

<https://doi.org/10.11646/zootaxa.4374.4.5>  
<http://zoobank.org/urn:lsid:zoobank.org:pub:DD722642-89AB-403B-8B19-10CB219156E9>

## A new species of fan-throated lizard of the genus *Sitana* Cuvier, 1829 from coastal Kerala, southern India

KALES SADASIVAN<sup>1</sup>, M. B. RAMESH<sup>1</sup>, MUHAMED JAFER PALOT<sup>2</sup>,  
MAYURESH AMBEKAR<sup>3</sup> & ZEECHAN A. MIRZA<sup>3,4</sup>

<sup>1</sup>Travancore Natural History Society, MBRRA 65, Jyothis, Mathrubumi Road, Vanchiyoor, Thiruvananthapuram, Kerala 695035, India

<sup>2</sup>Zoological Survey of India, Western Ghats Regional Centre, Jaferkhan Colony, Eranhipalam P.O., Kozhikode, Kerala 673006, India

<sup>3</sup>National Centre for Biological Sciences, Tata Institute for Fundamental Research, Bangalore, Karnataka 560065, India

<sup>4</sup>Corresponding author. E-mail: snakeszeeshan@gmail.com

### Abstract

We here describe *Sitana attenboroughii* sp. nov., a new species of fan-throated lizard of the genus *Sitana* Cuvier, 1829 from coastal Kerala in southern India. The new species morphologically is closer to *Sitana visiri* Deepak, 2016 (in Deepak et al. 2016a), however, differs in having higher numbers of ventral scales and a comparatively short but richly colored dewlap. Genetically the new species shows affinity to *Sitana marudhamneydhal* Deepak, Khandekar, Varma & Chaitanya, 2016 from which it differs in an uncorrected pairwise sequence divergence of 2.2% for a fragment of mitochondrial Nicotinamide adenine dinucleotide dehydrogenase (NADH) subunit 2 gene.

**Key words:** taxonomy, India, molecular phylogeny, mitochondrial DNA, Kerala

### Introduction

*Sitana* Cuvier, 1829 are ground-dwelling agamid lizards usually associated with open habitats such as scrublands, degraded forests, sandy beaches, and plateaus. Members of the genus are endemic to the Indian subcontinent and until recently were thought to be represented by four species (Deepak et al. 2016a, b; Kamath 2016). However, compilations by Amarasinghe et al. (2015), Deepak et al. (2016a; b) have greatly enhanced our understanding of the diversity within the genus. Furthermore, Deepak et al. (2016a) described a new allied genus, *Sarada* Deepak, Karanth and Giri, 2016 whose validity needs further investigation.

As part of an ongoing study on the reptilian fauna of Kerala, we collected specimens of a species of *Sitana* from coastal Kerala. Based on the key to *Sitana* species provided by Deepak et al. (2016a), the specimens from Kerala were found to show morphological affinities to *Sitana visiri* Deepak, 2016 (Deepak et al. 2016a) however they differed in several aspects. A detailed comparison of mensural and meristic character and molecular data from the two species highlight the distinctiveness of the specimens from Kerala which are herein described as a new species.

### Materials and methods

**Morphology:** Specimens were collected by hand, euthanized and fixed in 6% formalin. They were later washed and are stored in 70% ethanol. Tail and liver tissue were taken prior to fixation and stored for molecular work. The type specimens are deposited in the collection of the Bombay National History Society, Mumbai (BNHS). Specimens were measured using a Mitutoyo™ digital caliper. Descriptive style and morphometric/morphological characters were recorded follow Deepak et al. (2016a) with some modifications. The following measurements were taken: snout-vent length (SVL, from tip of snout to anterior border of cloaca), head length (HL, from snout tip to posterior

border of tympanum), head width (HW, distance from left to right outer edge of the head at its widest point), head height (HH, dorsoventral distance from top of head to underside of jaw at transverse plane intersecting angle of jaws), snout-eye length (SE, from snout tip to anterior border of orbit), eye to tympanum (ET, from posterior border of orbit to anterior border of tympanum), jaw length (JL, from rostrum to corner of jaw), interorbital width (IO, transverse distance between anterodorsal corners of left and right orbits), naris to eye (NE, distance from the anterior edge of orbit to posterior edge of naris), snout width/internasal distance (IN, transverse distance between left and right nares), tympanum diameter (TD, greatest diameter of tympanum), orbit diameter (OD, distance between anterior and posterior margins of orbit), lower arm length (LAL, distance from elbow to distal end of wrist, or just underside of forefoot when the limb is flexed), upper arm length (UAL, distance from anterior insertion of forelimb to elbow when the limb is flexed), finger lengths (F1, F2, F3, F4, F5) (e.g. F4 = Distance from juncture of 3rd and 4th digits to distalmost extent of 4th finger including the claw), femur length (FEL, length of femur from groin to knee), crus length (CL, length of crus (tibia) from knee to heel), hind foot length (HFL, distance from proximal end (heel) of hind foot to distal most point of fourth toe), hind limb length (HLL, from groin to tip of fourth toe), toe lengths (T1, T2, T3, T4) (e.g. T4 = Distance from juncture of 3rd and 4th digits to distal end of 4th digit on hind foot), trunk length (TrL, from forelimb insertion to hind limb insertion), trunk height (TrH, depth midway between the fore- and hind limb insertions), trunk width (TrW, width midway between the fore and hind limb insertions), tail length (TL, from posterior border of cloacal opening to tip of tail), tail height (TH) and tail width (TW) at tail base. Dewlap length (DWL, distance between posterior end of dewlap and tip of lower jaw), extent of dewlap in trunk (DWLT, measured from the axilla till the end of the dewlap). Meristic characters were counted for multiple individuals per species. The following characters were scored: mid-body scale rows (MBS, number of scale rows around the trunk at midbody), ventral scales (VEN, number of scales from below mental around the base of the dewlap to anterior border of cloaca), fourth toe lamellae (LAM4, number of 4th toe lamellae, from 1st lamella at the digit's cleft to the most distal lamella), dewlap scales (ESD, number of enlarged scale rows on the dewlap), supralabials (SL, posterior end defined by the last enlarged scale that contacts the infralabials at the corner of mouth), infralabials (IL, posterior end defined by the posteriormost enlarged scales that contact the supralabials at the corner of the mouth), ventral scales on the belly (VENB) number of scales posterior to the dewlap to the anterior border of cloaca, vertebral scales (VS) number of scales above the vertebral column counted from the mid-dorsal first nuchal spine to a level directly above the cloacal opening. Multivariate Principal Component Analysis (PCA) was performed in PAST vol. 3.14 (<http://folk.uio.no/ohammer/past/>) to statistically test the distinctiveness of the new species in morphospace with congeneric taxa. Morphometric data was log transformed; F1–F3, F5, T1–T3 and SVL were excluded from the analysis. Institution acronyms used are as follows: NCBS—National Centre for Biological Sciences, Bangalore, CES—Centre for Ecological Sciences, Bangalore.

**Molecular analysis:** Genomic DNA was extracted from liver tissue following Qiagen DNeasy™ Tissue kits following protocols specified by manufacturers. We amplified partial segment of mitochondrial Nicotinamide adenine dinucleotide dehydrogenase subunit 2 (*NADH* 2) gene with published primers L4437 5'-AAGCTTCGGGCCATACC-3' and H5540 5'-TTTAGGGCTTGAAAGGC-3' (Macey *et al.* 1997). A 12 $\mu$ l reaction was set containing 5 $\mu$ l of Qiagen Taq PCR Master Mix, 4 $\mu$ l of water, 0.5 $\mu$ l of each primer and 2 $\mu$ l template DNA, carried out with an Eppendorf Mastercycler Nexus GSX1. Thermo-cycle profile used for amplification were as follows: 94°C for 15 minutes, (denaturation temperature 94°C for 50 seconds, annealing temperature 59.1°C for 50 seconds, elongation temperature 72°C for 2 minutes) x 45 cycles, 72°C for 15 minutes, hold at 4°C. PCR product was cleaned using QIAquick PCR Purification Kit and sequenced with a 3730 DNA Analyzer. Sequences were cleaned and edited in Geneious R6 v.6.18. (Kearse *et al.* 2012) and were also manually checked in MEGA6. Taxon selection for phylogenetic analysis follows Deepak *et al.* (2015). Multiple taxa were selected that include members of the subfamily Draconinae, namely *Calotes*, *Japalura*, *Ceratophora*, *Lyriocephalus*, *Cophotis*, *Salea*, *Draco*, *Ptyctolaemus* and *Otocryptis* rooted with the outgroup *Bufo**niceps laungwalaensis*. The sequence of *Sitana* from Kanyakumari (KX371915) is here referred as *Sitana* sp. as it shows unresolved relationship with the new species and *S. marudhamneydhal*. Sequences were aligned with ClustalW (Thompson & Gibson 2002) in MEGA6 (Tamura *et al.* 2013). Aligned data comprised of 1017 bp which was analyzed with PartitionFinder (Lanfear *et al.* 2012) for optimal partitioning strategy and evolutionary substitution model. Maximum Likelihood (ML) and Bayesian Inference (BI) analyses were employed to infer phylogenetic relationships in RAxML (Silvestro & Michalak 2012) and MrBayes 3.2.2. (Ronquist & Huelsenbeck

2003) respectively with data partitioned by codon. ML analysis was run for 1000 bootstrap replicates under GTR + I + G model to assess clade support. BI was run for 10 million generations and was terminated after the analysis reached a standard split frequency of 0.01. GenBank accession numbers for the sequences generated for the types are KY393125 and KY381121 for the holotype and male paratype respectively.

