18) FP, 2 (1–3) SBFP, and six rows of ventrals. All specimens also had the lower eyelid fused, the presence of an enlarged tympanic scale, and smooth and upward pointing scales on the flank. The only three characters with meaningful variation between the three lineages are the number of dorsal scales (mean 121, 130, 140), RBS (53, 58, 59) and ESFL (28, 34, 38) (Table 2).

Attempting to summarize morphological variation using a principal components analysis had substantial overlap between the three lineages across the first three principal components using ratios, as well as ratios and the three variable meristic characters (not shown). Discriminant function analyses using both the morphological data sets were able to separate the three lineages in morphospace (Figure 2 shows a plot of discriminant function 1 from ratio only data versus DS).

Table 3. Uncorrected pairwise % cytochrome *b* sequence divergence between and within (along diagonal) members of the *Ophisops microlepis* complex.

		1	2	3
1	*Ophisops microlepis*	0.3–0.9		
2	*Ophisops pushkarensis* sp. nov.	5.9–6.3	0.1–0.5	
3	*Ophisops kutchensis* sp. nov.	7.6–9.4	8.1–9.5	0.4–1.6

Below, we provide a definition for *O. microlepis* sensu stricto, and describe the two unnamed lineages using morphology to support the distinctiveness of these genetically divergent, allopatric lineages. We also provide a key to Indian *Ophisops*.

Taxonomy

Ophisops microlepis (Blanford 1870)
Small-scaled snake-eye
Figures 3–7

Ophiops [*Gymnops*] *Microlepis* Blanford, 1870: 351–354, Plate XV.

Holotype. ZSI 2236, 'Korba in Bilaspur, the eastern part of Chhatisgarh division, Central Province' (in Chhattisgarh, central India) (Figure 3).

Additional material. NCBS AU739–740, adult males, near Chuhiya, Korba District, Chhattisgarh, India [22.48307°N, 82.68985°E; elevation 300 m above sea level, (asl)], collected 4 May 2015; NCBS AU741–742, adult males, NCBS AU743, adult female, near Ksheersagar (23.40423°N, 81.44724°E; 400 m asl), 6 May 2015 and NCBS AU744–745 adult females, NCBS AU746–748 adult males, near Tikri (24.16784°N, 81.89611°E; 325 m asl), 7 May 2015; latter two localities in Shahdol District, Madhya Pradesh, India; collected by A. Khandekar, T. Khichi and I. Agarwal.

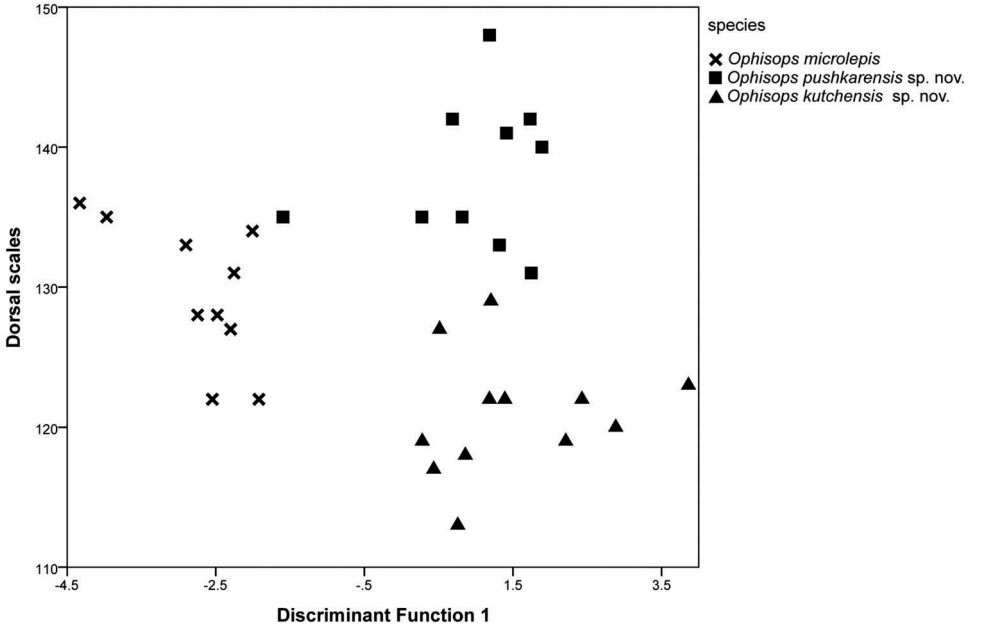

Figure 2. Plot of Discriminant Function 1 versus number of dorsal scales, illustrating the separation of the three lineages.

Figure 3. *Ophisops microlepis* in dorsal, ventral and lateral view (holotype ZSI 2236).

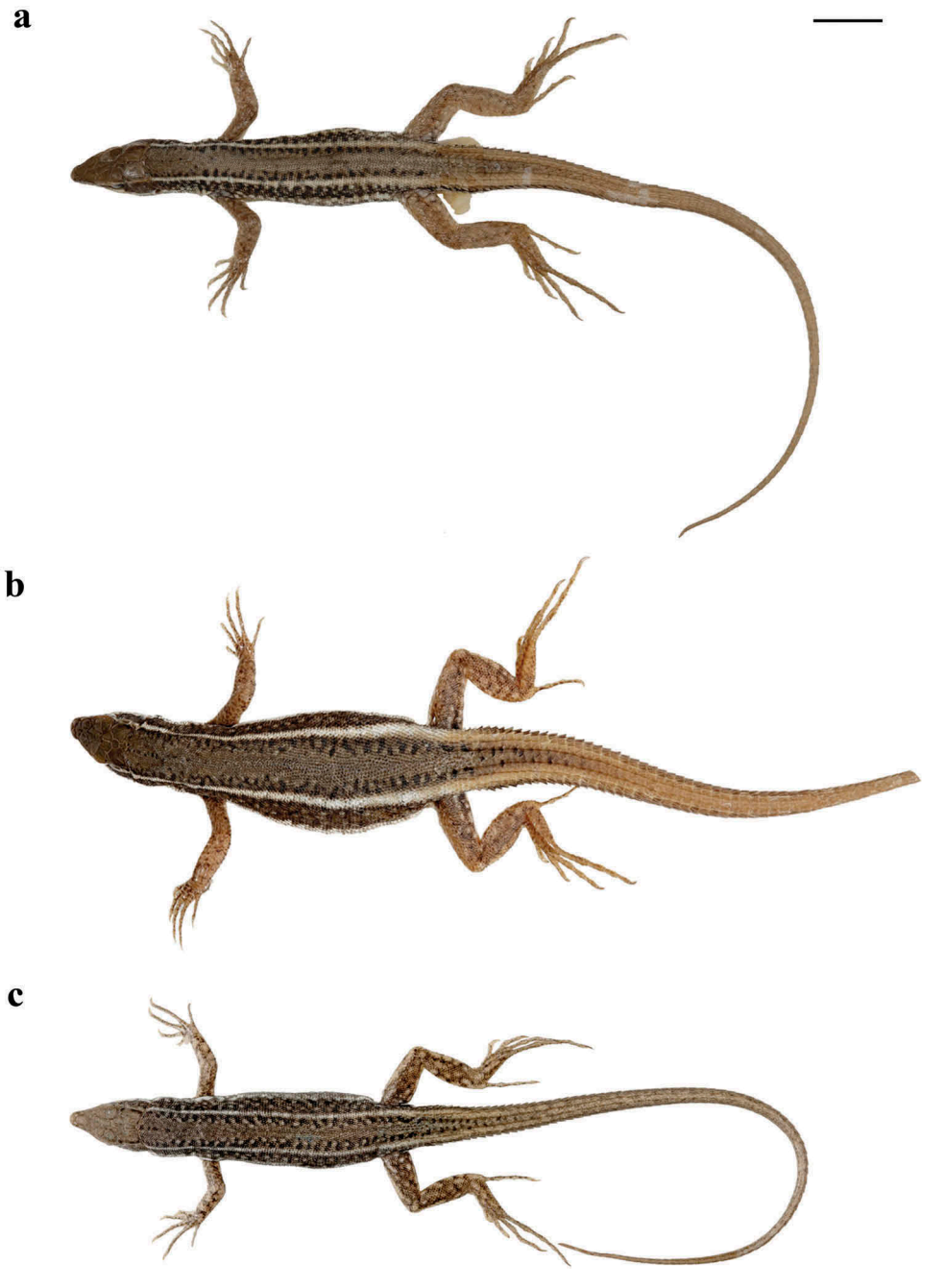

Figure 4. Dorsal view of (a) *Ophisops microlepis*, NCBS AU747; (b) holotype of *Ophisops pushkarensis* sp. nov., BNHS 2031; (c) holotype of *Ophisops kutchensis* sp. nov., NCBS AU760. Scale bar 10 mm.

Diagnosis. *Ophisops microlepis* can be distinguished from members of the small-bodied clade of *Ophisops* by its larger body size (SVL up to 61.5 mm versus SVL < 45 mm in *O. beddomei*, *O. jerdonii* and *O. nictans*), the higher number of scales in

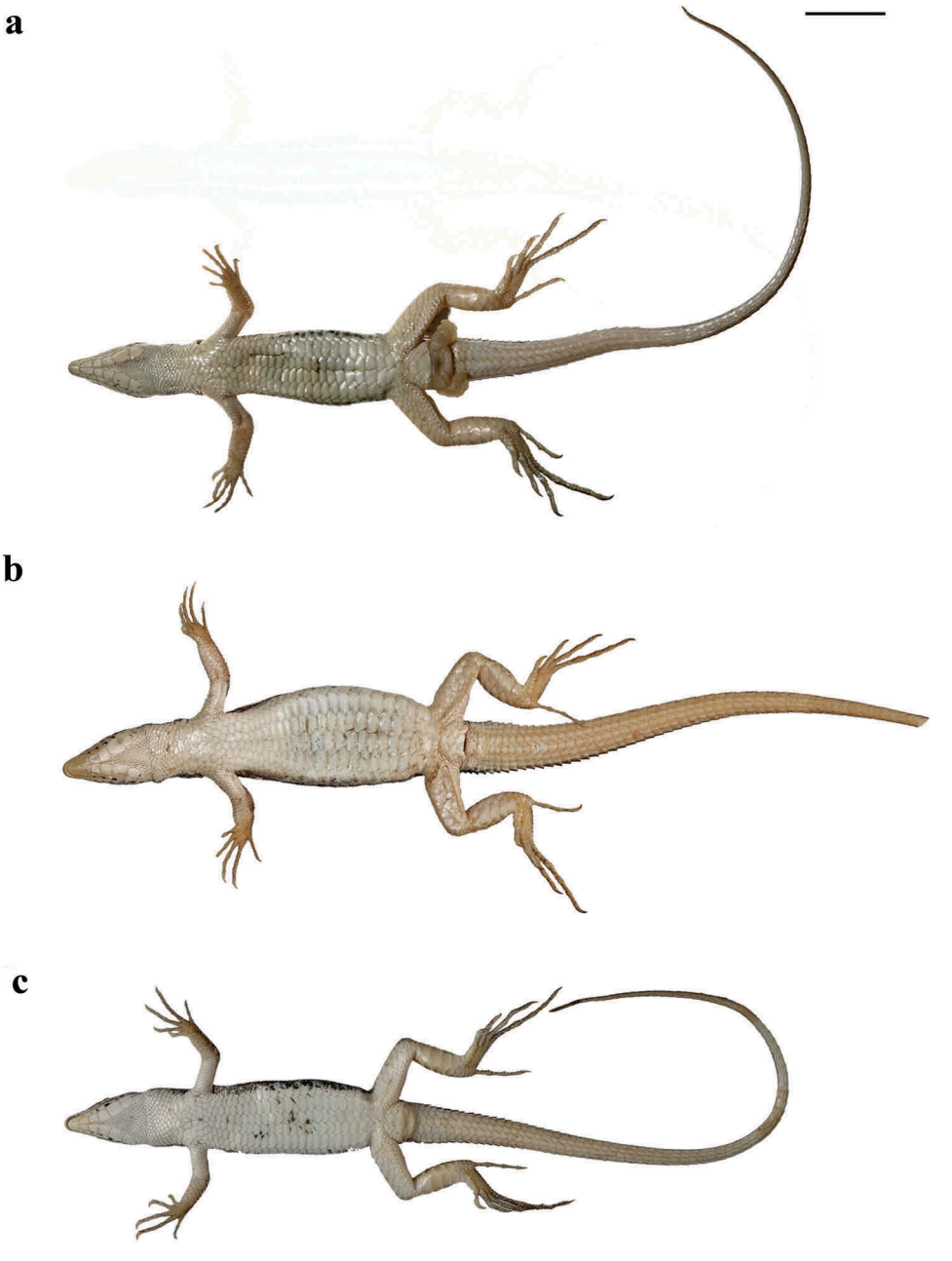

Figure 5. Ventral view of (a) *Ophisops microlepis*, NCBS AU747; (b) holotype of *Ophisops pushkarensis* sp. nov., BNHS 2031; (c) holotype of *Ophisops kutchensis* sp. nov., NCBS AU760. Scale bar 10 mm.

a transverse row around midbody (RBS 56–61 versus < 35 in *O. beddomei*, *O. jerdonii* and *O. nictans*) and the higher number of dorsal scales in a longitudinal series (DS > 120 versus < 52 in *O. beddomei*, *O. jerdonii* and *O. nictans*). *Ophisops microlepis* can be distinguished from the other large-bodied Indian congener,