## Results

### *Sitana attenboroughii* sp. nov.

Figs. 1–6, Table 1

Holotype.—Adult male, BNHS 2481, Trivandrum, Kerala, India ( $8.313387^{\circ}$ ,  $77.070933^{\circ}$ , elevation 9 m), collected by Muhammed Jafer Palot, 15.06.16.

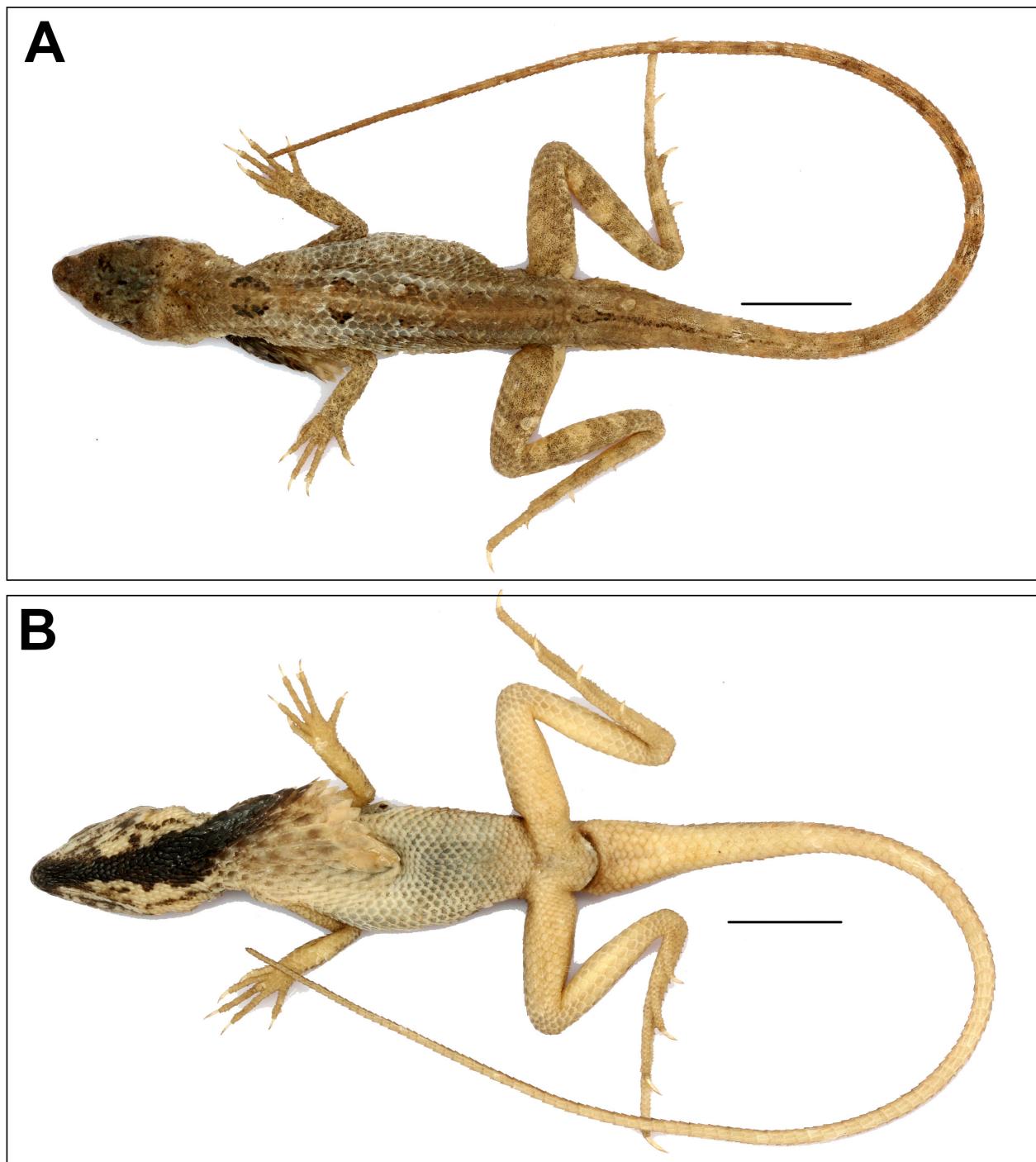
Paratypes (n=2).—Adult male, BNHS 2482 collected by Muhammed Jafer Palot, Kalesh Sadasivan and Ramesh M. B, on 15.06.16.; adult female, BNHS 2483, from the same locality and collectors 15.06.16.

**Diagnosis.** A moderately large sized species in relation to other members of the genus, SVL 55.6 mm. Dewlap colouration in breeding male iridescent blue and bright orange. Enlarged scales on dewlap moderately serrated. Dewlap moderately large, extending up to 36% of the trunk. More than 72–74 ventral scales and 35–38 vertebral scales.

*Sitana attenboroughii* sp. nov. differs from members of the genus *Sarada* by having an enlarged spine-like scale on the thigh and maximum SVL of 55.7 mm (vs. SVL >60 mm and an enlarged spine-like scale absent on the thigh in *Sarada deccanensis*, *Sarada darwini* and *Sarada superba*); differs from members of the genus *Sitana* in the dewlap coloration being vibrant orange and blue (vs. dewlap coloration yellowish white and may bear a faint blue line in *S. sivalensis* complex, *S. laticeps* and *S. spinaecephalus*); dewlap extending to over 36% of the trunk length (vs. 56% in *S. visiri*, 33% in *S. devakai*, 29% in *S. bahiri*, 46% in *S. ponticeriana*, 64% in *S. marudhamneydhal*); SVL 45.7–55.8 (vs. SVL 42–54 in *S. marudhamneydhal*, 36.36–44.5 in *S. ponticeriana*, 41.7–48.5 in *S. laticeps*); DWL 25.8–33.3 (vs. 37.3–40.5 in *S. marudhamneydhal*, 22.4–29.2 in *S. ponticeriana*, 24.5–39 in *S. visiri*, 26.1–32.6 in *S. spinaecephalus*, 20.7–27.1 in *S. laticeps*); ventral scales 72 or 73 (86–89 *S. bahiri*, 100–108 in *S. devakai*, 75–81 in *S. laticeps*, 80–84 in *S. marudhamneydhal*). The new species is most similar to *S. visiri* in general appearance from which it differs in possessing higher ventral counts 72–74 (vs. 65–69 in *S. visiri*). Other characters which may be used to distinguish the new species are presented in the key to the genus and an overview of selected characters are presented in Table 2.

**Description of holotype male BNHS 2481:** The holotype is in generally good condition, lacking any incisions or cuts. The tail is complete and fixed in a ‘U’ shaped curl against the body. Hemipenis not everted (Fig. 1A & 1B). Adult male SVL 55.8. Head relatively long (HL/SVL ratio 0.26), wide (HW/HL ratio 0.67), not depressed (HH/HL ratio 0.52), distinct from neck (Fig. 2). Snout moderately long (SE/HL ratio 0.43) bluntly conical; longer than eye diameter (OD/SE ratio 0.44) (Fig. 3). Eye large (OD/HL ratio 0.19); pupil round, eyelids covered with small pentagonal and hexagonal scales, supraciliaries short. Snout obtusely pointed when viewed dorsally, rostral much wider than deep, bordered posteriorly by two supralabials, prenasal and dorsally by three small scales. Canthus rostralis and supraciliary edge moderately sharp consisting of nine scales. Nostrils positioned in the centre of a large, undivided nasal plate, bordered by seven scales (right side), including one prenasal, two postnasals and one supranasal, and separated from rostral by prenasal and supralabials. Nine rectangular, weakly keeled supralabials, bordered above by a single row of slightly smaller, rectangular, keeled scales, terminating above eighth the supralabial. Loreal region concave, scales of the loreal region heterogeneous in size, flat, keeled, some roughly hexagonal. Scales on postorbital and temporal region homogenous, imbricate, strongly keeled, and directed posteriorly and dorsally. Orbital scales small but not granular. Tympanum naked. Canthals enlarged, overlapping, becoming slightly smaller along subimbricate supraciliaries, protruding slightly laterally on supraorbital ridge. Scales on dorsal surface of snout, forehead, interorbital, and occipital region heterogeneous in size, and shape; mostly elongate, imbricate, strongly keeled longitudinally; those on snout smaller, rhomboidal, those on forehead largest, greatly elongate; supraorbital scales increase in size becoming more elongate from supraciliaries to inner edges of orbits, of which the enlarged scales follow the curvature of the orbit posterolaterally; occipital region with slightly smaller, less elongate; imbricate, and keeled scales. Parietal plate with pineal eye, the plate slightly larger

than adjacent scales. Mental shield narrower than rostral; gular scales keeled. Dewlap moderately large, extends posteriorly over 36% of trunk length, with posterior scales extending slightly beyond axila, not extending to mid-venter, approximately four to five rows of anteriodorsal dewlap scales (blue in colour) smaller, elongate, pointed, keeled, remainder of scales much larger, keeled, lanceolate, bluntly pointed, gradually increasing in size towards margin, single marginal row largest with many more pointed scales. 16 enlarged rows of scales on dewlap. Nuchal and dorsal crest weak. Scales on nuchal region smaller, less than half the size of those on interorbital region, imbricate, strongly keeled. Body slender, 51 rows of scales around midbody, of these 10 to 12 rows of scales on back, from occiput to pectoral region homogenous in size, shape, slightly larger than those on neck, imbricate,