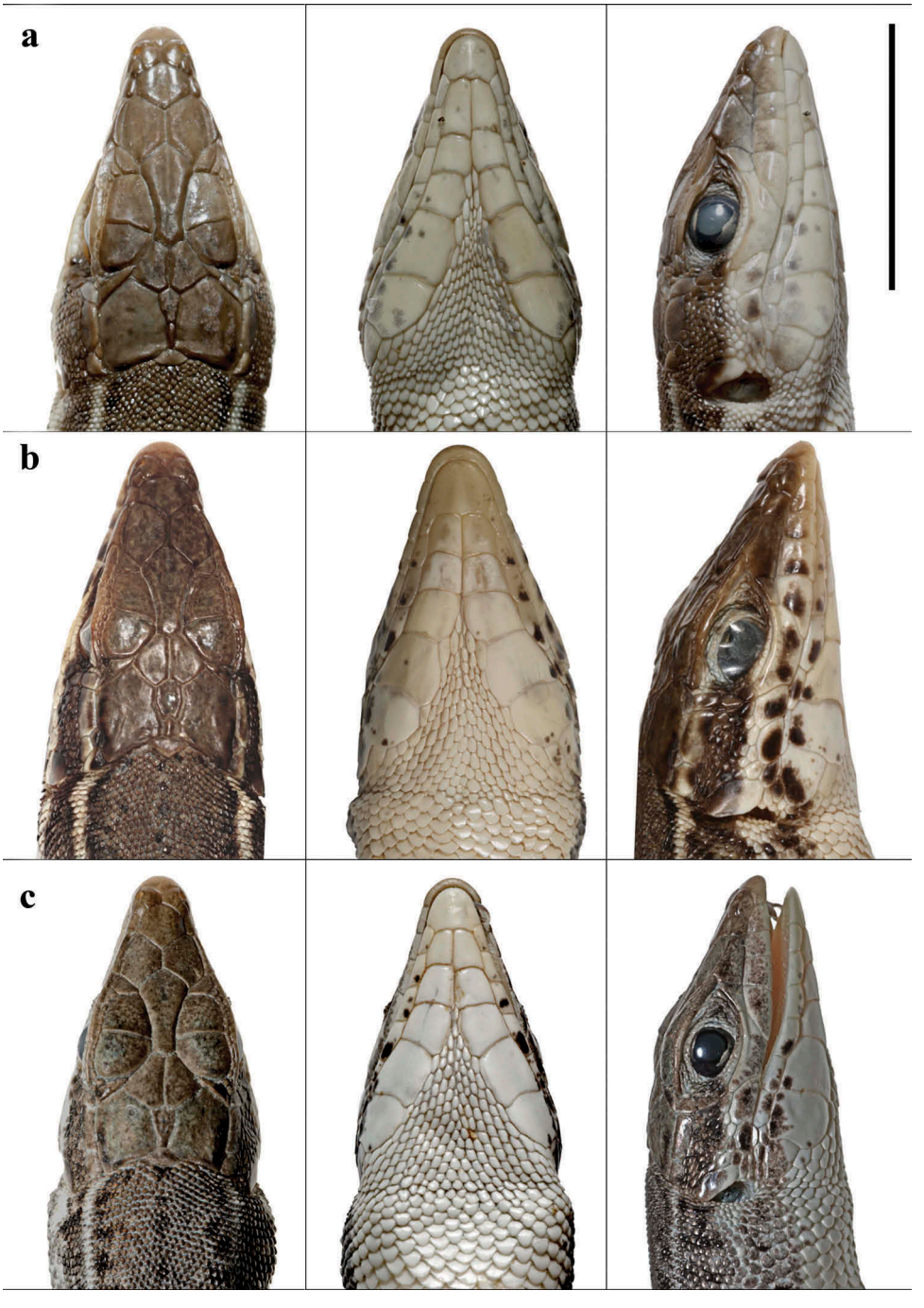

Figure 6. Dorsal, ventral and right lateral views of head of (a) *Ophisops microlepis*, NCBS AU747; (b) holotype of *Ophisops pushkarensis* sp. nov., BNHS 2031; (c) holotype of *Ophisops kutchensis* sp. nov., NCBS AU760. Scale bar 10 mm.

Figure 7. Members of the *Ophisops microlepis* complex in life: (a) *Ophisops microlepis*, NCBS AU739; (b) *Ophisops pushkarensis* sp. nov., holotype BNHS 2031; (c) *Ophisops kutchensis* sp. nov., paratype BNHS 2024.

O. leschenaulti by the larger body size of the former (SVL up to 61.5 mm versus SVL ≤ 50 mm), higher number of scales around midbody (56–61 versus 42–50) and the lower eyelid fused with the upper eyelid (versus lower eyelid distinct from upper in *O. leschenaulti*). *Ophisops microlepis* is most closely related to the two new species described herein, and diagnoses against the new species are provided after their descriptions.

Colouration in life (based on additional material examined, Figure 7). Dorsal ground colour dark khaki; two prominent lighter lateral stripes, a dorsolateral stripe extending from behind the eye (indistinct in temporal region) onto the tail, and a ventrolateral stripe that runs from the labials, above the forearm insertion and terminating at the groin. Dorsolateral and ventrolateral stripe buff anteriorly, the former with more rufous near hind limb insertions and on the tail; ventrolateral stripe lightly to heavily speckled between the limbs. Interspaces between stripes heavily mottled with darker and lighter markings, anterodorsal margin of dorsolateral stripe with mainly darker mottling extending up to ~2× width of the dorsolateral line, markings on each side well separated from one another in the vertebral region. Flanks, below ventrolateral stripe, with marbled lighter and darker markings, some enlarged belly scales that extend onto flanks with yellow-green markings. Limbs with scattered, irregular lighter and darker markings, largest and most prominent on femur where lighter spots are enclosed by darker reticulation. Head similar to dorsum in colouration, labials with dark blotches, temporal region with dark markings, iris bronze. Venter immaculate white. Dorsolateral stripes meet on the tail, flanked by narrow darker markings that fade to white on the tail venter.

Colouration in preservative (Figures 3–5). Similar to life colouration, except colours relatively faded and shades of yellow completely lost.

Distribution and natural history. This species was observed by us in flat and mildly undulating sandy habitats along the banks of large rivers with large tussocks of grass and other low vegetation (Figure 8). We only collected this species from three localities on a single fieldtrip in May 2015. These localities are at elevations of 300–400 m asl on the northeastern edge of the Satpuda and Vindhya Ranges, and are the only confirmed localities for *O. microlepis* sensu stricto.

***Ophisops pushkarensis* sp. nov.**

Pushkar small-scaled snake-eye

Figures 4–7, 9

Ophisops microlepis (non Blanford 1870)

Holotype. BNHS 2031, adult female, near Pushkar (26.49318°N 74.56021°E; 505 m asl), Rajasthan, India, collected by A. Datta-Roy, T. Khichi and I. Agarwal 25 September 2009.