**FIGURE 1.** *Sitana attenboroughii* sp. nov. holotype male BNHS 2481, (A) dorsal, (B) ventral. Scale bar 10mm.



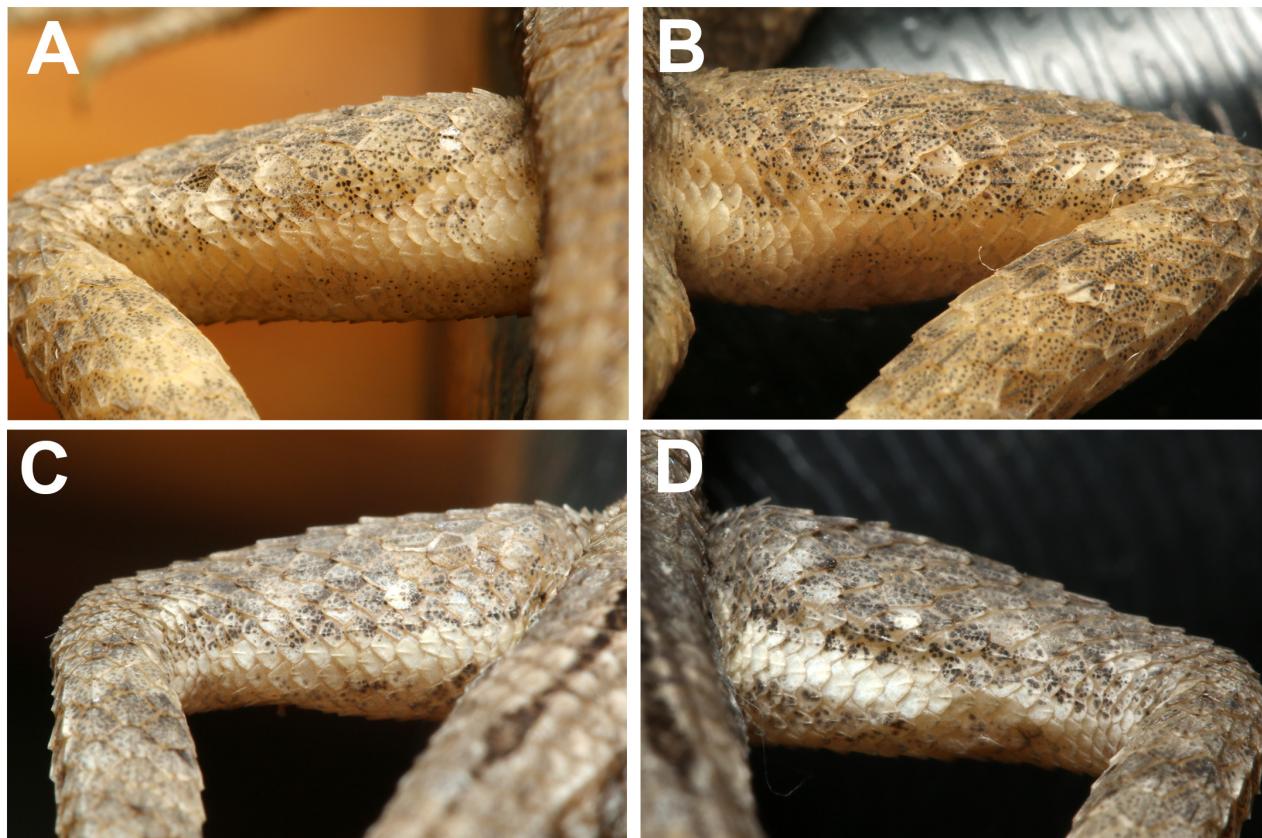
**FIGURE 2.** *Sitana attenboroughii* sp. nov. holotype male BNHS 2481 dorsal view of head. Scale bar 10mm.



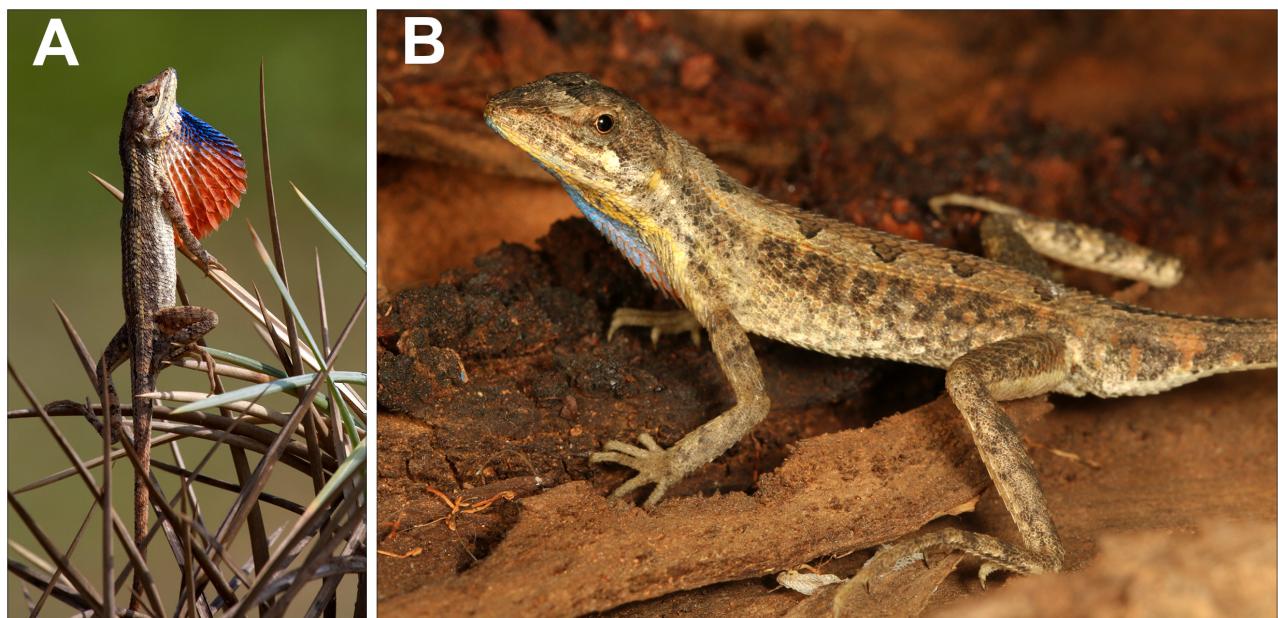
**FIGURE 3.** *Sitana attenboroughii* sp. nov. holotype male BNHS 2481 laterals view of head. Scale bar 10mm.

pointed, keeled, and directed posterioly forming regularly arranged longitudinal rows; those on flanks heterogeneous in size, shape, smaller than those on back, obtusely pointed, keeled, with irregularly scattered, slightly larger, pointed, keeled scales; scales of upper rows directed backwards and upwards; ventral rows backwards and downwards; ventral scales subimbricate, keeled, homogenous in size, shape, arranged in 72 rows; no precloacal or femoral pores. Fore and hind limbs relatively slender, tibia short (CL/SVL ratio 0.29); digits moderately long, ending in strong, elongate, slightly recurved claw; inter-digital webbing absent; subdigital lamellae entire, tri-mucronate, 25 subdigital lamellae on toe IV; relative length of fingers 4>3>2>5>1, toes

$4>3>2>1$ . Fore and hind limbs covered above and below with regularly arranged, enlarged, pointed, strongly keeled, scales. Enlarged projecting scale on thigh absent (Fig. 4). Tail entire; tail base swollen; tail uniformly covered with similar sized, keeled, weakly pointed, regularly arranged, posteriorly directed imbricate scales, no enlarged subcaudal row.



**FIGURE 4.** *Sitana attenboroughii* sp. nov. hind limb showing arrangement of scales on posterior aspect of thigh. (A–B) holotype male BNHS 2481, (C–D) paratype male BNHS 2482.



**FIGURE 5.** *Sitana attenboroughii* sp. nov. in life, (A) holotype male BNHS 2481, (B) paratype male BNHS 2482.



**FIGURE 6.** *Sitana attenboroughii* sp. nov. paratype male BNHS 2482 showing dewlap coloration.

Coloration in life (Fig. 5): Dark-brown above with five dark rhomboidal marks on the trunk, first mark present just posterior to the neck and the last one on the flank. Two lateral pale stripes running from posterior margin of the tympanum along the trunk above the flank. Limbs brown, banded with dark bands. Head coloration same as the body, except for the labials which are white with a tinge of yellow. Dewlap yellowish white at base, gradually turning into iridescent blue in its anterior one fourth region which in turn is replaced by bright-reddish orange, which covers the rest of the dewlap. A dark blue stripe runs along the line of attachment of the dewlap from the chin to insertion of the forelimb. The dewlap scale row attached to the trunk is white with a few scales with traces of the reddish orange color. Ventrally white.

Coloration in preservative (Fig. 1–3): Coloration much more faded, overall background coloration more yellowish. Rhomboidal marks turn much paler and almost diffused on towards the flank. Bands on legs almost vestigial. Blue coloration on the dewlap turns black, from the mental to the anterior half of the dewlap. A few black spots on around the dewlap on the lower jaw. The dark blue stripe runs along the line of attachment of the dewlap from the chin to insertion of the forelimb more prominent in the preserved specimen which appears black.