Paratypes. NCBS AU749, adult female, near Ajmer (26.44638°N 74.68600°E; 525 m asl), Rajasthan, India, collected by V. Deepak on 17 May 2014; NCBS AU750, NCBS AU754,

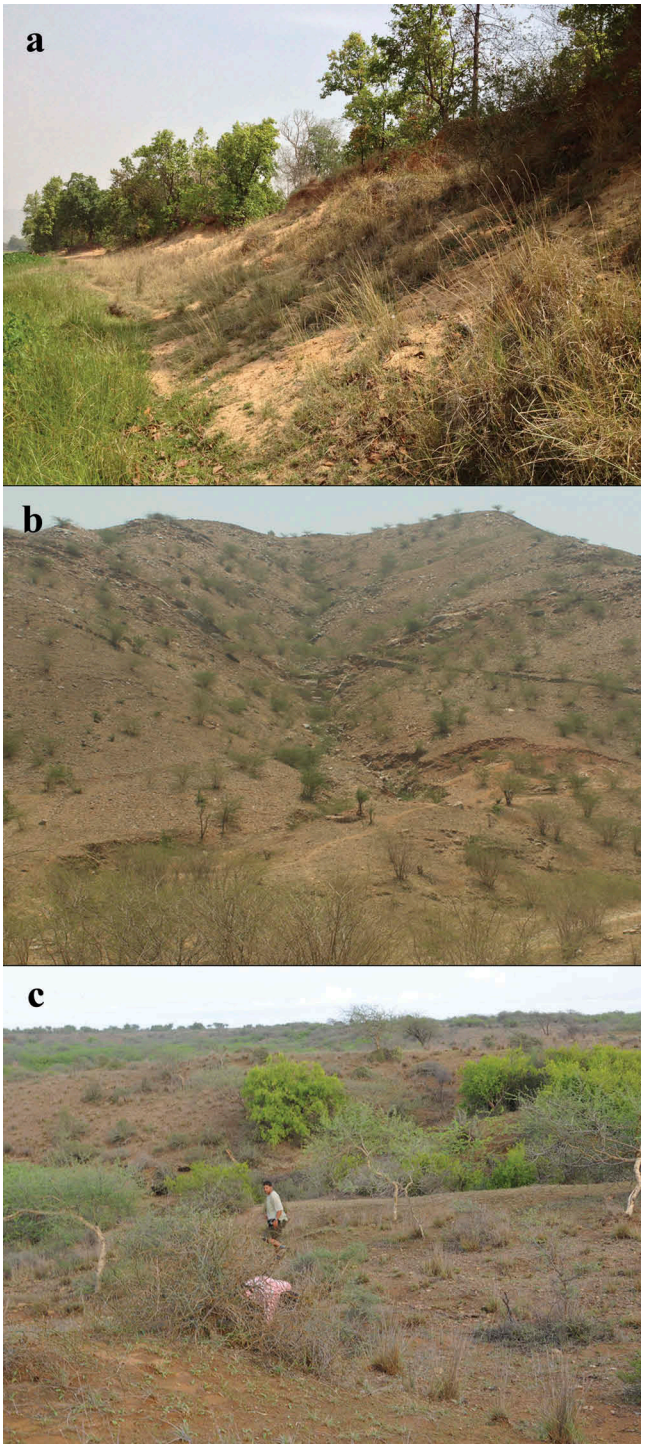

Figure 8. Habitats of members of the *Ophisops microlepis* complex: (a) *Ophisops microlepis*, Korba District, Chhattisgarh; (b) *Ophisops pushkarensis* sp. nov., Ajmer District, Rajasthan; (c) *Ophisops kutchensis* sp. nov., Kutch District, Gujarat.

Figure 9. Type series of *Ophisops pushkarensis* sp. nov.

adult males & NCBS AU751–753 adult females, near Ajmer (26.42913°N 74.67100°E, 520 m asl), Rajasthan, India, collected by A. Khandekar and C. Daniel, on 22 April 2017.

Etymology. The name is for the type locality of the new species, Pushkar, in Rajasthan, India.

Diagnosis. *Ophisops pushkarensis* sp. nov. can be distinguished from Indian congeners by the same characters that diagnose *O. microlepis* – large body size (SVL up to 62.7 mm), 57–62 scales around midbody and 133–148 DS (see diagnosis for *O. microlepis* for opposing character states in other *Ophisops* spp.). *Ophisops pushkarensis* sp. nov. is most closely related to *O. microlepis* and the new species described below (diagnosis against the new species provided after its description). *Ophisops pushkarensis* sp. nov. can be differentiated from *O. microlepis* by its higher number of dorsal scales (mean number of DS 139.1, range 133–148 versus 129.6, 122–136); the head relatively longer (HL 23.8% SVL, 21.1–25.0% versus HL 21.3% SVL, 20.1–22.0%) and narrower (HW/HL 0.544, 0.519–0.591 versus 0.603, 0.570–0.630).

Description of holotype. Adult female in relatively good condition apart from minor artefacts of preservation: left fore limb slightly extended, tail slightly sigmoid, tail tip collected as tissue sample, second finger on right manus without claw. SVL 62.7 mm. Head short (HL/SVL = 0.21), longer than wide (HL/HW = 1.63), not strongly depressed (HD/HL = 0.50), indistinct from neck. Loreal region slightly concave, canthus rostralis sharp. Snout acute (IN/IO = 0.27), slightly projecting beyond lower jaw. Eye small (ED/HL = 0.15); pupil round; supraciliary scales distinct, elongate, four on either side. Tympanum elongate, small (EL/HD = 0.26), covered anteriorly by a single scale,

slightly larger than ear opening; eye to ear distance more than twice eye diameter (EE/OD = 2.23). Nostril circular, dorsolaterally oriented, closer to the snout tip than to eye (NE/SE = 0.80) and between three protuberant nasals. Body slender (BW/SVL = 0.23), trunk not elongate (TRL/SVL = 0.43). Incomplete tail slightly longer than SVL (TL/SVL = 1.11). Fore limbs and hind limbs relatively well developed and slender; forearm short (FL/SVL = 0.13); tibia short (CL/SVL = 0.19); digits long and slender, ending in a sharp and slightly curved claw; subdigital lamellae distinct, entire, distinctly keeled, bicarinate on both manus and pes; number of subdigital lamellae including claw sheath: left manus 8–12-17–17-11; right manus 8–13-17–17-11; left pes 8–13-18–23-14; right pes 8–12-18–23-14. Relative length of digits (measurements in mm in parentheses, * denotes damaged digit): right manus I (2.3) < II (3.9*) < V (4.1) < III (6.4) < IV (6.8); right pes I (3.7) < II (5.8) < V (7.7) < III (9.6) < IV (13.7).

Rostral wider (2.5 mm) than high (1.0 mm), wedged between supranasals dorsally, in contact with first supralabials, nasals and supranasals. Paired supranasals roughly triangular, in contact medially, strongly in touch with slightly larger nasal laterally and smaller postnasals posteriolaterally. Frontonasal roughly hexagonal, similar in width (2.2 mm) and length (2 mm), strongly in contact with supranasals anteriorly; postnasals anteriolaterally and anterior loreal laterally.

A pair of roughly pentagonal prefrontals, in strong contact with each other medially, frontonasal anteriorly, and the posterior loreals laterally; in weak contact with the anterior loreals laterally and posteriorly in strong contact with first anterior supraocular and frontal.