**Etymology.** The specific epithet is a noun honoring the celebrated naturalist and broadcaster Sir David Frederick Attenborough for his contribution towards natural history documentation and wildlife conservation.

**Variation.** The paratypes resemble the holotype in most aspects with the holotype except for ventral belly scale number. The paratype male possesses 26 scales. Other morphometric and meristic characters are presented in Table 1.

**Natural history and distribution.** The species occurs on coastal sand dunes of Poovar in Trivandrum district, Kerala (Fig. 11). The locality receive 1835–1865 mm of rainfall annually. The vegetation at Poovar is dominated by spiny grasses (*Spinifex littoreus*), sprawling runners of *Ipomoea pes-caprae* and *Agave* spp. (Fig. 12). The locality is close to the Poovar estuary, where Neyyar River meets Arabian Sea. Adult males were seen basking and displaying on the *Agave* fronds in the month of October. The male paratype was collected in the month of June and is an adult individual. Survey conducted at the type locality in the month of July yielded only hatchlings and no adults hinting that this species likely breeds twice in a year. The females were seen running on the sand among the spiny tangles of this coastal vegetation. Many burrows and foot prints of the species were also observed from the

area. When disturbed, lizards sought shelter among the spiny bases of plants or within burrows. Males were active especially in the early mornings until noon when they were seen actively displaying their dewlap to other individuals. The area is under threat of human interference in form of construction activities, extraction of sand, beach litter, and fire. This is the only beach in southern Trivandrum where the sand dune and the lush growth of spiny grasses were noted during the survey and may be the only microhabitat in which *Sitana attenboroughi* resides. The type locality is under threat from tourism and fires. Immediate efforts must be made to ensure protection to the type locality.

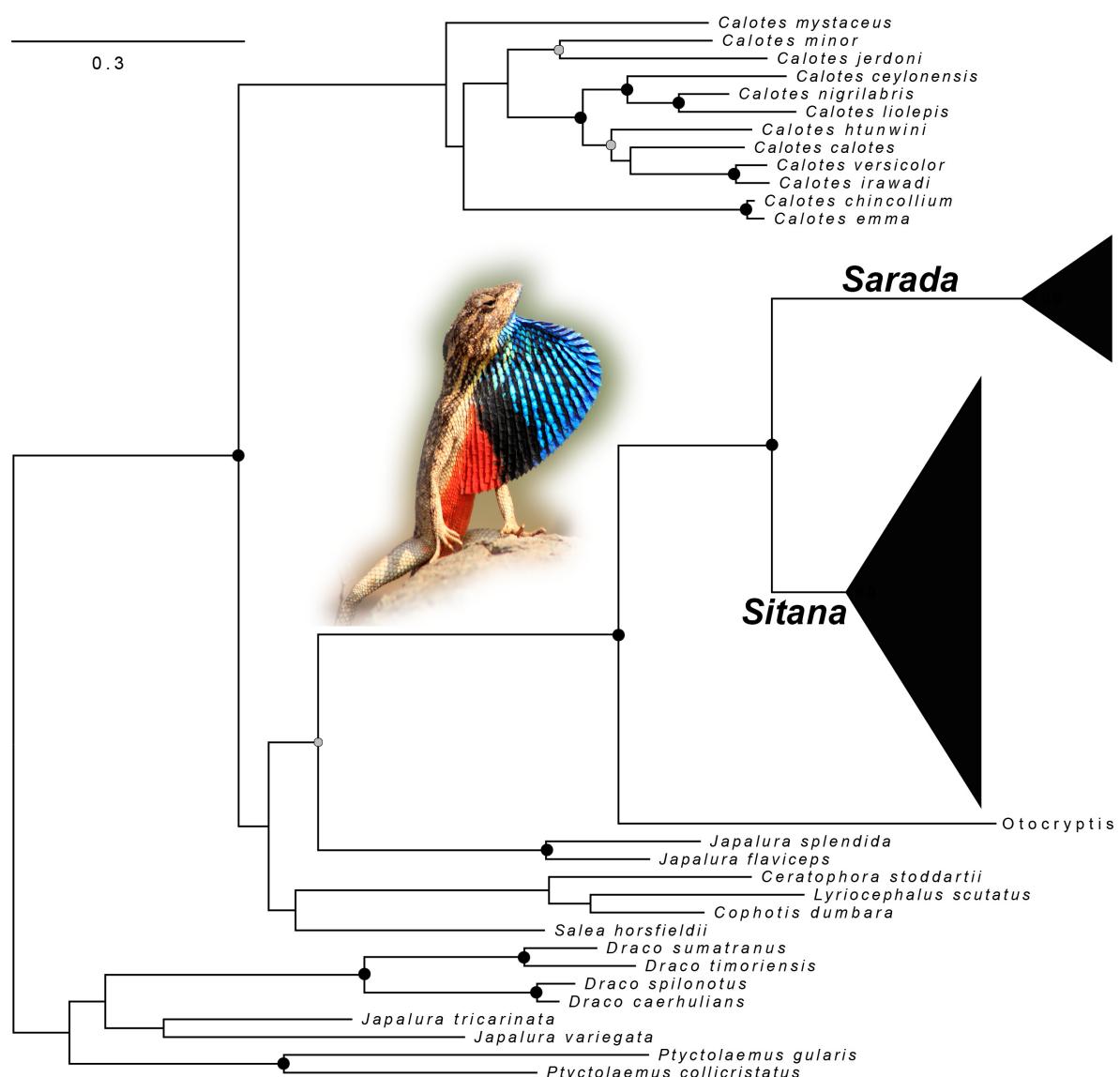
**Suggested common name.** Attenborough's fan-throated lizard.

**TABLE 1.** Measurements and morphological details of type specimens of *Sitana attenboroughii* sp. nov.

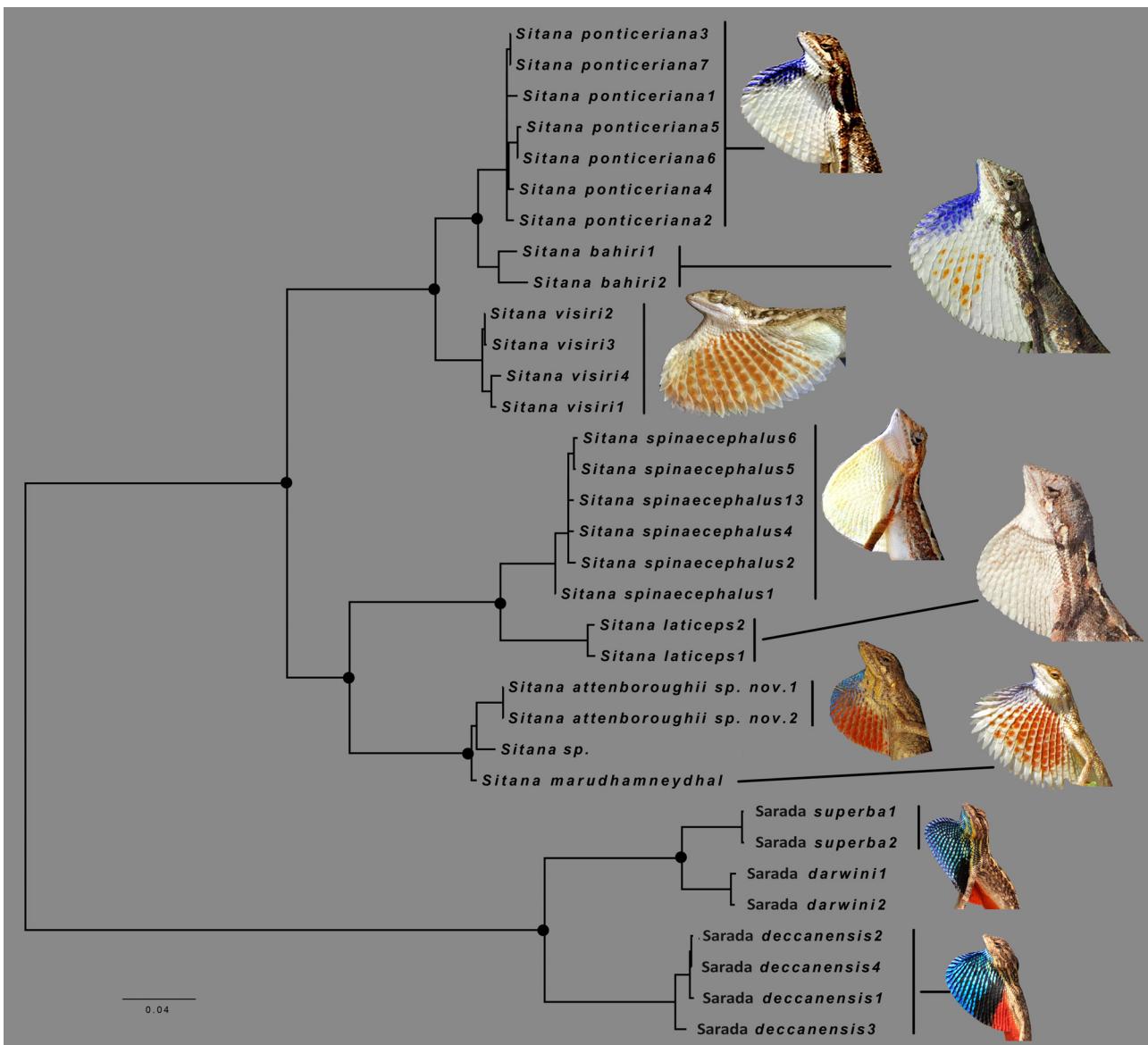
	Holotype BNHS 2481	Paratype BNHS 2483	Paratype BNHS 2482
Sex	Male	Female	Male
SVL	55.77	42.97	45.69
HL	14.38	11.69	12
HW	9.57	8.24	8
HH	7.48	6.43	6.65
EE	3.99	3.31	3.35
IO	6.91	6.26	6.36
JL	15.01	12.81	13.15
NE	4.72	3.28	3.44
SE	6.2	4.73	5.11
IN	2.91	2.84	2.26
DEWL	33.31	-	25.83
TD	1.17	1.16	1.16
OD	2.8	2.74	2.88
LAL	8.36	6.65	7.95
UAL	7.66	6.98	6.58
F1	3.17	2.94	2.42
F2	4.6	4.13	2.49
F3	5.87	5.28	3.2
F4	4.74	4.69	2.91
F5	3.67	3.35	2.29
FEL	12.58	10.04	12.18
CL	16.11	13.19	14.32
HFL	21.27	17.74	18.98
T1	2.78	2.5	3.15
T2	5.01	4	3.64
T3	6.8	5.86	5.44
T4	10.88	10.08	10.83
TL	119.77	-	-
TW	6.73	4.21	5.73
TH	3.8	3.52	4.19
TrL	28.2	18.57	24.77
TrW	8.19	7.75	9.27
TrH	6.62	*	6.61
DWLT	10.24	-	7.98