Frontal approximately pentagonal with slightly curved posterior margin, elongate (3.9 mm), becoming broader anteriorly; in strong contact with prefrontals anteriorly, laterally touching first, second and third supraoculars, and posteriorly in strong contact with frontoparietals. A pair of frontoparietals, roughly pentagonal, in contact with each other medially, anteriorly in strong contact with frontal, laterally touching third and fourth supraoculars, posteriolaterally touching parietals, posteriorly interparietal. Interparietal divided horizontally into a large anterior scale and smaller posterior; anterior one large, roughly pentagonal with distinct pineal eye, anteriorly in strong contact with frontoparietals, laterally touching parietals, posterior one much smaller, in contact with parietal laterally and occipital posteriorly. A pair of parietals, pentagonal, longer (3.7 mm) than broad (2.4 mm), separated from each other by interparietals, anteriorly in strong contact with fourth supraocular and frontoparietal on both sides, laterally touching three supratemporals on both sides. Occipital roughly triangular, broader than wide, in contact with parietals and posterior interparietal. Four supraoculars, the first and fourth smallest, separated from supraciliaries by a single row of 15 supraciliary granules on both sides (Figure 6).

Nostril circular, situated on contact line between nasal and supranasal. Postnasals smaller than the anterior loreal, bordered by frontonasal, supranasal, nasal and anterior loreal. Two loreals, anterior roughly rectangular and about the size of nasal, bordered by posterior loreal, prefrontal, frontonasal, postnasal, nasal, supralabials I and II; posterior loreal much larger than anterior, slightly smaller than prefrontal, becoming broader posteriorly, bordered by preoculars, supraciliary I, prefrontal, anterior loreal, supralabial II, III and IV. Preocular slightly smaller than anterior loreal, roughly rectangular. Eight supralabials, V being largest and forming the lower border of the eye, gradually decreasing in size in either direction. Three moderately enlarged postoculars, the most dorsal

the largest. Three supratemporals on the right and four on the left, the most anterior the largest. Temporal scales much smaller than postoculars, smooth, subimbricate, arranged in two to eight rows, those bordering supralabials largest.

Six infralabials on either side. Mental large, as wide (2.2 mm) as long (2.4 mm), in strong contact with infralabial I and first pair of chin shields. Six chin shields on either side, gradually increasing in size posteriorly, except the posterior-most, which is half the size of its adjacent chin shield, three anterior chin shields strongly in contact with each other medially, posterior three separated from each other by gular scales.

Dorsal pholidosis heterogeneous in shape, size, orientation and carination; composed of smaller, weakly pointed, imbricate scales throughout, 58 scales in a transverse row across midbody; 135 scales in longitudinal, vertebral series; scales on dorsal aspect strongly keeled, directed backwards and downwards, those on flanks smooth, directed backwards and upwards; scales on the neck smaller, gradually increasing in size posteriorly and laterally, most posterior two to three rows on flank largest. Ventral scales smooth, heterogeneous, arranged in six transverse rows on belly, midventral series with 34 scales in a longitudinal series; gular scales smaller, elongate, subimbricate, those on neck slightly larger than gular scales, weakly pointed and imbricate; scales on pectoral region larger than those on neck, strongly imbricate; those on belly much enlarged, subimbricate, rectangular, except single outermost row on either side cycloid. Indistinct collar, vaguely defined by a fold of skin with granular scales on shoulders and larger cycloid imbricate scales ventrally. Preanal scale large, elongate, smooth, anteriorly bordered by five and surrounded by two-to three rows of cycloid, imbricate scales of variable size, those on posterior aspect smallest. Femoral pores 15 on either side, medially interrupted by two poreless scales.

Scales on the fore limbs heterogeneous in shape and size, those on the palmar and plantar faces slightly smaller than the associated lamellae, imbricate, strongly keeled. Scales on dorsal surface of upper arm much larger than those on body dorsum, weakly pointed, strongly imbricate, smooth, except those on elbow, which are keeled. Ventral surface of upper arm with smaller, smooth, subimbricate scales. Scales on forearms similar to those on upper arms except three rows on anterior surface larger and smooth, of which single median row much enlarged, subimbricate and almost rhombus shaped.

Scales on hind limbs heterogeneous in shape and size, posterior surface of the thigh with much smaller, granular scales, becoming enlarged, pointed, strongly keeled, imbricate towards anterior surface, ventral surface of thigh covered with three to four rows of much enlarged, smooth, strongly imbricate scales, with anteriormost single row largest and rhombus shaped; scales on dorsal surface of shank like those on forearm but smaller in size, ventral aspect of shank covered with two rows of much enlarged, imbricate, smooth scales, of which the median row is largest and rhombus shaped.

Scales on the dorsal and lateral aspect of the unregenerated tail arranged in regular whorls, cycloid at the base, becoming gradually elongated distally, strongly keeled, imbricate and pointed, 16 scales in the 10th whorl behind the vent. Ventral aspect of the tail with strongly imbricate scales, weakly pointed except single median row, which is slightly smaller, more elongated and roughly triangular; scales near the base of the tail smooth, gradually becoming weakly keeled towards tip of the tail.

Colouration in life. Dorsal ground colour coffee brown, two prominent lighter lateral stripes, a dorsolateral stripe extending from behind the eye onto the tail, and a ventrolateral stripe that runs from the labials, just above the forearm insertion and terminating at the groin. Dorsolateral stripe buff to tan anteriorly, transitioning to slightly darker tan/ochre posteriorly; ventrolateral stripe dirty white. Interspaces between dorsolateral and ventrolateral stripes heavily mottled with darker and lighter markings, anterodorsal margin of dorsolateral line with mainly darker mottling extending up to 2× width of the dorsolateral line, markings on each side well separated from one another in the vertebral region. Flanks, below ventrolateral stripe, with marbled lighter and darker markings, some enlarged scales with yellow-green markings. Limbs slightly washed out relative to dorsum, with scattered, irregular lighter and darker markings, largest and most prominent on femur. Head dorsum suffused with scattered, indistinct black markings, labials with black blotches, temporal region with darker markings, iris copper. Venter immaculate white. Dorsolateral stripes meet on the tail, flanked by narrow darker markings that fade to white on the tail venter.

Colouration in preservative. Similar to life colouration, except colours faded and shades of yellow completely lost.

Variation and additional information from type series. Mensural data for the type series and additional material are given in Table 2. There are three male and two female specimens ranging in size from 54.3 mm to 62.7 mm. The paratypes are similar to the holotype in most characters, except, VG 0338 has seven infralabials on both sides; supratemporal scales – two on both sides in VG 0336, VG 0337, four on left and three on right side in VG 0338, three on either side in VG 0335, three on left and two on right in CES 458; scales in a transverse row across midbody – 57 in VG 339 and 62 VG 0338; femoral pores – 16 on either side in VG 0335; supralabial II and III touching posterior loreal on right in VG 0337 and on both sides in VG 0338; postoculars – two on both sides in VG 0335; occipital broken in VG 0337. Extent of irregular dorsal markings variable, most prominent in VG 0335 and VG 0339 and least distinct in VG 0338 and CES 459.