**TABLE 2.** A summary of diagnostic characters for males of selected *Sitana* spp.

Species	SVL	DWL	DWLT	VEN	VNB	VS
<i>Sitana attenboroughii</i> sp. nov.	45.7–55.8	25.8–33.3	8–10.2	72–73	26–27	35–38
<i>Sitana bahiri</i>	40.5–45	24.2–25.4	5.6–5.9	86–89	-	-
<i>Sitana devakai</i>	40.5–45	23.3–27.5	4.5–6.7	100–108	-	-
<i>Sitana laticeps</i>	41.7–48.5	20.7–27.1	1.3–4.9	75–81	-	-
<i>Sitana marudhamneydhal</i>	55–56	37.3–40.5	11.5–13.2	80–84	27	39–40
<i>Sitana ponticeriana</i>	36.6–44.5	22.4–29.2	3.7–8.1	64–76	-	-
<i>Sitana spinaecephalus</i>	45.3–56.6	26.1–32.6	4–8.3	70–88	-	-
<i>Sitana visiri</i>	40.3–56.3	24.5–39	5.3–12.1	65–85	-	-
<i>Sarada superba</i>	59.5–75.7	38.9–55	10.2–17.1	81–91	-	-
<i>Sarada deccanensis</i>	56.1–66.2	38.9–46.5	9.1–12.8	79–93	-	-
<i>Sarada darwini</i>	52.9–63.4	33.6–50	8.2–11.8	81–90	-	-



**FIGURE 7.** Maximum-likelihood phylogeny of Draconinae based on 1017bp of mitochondrial Nicotinamide adenine dinucleotide dehydrogenase (NADH) subunit 2 gene. Nodes with high support indicated by black circle (ML  $\geq 95$ , Bayesian PP  $> 0.99$ ), nodes with support only from Bayesian analyses indicated by grey circles. Species of the genus *Sitana* have been collapsed for representation purpose. Outgroup, *Bufoinceps laungwalaensis* has been removed.



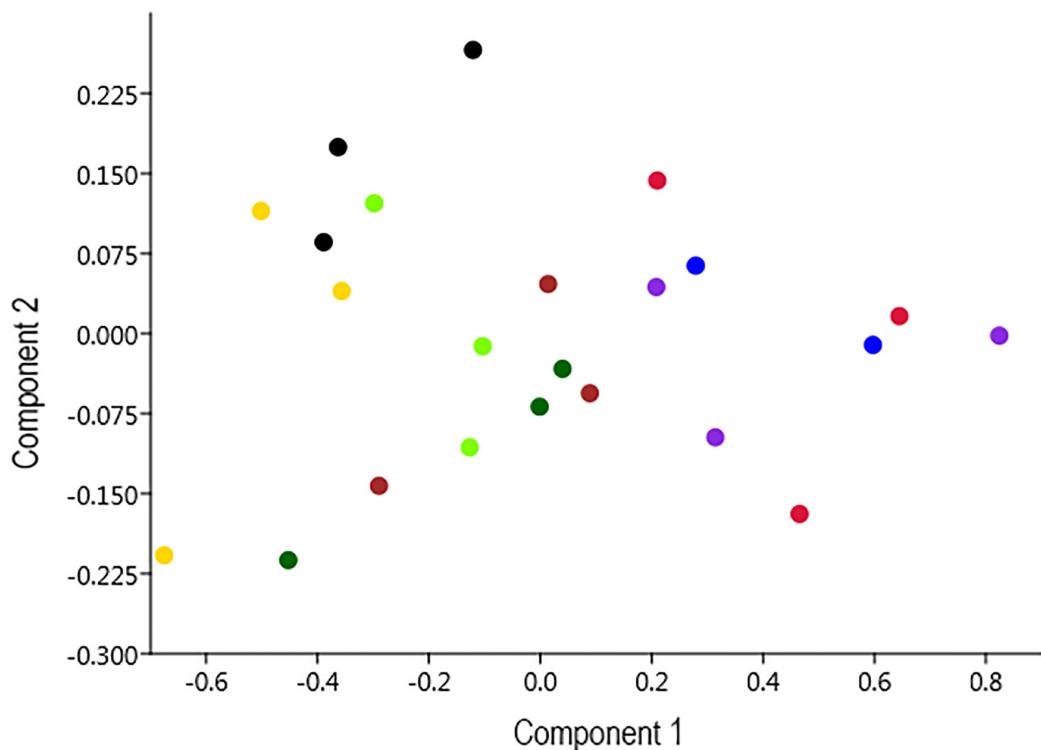
**FIGURE 8.** Maximum-likelihood phylogeny of *Sitana* based on 1017bp of mitochondrial Nicotinamide adenine dinucleotide dehydrogenase (NADH) subunit 2 gene. Nodes with high support indicated by black circle (ML ≥ 95, Bayesian PP > 0.99).

## Discussion

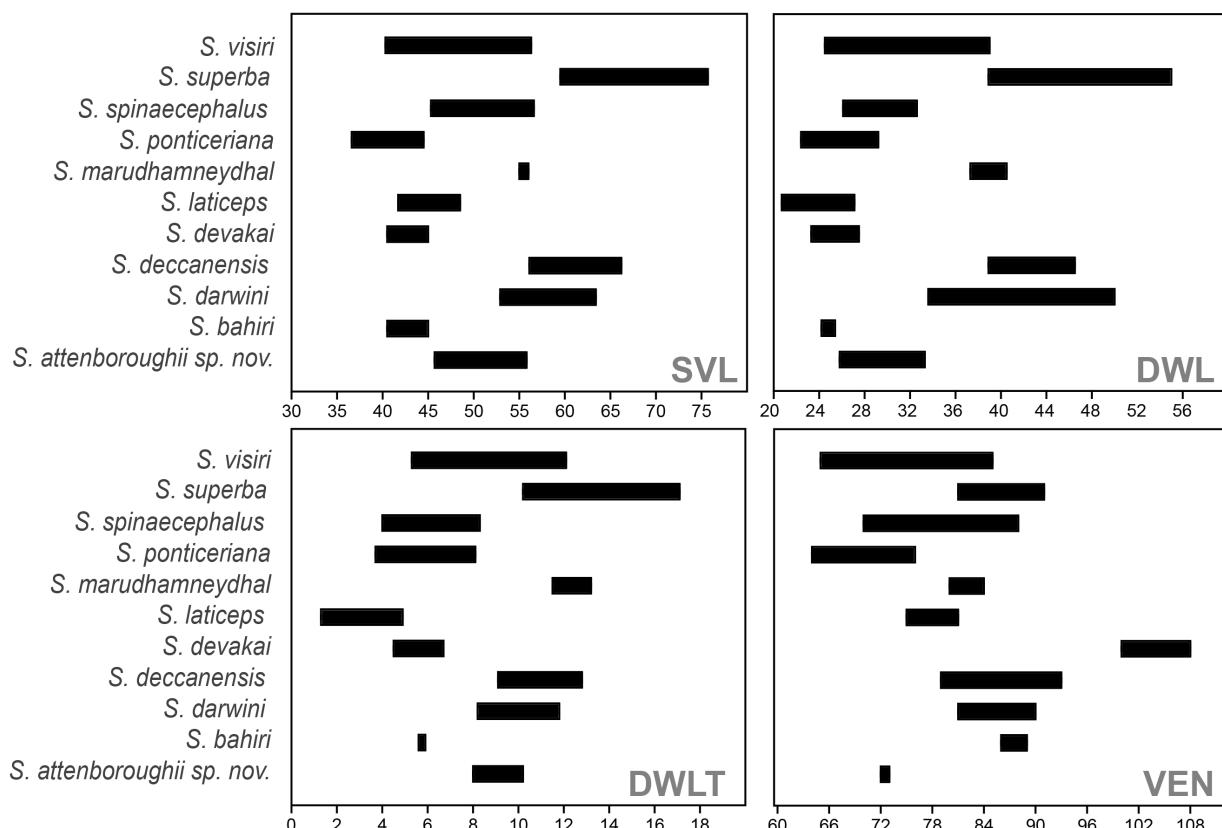
*Sitana attenboroughii* sp. nov. was found to be a member of “Clade 2” of Deepak *et al.* (2016a) and Deepak *et al.* (2016b) that contain *S. marudhamneydhal*, *S. laticeps* and *S. spinaecephalus*. The new species and *S. marudhamneydhal* form a clade, however their relationship remain unresolved due to lack of addition sequences of *S. marudhamneydhal*, especially from the type locality (Fig. 7–8). *Sitana attenboroughii* sp. nov. shows an uncorrected pairwise sequence divergence of 2.2% from the holotype of *S. marudhamneydhal*. The low molecular divergence might likely due to recent diversification. A revised phylogeny of *Sitana* with addition data for mitochondrial genes is necessary to help identify cryptic species.

Phylogenetic relationships recovered from our analyses are congruent with results from Pyron *et al.* (2013), Deepak *et al.* (2015) and Grismer *et al.* (2016). Multivariate PCA further attests to the distinctiveness of the new species from *S. marudhamneydhal* and *S. visiri*, where PC1+PC2 explain 71.49+6.87% of the total variance (Fig. 9). Further, *S. marudhamneydhal* occurs in the rain shadow region which receives an annual rainfall of ~1070 mm whereas *Sitana attenboroughii* sp. nov. occurs in coastal zones of southern Kerala which receives ~1865 mm of

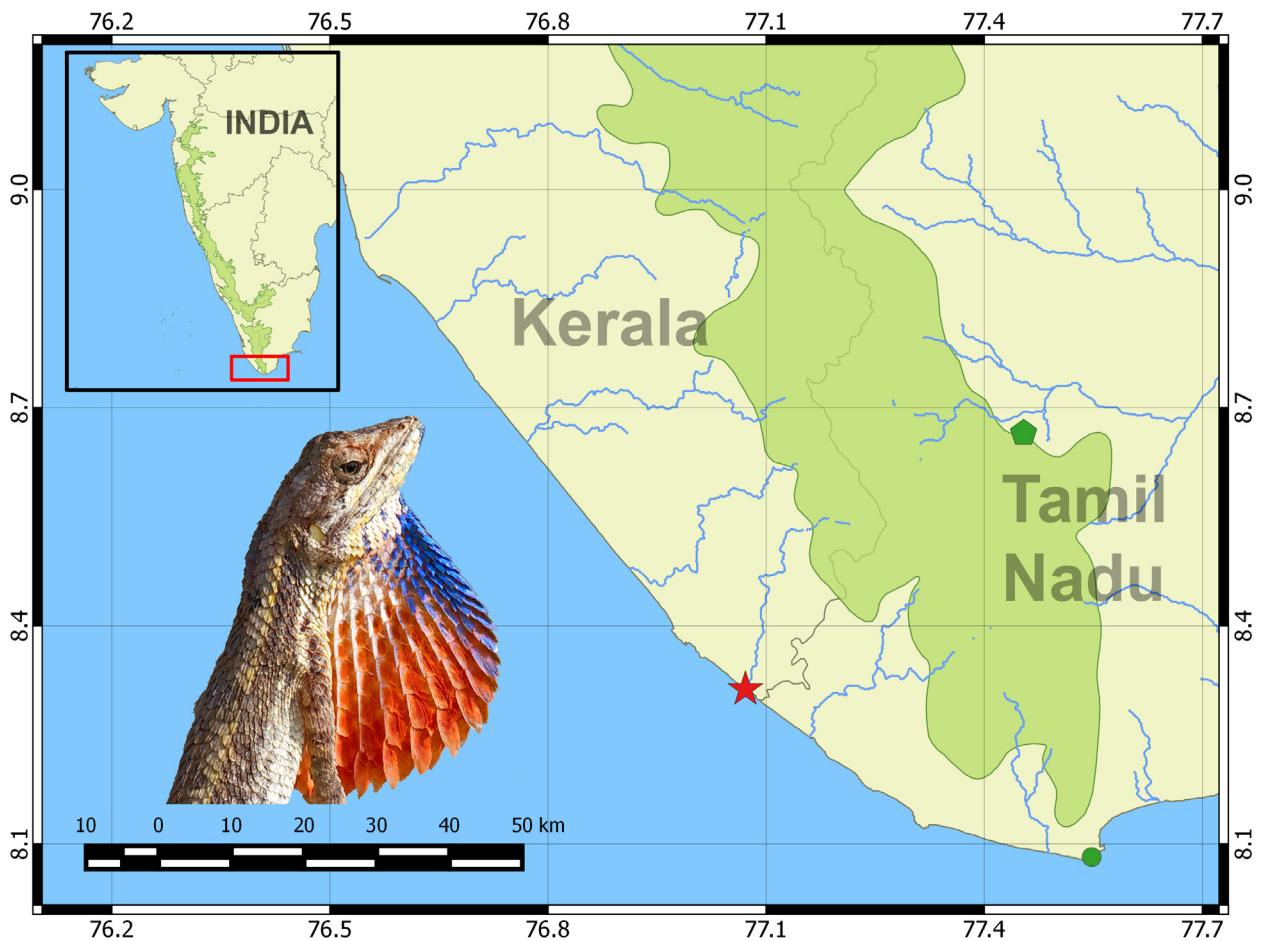
rainfall annually (Fig. 11). A summary of morphological and meristic details of selected characters of *Sitana* spp. are listed and presented in Table 2 & Fig. 10.



**FIGURE 9.** PCA plot for *Sitana* spp. showing separation of *Sitana attenboroughii* sp. nov. (black) from related species, *Sarada deccanensis* (blue), *Sarada darwini* (purple), *Sarada superba* (red), *Sitana visiri* (brown), *Sitana spinaecephalus* (light green), *Sitana laticeps* (yellow), *Sitana marudhamneydhal* (dark green).



**FIGURE 10.** A graphical summary of diagnostic characters for males of selected *Sitana* spp.



**FIGURE 11.** Map showing southern India with collection localities for *Sitana attenboroughii* sp. nov. (red star: type locality; *S. marudhamneydhal* type locality green polygon, green circle Kanyakumari).

Description of yet another species of the genus *Sitana* raises the number of species within the genus to twelve. It is likely that dedicated surveys across India will yield additional undescribed species as some species of the genus are likely to be narrowly distributed as seen in case of *Sitana attenboroughii* sp. nov. and *Sarada superba*. Description of seven new species of the genus *Sitana* (Deepak *et al.* 2016a; b), a new snake genus *Wallaceophis* Mirza, Vyas, Patel & Sanap, 2016 (Mirza *et al.* 2016), new lizard species *Cyrtodactylus varadgirii* Agarwal, Mirza, Pal, Maddock, Mishra & Bauer, 2016 (Agarwal *et al.* 2016) in a year merely highlight the poor nature of reptile documentation in India warranting dedicated herpetofaunal surveys across the country.

#### Updated key to the genus *Sarada* and *Sitana* (Modified after Deepak *et al.* 2016a)

- |     |   |                           |
|-----|---|---------------------------|
| 1a. | SVL >52mm, dewlap large with iridescent blue, orange and black coloration .....   | 2                         |
| 1b. | SVL <52mm, dewlap small to medium sized with pale yellow, white, blue or orange coloration .....  | 4                         |
| 2a. | Hind limb length exceeds SVL, dewlap large (extending over up to 55% of trunk), average SVL 62.2 mm, relatively large feet (0.42 HFL/SVL) ..... | <i>Sarada deccanensis</i> |
| 2b. | Hind limb length not exceeding SVL .....  | 3                         |
| 3a. | Dewlap very large (extending over up to 52% of trunk), average SVL 54.5 mm, relatively large feet (0.40 HFL/SVL) .....                          | <i>Sarada darwini</i>     |
| 3b. | Dewlap very large (extending over up to 59% of trunk), average SVL 67.9 mm, relatively small feet (0.37 HFL/SVL) .....                          | <i>Sarada superba</i>     |
| 4a. | Dewlap coloration in breeding males' blue, iridescent white and orange .....  | 5                         |
| 4b. | Dewlap in breeding male yellowish white with only a single blue line .....  | 8                         |
| 5a. | Dewlap coloration rich/vibrant .....  | 6                         |

5b.	Dewlap coloration paler/faded .....	7
6a.	Dewlap very large (extending over up to 56% of the trunk), with enlarged scales and strongly serrated margins; average SVL 50 mm; 65-69 ventral scales .....	<i>Sitana visiri</i>
6b.	Dewlap large (extending over up to 33% of trunk), with enlarged scales and strongly serrated margins, average SVL 35 mm, 100-108 ventral scales.....	<i>Sitana devakai</i>
6c.	Dewlap large (extending over up to 36% of trunk), with enlarged scales and moderately serrated margins, average SVL 48 mm, 72-74 ventral scales.....	<i>Sitana attenboroughii</i> sp. nov.
7a.	Dewlap of medium size (extending over up to 29% of trunk), with enlarged scales and strongly serrated margins, average SVL 34 mm, 86-89 ventral scales .....	<i>Sitana bahiri</i>
7b.	Dewlap large (extending over up to 46% of the trunk), with strongly serrated margins, average SVL 40.5 mm, 64-76 ventral scales .....	<i>Sitana ponticeriana</i>
7c.	Dewlap large (extending over up to 64% of the trunk), with strongly serrated margins, average SVL 51 mm, 80-84 ventral scales .....	<i>Sitana marudhamneydhal</i>
8a.	Dewlap small, weakly serrated, not reaching axilla.....	<i>Sitana sivalensis</i> complex
8b.	Dewlap medium to large, weakly serrated, extending beyond axilla.....	9
9a.	Dewlap medium (extending over up to 29% of trunk), four small yet enlarged spine-like scales bordering occipital region.....	<i>Sitana laticeps</i>
9b.	Dewlap large (extending over up to 45% of trunk), four prominent enlarged spine-like scales bordering occipital region .....	<i>Sitana spinaecephalus</i>



**FIGURE 12.** Habitat at the type locality of *Sitana attenboroughii* sp. nov. where all the type specimens were collected.