Notes. Specimens from Jessore Wildlife Sanctuary, Gujarat (BNHS 1726, BNHS 1727 and NCBS AU701) are allocated to this species in the absence of molecular data based on the high number of dorsal scales in longitudinal, vertebral series (142 DS versus DS 139.1, range 133–148 in *O. pushkarensis* sp. nov.) and morphometric data (Figure 2); even though the ventrolateral stripe is not very distinct in BNHS 1726. Confirming our allocation of these specimens to *O. pushkarensis* sp. nov. requires additional samples and genetic data. The specimen from Ajmer reported by Sharma et al. (2015) is likely to be a member of the new species based on its locality and general appearance in the low-resolution photographs provided. However, their record of cannibalism may have been of predation by *O. pushkarensis* sp. nov. upon *O. jerdonii* (based on the apparently large dorsal scales of a photograph of the partially digested lizard in Sharma et al. 2015). Records from Jodhpur and Pali District are likely to represent the new species (Figure 1), but require verification with specimen data.

Distribution and natural history. *Ophisops pushkarensis* sp. nov. has been collected from rocky and sandy open scrub habitats around Pushkar and Ajmer (Figure 8) at elevations between 505 and 525 m asl. The other localities around Jessore, Gujarat are ~300 km southwest of the type locality and at somewhat lower elevations (200–215 m asl). BNHS 2031 was gravid when collected in July 2009 and laid 10 eggs in captivity. This diurnal species has been observed active in April, May and July; though it is likely to be seen throughout the year except outside peak winter.

***Ophisops kutchensis* sp. nov.**

Kutch small-scaled snake-eye

Figures 4–7, 10

Ophisops microlepis (non Blanford 1870)

Holotype. NCBS AU760, adult female, near Vithon, Kutch district, Gujarat, India (23.3430556°N 69.354444°E, 195 m asl), collected by A. Khandekar and C. Daniel on 19 April 2017.

Paratypes. BNHS 2024, adult female, near Tera, Kutch District, India (23.34664°N 69.00720°E; 55 m asl), collected by A. Datta-Roy, T. Khichi and I. Agarwal 2009; NCBS AU756, NCBS AU762–764 adult males & NCBS AU755, NCBS AU757–761, NCBS AU765 adult females, same collection data as holotype.

Etymology. The name is for the type locality of the new species, in Kutch District, India.

Diagnosis. *Ophisops kutchensis* sp. nov. can be distinguished from Indian congeners by the same characters that diagnose *O. microlepis* – large body size (SVL up to 53.4 mm), 50–58 scales around midbody and 113–129 DS (see diagnosis for *O. microlepis* for

Figure 10. Type series of *Ophisops kutchensis* sp. nov.

opposing character states for other Indian *Ophisops* spp.). *Ophisops kutchensis* sp. nov. is most closely related to *O. microlepis* and *O. pushkarensis* sp. nov. and can be diagnosed from these species by the lower number of scales in the longitudinal vertebral series (mean DSR 120.9, range 113–129 versus mean 129.6, range 122–136 in *O. microlepis* and mean DSR 139.1, range 133–148 in *O. pushkarensis* sp. nov.) and fewer scales around midbody (mean RBS 52.7, range 50–58 versus 57.7, 56–61 in *O. microlepis* and 58.7, 57–62 in *O. pushkarensis* sp. nov.). *Ophisops kutchensis* sp. nov. has a narrow, indistinct dorsolateral stripe (versus broader, distinct ventrolateral stripes in both *O. microlepis* and *O. pushkarensis* sp. nov.) and strong mottling between the dorsolateral stripes, which almost meet on the vertebral region (versus mottling only close to the dorsolateral stripe, widely separated in vertebral region in *O. microlepis* and *O. pushkarensis* sp. nov.).

Description of holotype. Adult female in good state of preservation except tail is bent towards the left. SVL 48.5 mm. Head short (HL/SVL = 0.24), longer than wide (HL/HW = 1.79), not strongly depressed (HD/HL = 0.46), indistinct from neck. Loreal region slightly concave, canthus rostralis sharp. Snout acute (IN/IO = 0.33), slightly projecting beyond lower jaw. Eye small (ED/HL = 0.15); pupil round; supraciliary scales distinct, elongate, four on either side. Tympanum elongate, small (EL/HD = 0.14), covered anteriorly by a single scale, slightly larger than ear opening; eye to ear distance more than twice eye diameter (EE/OD = 2.16). Nostril circular, dorsally oriented, closer to snout tip than eye (NE/SE = 0.77) and between three protuberant nasals. Body slender (BW/SVL = 0.18), trunk not elongate (TRL/SVL = 0.44). Length of tail twice SVL (TL/SVL = 2.17). Fore limbs and hind limbs relatively well developed and slender; forearm short (FL/SVL = 0.15); tibia short (CL/SVL = 0.23); digits long and slender, ending in sharp and slightly curved claw; subdigital lamellae distinct, entire, distinctly keeled, bicarinate on both manus and pes; number of subdigital lamellae including claw sheath: left manus 8–11-16–18-10; right manus 8–12-16–17-10; left pes 8–14-17–21-14; right pes 7–12-17–21-14. Relative length of digits (measurements in mm in parentheses): right manus I (2.2) < V (3.1) < II (3.3) < III (5.3) < IV (6.1); right pes I (3.7) < II (6) < V (7.4) < III (9.5) < IV (13.7).

Rostral wider (2 mm) than high (1.2 mm), wedged between supranasals dorsally, in contact with first supralabial, nasal and supranasal on either side. Paired supranasals roughly triangular, in contact medially, strongly in touch with slightly larger nasal laterally and smaller postnasals posteriolaterally. Frontonasal roughly hexagonal, similar in width (1.9 mm) and length (1.9 mm), strongly in contact with supranasals and postnasals anteriolaterally and anterior loreal laterally. A pair of roughly pentagonal prefrontals, in strong contact with each other medially, frontonasal anteriorly, and the posterior loreals laterally; in weak contact with the anterior loreals laterally and posteriorly in strong contact with first anterior supraocular and frontal.

Frontal approximately pentagonal with slightly curved posterior margin, elongate (3.6 mm), becoming broader anteriorly; in strong contact with prefrontals anteriorly, laterally touching first, second and third supraoculars and posteriorly in strong contact with frontoparietals.

A pair of roughly pentagonal frontoparietals in contact with each other medially, anteriorly in strong contact with frontal, laterally touching third and fourth supraoculars, posteriolaterally touching parietals, posteriorly interparietal. Interparietal single, roughly pentagonal slightly broad anteriorly with distinct pineal eye, anteriorly in strong contact

with frontoparietals, laterally touching parietals and occipital posteriorly. A pair of pentagonal parietals, slightly longer (3.2 mm) than broad (2.4 mm), separated from each other by interparietal and occipital, anteriorly in strong contact with fourth supraocular and frontoparietal on both sides, laterally touching two supratemporals on both sides. Occipital roughly triangular, broader than wide in contact with parietals and interparietal. Four supraoculars, the first and fourth smallest, separated from supraciliaries by a single row of 14 supraciliary granules on both sides (Figure 6).

Nostril circular, situated on contact line between nasal and supranasal. Nasal elongate equal in length to supranasal and postnasal together, bordered by postnasal, supranasal, rostral, supralabial I and anterior loreal. Postnasals smaller than the anterior loreal, bordered by frontonasal, supranasal, nasal and anterior loreal. Two loreals, anterior roughly rectangular and about the size of nasal, bordered by posterior loreal, prefrontal, frontonasal, postnasal, nasal, supralabials I and II; posterior loreal much larger than anterior, slightly smaller than prefrontal, becoming broader posteriorly, bordered by preocular, supraciliary I, prefrontal, anterior loreal, supralabial II and III. Preocular slightly longer than anterior loreal, roughly rectangular. Seven supralabials, V being largest and forming the lower border of the eye, gradually decreasing in either direction. Three moderately enlarged postoculars, lower smallest. Two supratemporals on either side, the most anterior the largest. Temporal scales much smaller than postoculars, smooth, subimbricate, arranged in three to eight rows, those bordering supralabials and postoculars largest.

Six infralabials on either side. Mental large, as wide (1.8 mm) as long (1.7 mm), in strong contact with infralabial I and first pair of chin shields. Six chin shields on either side, gradually increasing size posteriorly, except the posterior-most, which is half the size of its adjacent chin shield, two anterior chin shields strongly in contact with each other medially, remaining separated from each other by gular scales.

Dorsal pholidosis heterogeneous in shape, size, orientation and carination; composed of smaller, weakly pointed, imbricate scales throughout, 53 scales in a transverse row across midbody; 123 scales in longitudinal, vertebral series; scales on dorsal aspect strongly keeled, directed backwards and downwards, those on flank smooth, directed backwards and upwards; scales on the neck smaller, gradually increasing in size posteriorly and laterally, most posterior two to three rows on flank largest. Ventral scales smooth, heterogeneous in shape and size, arranged in six transverse rows on belly, midventral row with 32 scales in a longitudinal series; gular scales smaller, elongate, juxtapose; scales on neck slightly larger than gular scales, weakly pointed and imbricate; scales on pectoral region larger than those on neck, strongly imbricate; those on belly much enlarged, subimbricate, rectangular, except two midventral rows slightly smaller. Collar indistinct, vaguely defined by a fold of skin with granular scales on shoulders and larger, cycloid, imbricate scales ventrally. Preanal scale large, elongate, smooth, anteriorly bordered by six and surrounded by two rows of cycloid, imbricate scales of variable size, those on posterior aspect smallest. Femoral pores 12 on either side, medially interrupted by two poreless scales.

Scales on the fore limbs heterogeneous in shape and size, those on the palmar and plantar faces slightly smaller than the associated lamellae, imbricate, strongly keeled. Scales on dorsal surface of upper arm much larger than those on body dorsum, weakly pointed, strongly imbricate, smooth, except those on elbow, which are keeled; ventral

surface of upper arm with smaller, smooth, subimbricate scales; scales on forearms similar to those on upper arms all keeled except three rows on anterior surface larger and smooth, of which single median row much enlarged, subimbricate and almost rhombus shaped.

Scales on hind limbs heterogeneous in shape and size, posterior surface of the thigh with much smaller, granular scales, becoming enlarged, pointed, strongly keeled, imbricate towards anterior surface; ventral surface of thigh covered with two to five rows of much enlarged, smooth, strongly imbricate scales, with anterior-most single row largest and rhombus shaped; scales on dorsal surface of shank like those on forearm but smaller in size; ventral aspect of shank covered with two rows of much enlarged, imbricate, smooth scales, of which the median row is largest and rhombus shaped.

Scales on the dorsal and lateral aspect of the tail arranged in regular whorls, cycloid at the base, becoming gradually elongated distally, strongly keeled, imbricate and pointed, 15 scales in the 10th whorl behind the vent; ventral aspect of the tail with strongly imbricate scales, weakly pointed except single median row, which is slightly smaller, more elongated and roughly triangular; scales near the base of the tail smooth, gradually becoming weakly keeled towards tip of the tail.

Colouration in life. Dorsal ground colour olive brown, two indistinct lighter lateral stripes, a dorsolateral stripe extending from behind the eye onto the tail, and a just discernible ventrolateral stripe that runs from the labials, just above the forearm insertion and terminating at groin. Interspaces between dorsolateral and ventrolateral stripes thickly reticulated with darker and lighter markings, anterodorsal margin of dorsolateral line with light and dark mottling, markings from either side almost meeting in vertebral region. Flanks below ventrolateral stripe with marbled lighter and darker markings, some enlarged scales with blue-green markings. Fore limbs with scattered, irregular lighter and darker spotting, hind limbs with thick dark reticulations outlining lighter blotches. Head dorsum suffused with scattered, indistinct black markings and a few small spots, labials with black blotches, temporal region with some darker markings, iris copper. Venter immaculate white. Dorsolateral stripes on tail flanked by narrow darker and lighter markings that fade to white on the tail venter.

Colouration in preservative. Similar to life colouration, except colours faded and shades of yellow lost.

Variation and additional information from type series. Mensural data for the type series and additional material are given in Table 2. There are 12 specimens ranging in size from 41.1 mm to 53.4 mm. The paratypes are similar to the holotype in most characters except, VG 0300, VG 0301, VG 0308, VG 0309 have eight supralabial on both sides; scales in a transverse row across midbody – 50 in VG 299, VG 300 and 58 in VG 0301; scales in longitudinal, vertebral series – 113 in BNHS 2024 and 129 in VG 301; femoral pores – 11 in VG 299 and 13 on right and 15 on left in BNHS 2024; interparietal – divided into VG 301; supralabial IV strongly touching posterior loreal on both sides in VG 0335 and weakly touching on both sides in BNHS 2024. Extent of irregular

light and dark markings variable, from few irregular markings in VG 0302 to very broken up markings in BNHS 2024.

Distribution and natural history. *Ophisops kutchensis* sp. nov.has been collected from open scrub habitats in Kutch, with photographic records from the Banni Grasslands and Lakhpat Fort in Gujarat (Figure 1). This diurnal species has been seen active in April and August, with subadults observed in April 2017 and numerous adults observed (and one collected) in August 2009. Sharma (1982) recorded this species from Bhuj (Kutch District), Okha (Jamnagar District) and Rajkot (Rajkot District) besides Nal Sarovar Dam in Gujarat. The text in Sharma (1982) mentions 46–60 RBS (which overlaps with our data for *Ophisops kutchensis* sp. nov. (50–58 RBS) while a table has 52–66 RBS (which exceeds the number known for any members of the *O. microlepis* complex, and in all likelihood includes the series of six ventral plates). As these localities are close to confirmed localities for the new species, and it seems likely that the table has RBS + ventral plates, we tentatively assign these localities to the distribution of *O. kutchensis* sp. nov. (Figure 1).