### Acknowledgments

Part of the research was carried with funding from the Rufford Small Grant and funds from Tulika Kedia through the Singinawa Conservation Foundation to ZM. Special thanks to the Forest and Wildlife department of Kerala for necessary permission to carryout fieldwork (Permit no. WL.10. 4950/2014). We thank members of Travancore Natural History Society (TNHS), Trivandrum for their help in the field. A lot of people contributed images of *Sitana* spp. for which we really thank them: Ambika Kamath (*S. marudhamneydhal*), Pratik Joshi (*S. deccanensis*), Vishal Mane (*S. laticeps*), David Raju (*S. spinaecephalus*) Amod Zambre, and Suranjan Karunarathna (*S. bahiri*).

Aaron Bauer provided impossible to find literature from which the work greatly benefited and Harshil Patel for timely advice and helpful discussions on agamid taxonomy. MJP is thankful to the Director, Zoological Survey of India, Kolkata and the Officer-in-Charge, ZSI, Kozhikode for facilities and encouragements. Special thanks to Rahul Khot (BNHS, Mumbai) for help with registration of type specimens and specimen details from the museum collection. Special thanks to an anonymous review for constructive comments from which the manuscript benefitted. Special thanks to Varad Giri and Krushnamegh Kunte for granting permission to examine Sitana types at the National Centre for Biological Sciences.

## References

- Agarwal, I., Mirza, Z.A., Pal, S., Maddock, S.T., Mishra, A. & Bauer, A.M. (2016) A new species of the *Cyrtodactylus (Geckoella) collegalensis* (Beddome, 1870) complex (Squamata: Gekkonidae) from Western India. *Zootaxa*, 4170 (2), 339–354.  
<https://doi.org/10.11646/zootaxa.4170.2.7>
- Amarasinghe, A.A.T., Ineich, I., Karunarathna, D.M.S.S., Botejue, W.M.S. & Campbell, P.D. (2015) Two new species of the genus *Sitana* Cuvier, 1829 (Reptilia: Agamidae) from Sri Lanka, including a taxonomic revision of the Indian *Sitana* species. *Zootaxa*, 3915 (1), 67–98.  
<https://doi.org/10.11646/zootaxa.3915.1.3>
- Deepak, V., Giri, V.B., Asif, M., Dutta, S.K., Vyas, R., Zambre, A.M., Bhosale, H. & Karanth, P. (2016a) Systematics and phylogeny of *Sitana* ( Reptilia : Agamidae ) of Peninsular India , with the description of one new genus and five new species. *Contributions to Zoology*, 85, 67–111.
- Deepak, V., Khandekar, A., Varma, S. & Chaitanya, R. (2016)b) Description of a new species of *Sitana* Cuvier, 1829 from southern India. *Zootaxa*, 4139 (2), 167–182.  
<https://doi.org/10.11646/zootaxa.4139.2.2>
- Deepak, V., Vyas, R., Giri, V.B. & Praveen Karanth, K. (2015) A taxonomic mystery for more than 180 years: The identity and systematic position of *Brachysaura minor* (HARDWICKE & GRAY, 1827). *Vertebrate Zoology*, 65, 371–381.
- Grismer, J.L., Schulte, J.A., Alexander, A., Wagner, P., Travers, S.L., Buehler, M.D., Welton, L.J. & Brown, R.M. (2016) The Eurasian invasion: phylogenomic data reveal multiple Southeast Asian origins for Indian Dragon Lizards. *BMC Evolutionary Biology*, 16, 43.  
<https://doi.org/10.1186/s12862-016-0611-6>
- Kamath, A. (2016) Variation in Display Behavior, Ornament Morphology, Sexual Size Dimorphism, and Habitat Structure in the Fan-Throated Lizard (*Sitana*, Agamidae). *Journal of Herpetology*, 50, 394–403.  
<https://doi.org/10.1670/15-040>
- Kearse, M., Moir, R. & Wilson, A. (2012) Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics*, 28, 1647–1649.  
<https://doi.org/10.1093/bioinformatics/bts199>
- Lanfear, R., Calcott, B., Ho, S. & Guindon, S. (2012) PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution*, 29, 1695–1701.  
<https://doi.org/10.1093/molbev/mss020>
- Macey, J.R., Larson, A., Ananjeva, N., Fand, Z. & Papenfuss, T.J. (1997) Two novel gene orders and the role of light-strand replication in rearrangement of the vertebrate mitochondrial genome. *Molecular Biology and Evolution*, 14, 91–104.  
<https://doi.org/10.1093/oxfordjournals.molbev.a025706>
- Mirza, Z.A., Vyas, R., Patel, H., Maheta, J. & Sanap, R. V (2016) A New Miocene-Divergent Lineage of Old World Racer Snake from India. *PloS one*, 11 (3) , e0, 1–17.  
<https://doi.org/10.1371/journal.pone.0148380>
- Pyron, R., Burbrink, F. & Wiens, J. (2013) A phylogeny and revised classification of Squamata, including 4161 species of lizards and snakes. *BMC Evolutionary Biology*, 13 (93), 1–53.  
<https://doi.org/10.1186/1471-2148-13-93>
- Ronquist, F. & Huelsenbeck, J. (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics*, 19, 1572–1574.
- Silvestro, D. & Michalak, I. (2012) raxmlGUI: a graphical front-end for RAxML. *Organisms Diversity & Evolution*, 12, 335–337.
- Tamura, K., Stecher, G., Peterson, D., Filipski, A. & Kumar, S. (2013) MEGA6: Molecular Evolutionary Genetics Analysis version 6.0. *Molecular biology and evolution*, 30, 2725–2729.  
<https://doi.org/10.1093/molbev/mst197>
- Thompson, J. & Gibson, T. (2002) Multiple sequence alignment using ClustalW and ClustalX. *Current protocols in*. [published online]  
<https://doi.org/10.1002/0471250953.bi0203s00>

**APPENDIX 1.** Species and their GenBank accession numbers used in the present study.

Species	Accession number
<i>Calotes versicolor</i>	DQ289478
<i>Calotes irawadi</i>	DQ289465
<i>Calotes htunwini</i>	DQ289464
<i>Calotes emma</i>	DQ289460
<i>Calotes chincollium</i>	DQ289459
<i>Calotes calotes</i>	AF128482
<i>Calotes jerdoni</i>	GQ502783
<i>Calotes minor</i>	KT952397
<i>Calotes liolepis</i>	AF128485
<i>Calotes nigrilabris</i>	AF128486
<i>Calotes ceylonensis</i>	AF128483
<i>Calotes mystaceus</i>	AF128487
<i>Otocryptis wiegmanni</i>	AF128480
<i>Ceratophora stoddartii</i>	AF364054
<i>Cophotis dumbara</i>	GQ502785
<i>Lyriocephalus scutatus</i>	AF364052
<i>Salea horsfieldii</i>	AF128490
<i>Japalura splendida</i>	AF288230
<i>Japalura variegata</i>	AF128479
<i>Japalura tricarinata</i>	AF128478
<i>Japalura flaviceps</i>	AF128500
<i>Ptyctolaemus gularis</i>	AY555838
<i>Ptyctolaemus collicristatus</i>	AY555837
<i>Draco caerhulians</i>	AF288281
<i>Draco timoriensis</i>	AF288275
<i>Draco spilonotus</i>	AF288282
<i>Draco sumatranaus</i>	AF288264
<i>Bufoinceps laungwalaensis</i>	DQ008214
<i>Otocryptis wiegmanni</i>	AF128480
<i>Sitana bahiri</i>	AF12848
<i>Sitana bahiri</i>	KT831321
<i>Sitana bahiri</i>	KT831322
<i>Sarada darwini</i>	KT831313
<i>Sarada darwini</i>	KT831314
<i>Sarada deccanensis</i>	KT831315
<i>Sarada deccanensis</i>	KT831316
<i>Sarada deccanensis</i>	KT831317
<i>Sarada deccanensis</i>	KT831318
<i>Sitana laticeps</i>	KT831323
<i>Sitana laticeps</i>	KT831324
<i>Sitana ponticeriana</i>	KT831325
<i>Sitana ponticeriana</i>	KT831326

*.....continued on the next page*

Species	Accession number
<i>Sitana ponticeriana</i>	KT831327
<i>Sitana ponticeriana</i>	KT831328
<i>Sitana ponticeriana</i>	KT831329
<i>Sitana ponticeriana</i>	KT831330
<i>Sitana ponticeriana</i>	KT831331
<i>Sitana spinaecephalus</i>	KT831332
<i>Sitana spinaecephalus</i>	KT831333
<i>Sitana spinaecephalus</i>	KT831334
<i>Sitana spinaecephalus</i>	KT831335
<i>Sitana spinaecephalus</i>	KT831336
<i>Sitana spinaecephalus</i>	KT831337
<i>Sarada superba</i>	KT831319
<i>Sarada superba</i>	KT831320
<i>Sitana visiri</i>	KT831338
<i>Sitana visiri</i>	KT831339
<i>Sitana visiri</i>	KT831340
<i>Sitana visiri</i>	KT831341
<i>Sitana</i> sp.	KX371915
<i>Sitana marudhamneydhal</i>	KX371916

**APPENDIX 2.** Un-corrected p-distance (in %) for NADH2 gene for selected members of Agamidae.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
<i>Otocryptis_wiegmanni</i>	0.27																
<i>Sarada_darwinii</i>	0.26	0.01															
<i>Sarada_deccanensis1</i>	0.28	0.11	0.11														
<i>Sarada_deccanensis2</i>	0.28	0.11	0.11	0.00													
<i>Sarada_deccanensis3</i>	0.28	0.11	0.11	0.01	0.01												
<i>Sarada_deccanensis4</i>	0.28	0.11	0.11	0.00	0.00	0.01											
<i>Sarada_superba1</i>	0.27	0.05	0.05	0.11	0.11	0.12	0.11										
<i>Sarada_superba2</i>	0.27	0.05	0.05	0.11	0.11	0.12	0.11	0.00									
<i>Sitana_laticeps1</i>	0.27	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.23	0.23	0.23	0.23	0.23	0.23	0.23	0.23	0.23
<i>Sitana_bahir1</i>	0.27	0.23	0.23	0.23	0.23	0.23	0.23	0.23	0.23	0.23	0.23	0.23	0.23	0.23	0.23	0.23	0.23
<i>Sitana_bahir2</i>	0.27	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22
<i>Sitana_laticeps2</i>	0.27	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22
<i>Sitana_ponticeriana1</i>	0.27	0.23	0.23	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21
<i>Sitana_ponticeriana2</i>	0.27	0.23	0.23	0.22	0.22	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21
<i>Sitana_ponticeriana3</i>	0.27	0.22	0.22	0.22	0.22	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21
<i>Sitana_ponticeriana4</i>	0.27	0.22	0.22	0.22	0.22	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21
<i>Sitana_ponticeriana5</i>	0.27	0.23	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22
<i>Sitana_ponticeriana6</i>	0.27	0.23	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22
<i>Sitana_ponticeriana7</i>	0.27	0.22	0.22	0.22	0.22	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21
<i>Sitana_spinacephalus1</i>	0.27	0.22	0.22	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21
<i>Sitana_spinacephalus2</i>	0.27	0.23	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22
<i>Sitana_spinacephalus13</i>	0.27	0.23	0.23	0.22	0.22	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21
<i>Sitana_spinacephalus4</i>	0.27	0.23	0.23	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22	0.22
<i>Sitana_spinacephalus5</i>	0.27	0.22	0.22	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21
<i>Sitana_spinacephalus6</i>	0.27	0.22	0.22	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21
<i>Sitana_visiri1</i>	0.27	0.22	0.22	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21
<i>Sitana_visiri2</i>	0.27	0.22	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21
<i>Sitana_visiri3</i>	0.27	0.22	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21
<i>Sitana_visiri4</i>	0.27	0.22	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21
<i>Sitana_attenboroughii_sp_nov_1</i>	0.27	0.21	0.21	0.20	0.20	0.20	0.20	0.20	0.20	0.20	0.20	0.20	0.20	0.20	0.20	0.20	0.20
<i>Sitana_attenboroughii_sp_nov_2</i>	0.27	0.22	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21
<i>Sitana_marudhamneydhal1</i>	0.27	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21
<i>Sitana_sp.</i>	0.27	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21

.....continued on the next page

## APPENDIX 2. (Continued)

	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
<i>Otoxypitis_wiegmanni</i>																
<i>Sarada_darwini1</i>																
<i>Sarada_darwini2</i>																
<i>Sarada_deccanensis1</i>																
<i>Sarada_deccanensis2</i>																
<i>Sarada_deccanensis3</i>																
<i>Sarada_deccanensis4</i>																
<i>Sarada_deccanensis5</i>																
<i>Sarada_superba1</i>																
<i>Sarada_superba2</i>																
<i>Sitana_laticeps1</i>																
<i>Sitana_bahiri1</i>																
<i>Sitana_bahiri2</i>																
<i>Sitana_laticeps2</i>																
<i>Sitana_ponticeriana1</i>																
<i>Sitana_ponticeriana2</i>																
<i>Sitana_ponticeriana3</i>																
<i>Sitana_ponticeriana4</i>																
<i>Sitana_ponticeriana5</i>																
<i>Sitana_ponticeriana6</i>																
<i>Sitana_ponticeriana7</i>	0.00	0.01	0.01													
<i>Sitana_spinaeccephalus1</i>	0.15	0.15	0.15	0.15												
<i>Sitana_spinaeccephalus2</i>	0.15	0.15	0.15	0.15	0.01											
<i>Sitana_spinaeccephalus3</i>	0.15	0.15	0.15	0.16	0.01	0.01										
<i>Sitana_spinaeccephalus4</i>	0.15	0.15	0.15	0.15	0.01	0.01	0.01									
<i>Sitana_spinaeccephalus5</i>	0.15	0.15	0.15	0.16	0.01	0.01	0.01	0.01								
<i>Sitana_spinaeccephalus6</i>	0.15	0.15	0.15	0.15	0.01	0.01	0.01	0.01	0.00							
<i>Sitana_visir1</i>	0.06	0.06	0.06	0.06	0.14	0.14	0.14	0.14	0.14	0.14	0.14	0.14	0.14	0.14	0.14	0.14
<i>Sitana_visir2</i>	0.06	0.06	0.06	0.06	0.14	0.14	0.14	0.14	0.14	0.14	0.14	0.14	0.14	0.14	0.14	0.14
<i>Sitana_visir3</i>	0.06	0.06	0.06	0.06	0.14	0.14	0.14	0.14	0.14	0.14	0.14	0.14	0.14	0.14	0.14	0.14
<i>Sitana_visir4</i>	0.06	0.06	0.06	0.06	0.14	0.15	0.15	0.15	0.15	0.15	0.15	0.15	0.15	0.15	0.15	0.15
<i>Sitana_attenboroughii_sp_nov.1</i>	0.12	0.12	0.13	0.11	0.12	0.12	0.12	0.12	0.12	0.12	0.12	0.12	0.12	0.12	0.12	0.12
<i>Sitana_attenboroughii_sp_nov.2</i>	0.12	0.12	0.12	0.13	0.11	0.12	0.12	0.12	0.12	0.12	0.12	0.12	0.12	0.12	0.12	0.12
<i>Sitana_marudhamneydhall</i>	0.13	0.13	0.13	0.13	0.11	0.12	0.12	0.12	0.12	0.12	0.12	0.12	0.12	0.12	0.12	0.12
<i>Sitana</i> sp.	0.13	0.13	0.13	0.13	0.11	0.12	0.12	0.12	0.12	0.12	0.12	0.12	0.12	0.12	0.12	0.12

**APPENDIX 3.** Optimal partitioning strategy and evolutionary substitution model suggested by PartitionFinder.

Software	Gene	PartitionFinder	Implemented
RAXML	nd2_pos1	TVM+I+G	GTR+I+G
	nd2_pos2	GTR+G	GTR+I+G
	nd2_pos3	GTR+I+G	GTR+I+G
MrBayes	nd2_pos1	TVM+I+G	GTR+I+G
	nd2_pos2	GTR+G	GTR+G
	nd2_pos3	GTR+I+G	GTR+I+G

**APPENDIX 4.** Eigenvalues and the variance explained by each Principal component derived from PCA.

PC	Eigenvalue	% variance
1	0.158175	71.49
2	0.015199	6.87
3	0.013305	6.01
4	0.007953	3.59
5	0.006462	2.92
6	0.004845	2.19
7	0.004055	1.83
8	0.002631	1.19
9	0.002033	0.92
10	0.001692	0.76
11	0.001087	0.49
12	0.000976	0.44
13	0.000785	0.36
14	0.000675	0.31
15	0.000502	0.23
16	0.000323	0.15
17	0.000301	0.14
18	0.0001	0.05
19	8.78E-05	0.04
20	3.28E-05	0.01
21	2.20E-05	0.01
22	5.87E-06	0.00

**APPENDIX 5.** Factor loadings on the principal components for each morphometric variable derived from PCA.

	PC 1	PC 2
HL	0.19463	0.013783
HW	0.19176	-0.01148
HH	0.24294	0.053643
EE	0.25879	0.062082
IO	0.16017	0.20529
JL	0.14491	0.20637
NE	0.1501	0.2073
SE	0.15094	0.046456
IN	0.16674	0.010794
DEWL	0.17262	-0.19748
TD	0.18518	-0.5072
OD	0.19863	-0.29896
LAL	0.32586	0.28651
UAL	0.29497	0.090175
F4	0.25264	-0.02628
FEL	0.19173	-0.01546
CL	0.17619	0.022214
HFL	0.13529	-0.01849
T4	0.13954	0.13267
TL	0.061911	0.11178
TW	0.18323	0.30133
TH	0.22436	0.071296
TrL	0.11747	0.013484
TrW	0.22146	-0.46516
TrH	0.25072	-0.20692