Key to Indian species of *Ophisops* with notes on *Cabrita jerdonii*

The genus *Cabrita*, diagnosed by distinct upper and lower eyelids, was synonymized with *Ophisops* by Arnold (1989) based on morphology, further corroborated by the genetic data presented by Agarwal and Ramakrishnan (2017). As *Ophisops jerdonii* Blyth was pre-occupied, Arnold (1989) provided the replacement name *Ophisops nictans* Arnold for *Cabrita jerdonii* Beddome, 1870, overlooking the Sri Lankan endemic subspecies *Cabrita jerdonii minor* Deraniyagala, 1971 – the next available name for *Ophisops (Cabrita) jerdonii* (Böhme and Bischoff 1991). However, following the preliminary genetic results of Agarwal and Ramakrishnan (2017) that reveal divergent lineages within this complex, and pending a more thorough taxonomic revision of the Sri Lankan and Indian members of this group, we use the name *O. nictans* with its type locality in southern India (Beddome 1870) to refer to Indian members of this group and restrict *O. minor* (Deraniyagala) to Sri Lanka.

Below is a key to the currently recognized Indian *Ophisops* species:

1. SVL of adults <45 mm, fewer than 35 scales in a row across midbody 2
   SVL of adults > 50 mm, more than 40 scales in a row across midbody 4

2. Strongly spotted throat, lower eyelid distinct from upper ..... *Ophisops nictans*
   Throat immaculate or lightly spotted, lower eyelid fused with upper 3

3. A single frontonasal ..... *Ophisops jerdonii*
   2–3 frontonasals ..... *Ophisops beddomei*

4. Lower eyelid fused with upper 5
   Lower eyelid distinct from upper ..... *Ophisops leschenaultii*

5. 50–58 scales in a row across midbody, ventrolateral stripe indistinct, heavily speckled ..... *Ophisops kutchensis* sp. nov.

56–62 scales in a row across midbody, ventrolateral stripe distinct, immaculate to moderately speckled..... 6

6. 122–136 dorsal scales in longitudinal, vertebral series; ventrolateral stripe lightly to moderately speckled..... *Ophisops microlepis*
133–148 dorsal scales in longitudinal, vertebral series; ventrolateral stripe usually immaculate (occasionally faintly speckled)..... ..... *Ophisops pushkarensis* sp. nov.

Discussion

Ophisops kutchensis and *O. pushkarensis* are the first *Ophisops* to be described since 1971 and the first from India since 1870 (Uetz et al. 2017). These are also the first reptiles endemic to western Gujarat and the Aravalli Range respectively (though undescribed members of the *Cyrtopodion aravallensis* (Gill, 1997) complex are found in both regions; Agarwal et al. 2014). The three species of the *O. microlepis* complex are allopatrically distributed, the type localities ~ 600, > 900 and > 1400 km apart from one another (Figure 1). The group as a whole is likely to be much more widely distributed than currently understood, as these lizards have been recorded from a range of open habitats with sandy and rocky substrates across northern India (Figure 1, 8), which has vast expanses of suitable, unsampled habitat. It is unclear if the form from the far east of the range is conspecific with *O. microlepis*, and similarly, if the animals from central and eastern Rajasthan represent *O. pushkarensis* and/or *O. microlepis*; and which of these, if any, might represent additional new species. As is the case for Indian reptiles in general, evaluating the true diversity of the *Ophisops microlepis* complex and the distribution of individual species requires extensive collections across areas of suitable habitat combined with the examination of existing museum specimens and genetic data. The habitats that these endemic species inhabit are of particular conservation attention as they are understudied and consequently often overlooked as native habitats with endemic biodiversity (Putz and Redford 2010; Parr et al. 2014; Veldman et al., 2015a, 2015b). It is important to survey the biodiversity of and map the extents of natural open, grassy habitats and ensure that these areas are adequately protected from development and tree planting.

India is at the cusp of a second discovery phase in alpha taxonomy, at least when it comes to lizards, with 35 species described in the decade 2008–2017 (Uetz et al. 2017). The only time more species were described within a decade from India was 46 species between 1870 and 1880, mainly driven by 25 new descriptions, including 13 by Beddome, in 1870. Besides two from northeast India and four from the Andaman & Nicobar Islands, 29 of the 35 new species are from peninsular India. These include two from the Eastern Ghats, four from the Western Ghats and 19 from the rest of peninsular India (Uetz et al. 2017). Although all the new species were diagnosed based on morphological data, 16 of the 28 new species descriptions included genetic data. As with at least some of those papers (e.g. Agarwal et al. 2011; Agarwal 2016; Deepak et al. 2016), genetic data was the basis for first recognizing the existence of deeply divergent lineages within superficially similar animals.

Members of the *O. microlepis* complex are cryptic, with even the most distinctive species, *O. kutchensis*, differing from the other two species in only a few meristic characters and colour pattern; while *O. pushkarensis* and *O. microlepis* are virtually indistinguishable in overall pattern and scalation. Diversification in at least two other cryptic species complexes in the region is associated with expanding arid habitats from the late Miocene onward, potentially in the absence of ecologically similar lizards (*Cyrtopodion aravallensis*, Agarwal et al. 2014; and the small bodied clade of *Ophisops*, Agarwal and Ramakrishnan 2017). Similarly, species in the *O. microlepis* complex diverged from one another in the late Miocene to early Pliocene (Agarwal and Ramakrishnan 2017), and these are the only large-bodied lacertids across most of their range (except sandy habitats in western Gujarat and Rajasthan, where *Acanthodactylus cantoris* also occurs). However, a precise estimate of species richness and morphological diversity is necessary to unravel patterns of morphological evolution within this group, which would also allow insights into more general patterns of biogeography.

Our study highlights additional cryptic diversity in areas assumed to be biodiversity poor in the Indian subcontinent. Reptiles and small vertebrates are generally not well represented by protected areas in the region (e.g. Pawar et al. 2007), and given how poor our understanding of species diversity and distributions, current efforts to protect biodiversity are unlikely to capture a vast number of smaller, cryptic or overlooked species. Primary field sampling in conjunction with integrative taxonomic approaches, as used in this paper, is the first step toward addressing these gaps in knowledge.

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Disclosure statement

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Appendix 1. Specimens examined

Ophisops jerdonii: IAL 062, IAL 063 near Jalna, Jalna district, Maharashtra, India; IAL 113, IAL 114 near Satna, Satna district, Madhya Pradesh, India.

Ophisops beddomei: VG 0278, VG 0279, VG 0343, VG 0344 Amboli, Sindhudurg district, Maharashtra, India.

Ophisops nictans: IAL 068, IAL 069, near Kuntalakhurd, Adilabad district, Telanga, India; IAL 087, near Asifabad, Adilabad district, Telangana; G540, Srisailam, Kurnool district, Andhra Pradesh, India.

Ophisops leschenaultii: IAL 050, IAL 051, near Penukonda, Tumkur district, Karnataka, Inda; IAL 207, Gingee, Villupuram district, Tamil Nadu.