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Article *in* Zootaxa · February 2018

DOI: 10.11646/zootaxa.4384.1.1

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Zootaxa 4384 (1): 001–088
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Monograph

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.4384.1.1
http://zoobank.org/urn:lsid:zoobank.org:pub:18DD1320-7914-4E09-A46C-707069DC69F5

ZOOTAXA

4384

An integrative taxonomic review of the South Asian microhylid genus *Uperodon*

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Magnolia Press
Auckland, New Zealand

Accepted by M. Vences: 4 Dec. 2018; published: 23 Feb. 2018

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An integrative taxonomic review of the South Asian microhylid genus *Uperodon*
(*Zootaxa* 4384)

88 pp.; 30 cm.

22 Feb. 2018

ISBN 978-1-77670-315-9 (paperback)

ISBN 978-1-77670-316-6 (Online edition)

FIRST PUBLISHED IN 2018 BY

Magnolia Press

P.O. Box 41-383

Auckland 1346

New Zealand

e-mail: magnolia@mapress.com

http://www.mapress.com/j/zt

ISSN 1175-5326 (Print edition)

ISSN 1175-5334 (Online edition)

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Abstract

Based on a recent molecular phylogenetic study, the South Asian microhylid genus *Uperodon* (subfamily Microhylinae) currently comprises of 12 valid species that are largely restricted to India and Sri Lanka. Considering the revised generic-level status of its various members, here we review the taxonomy of all known species in this genus and clarify their nomenclatural status and geographical distribution, by integrating evidence from genetics, adult and tadpole morphology, breeding ecology, and bioacoustics. Our molecular analyses of a mitochondrial 16S rRNA gene fragment combined with external and internal morphological studies also revealed a distinct new species in the genus. This species, formally described as *Uperodon rohani* **sp. nov.**, is endemic to Sri Lanka and widely distributed at lower elevations in the island. For nomenclatural stability of various previously known members, the following actions are also undertaken: (1) redescription of the poorly-defined species *Ramanella anamalaiensis* Rao (= *Uperodon anamalaiensis*) and *Hylaedactylus montanus* Jerdon (= *Uperodon montanus*); (2) neotype designation for *Ramanella anamalaiensis* Rao (= *Uperodon anamalaiensis*), *Ramanella minor* Rao, *Ramanella mormorata* Rao (= *Uperodon mormorata*), and *Ramanella triangularis rufeventris* Rao; (3) lectotype designation for *Callula variegata* Stoliczka (= *Uperodon variegatus*); and (4) synonymization of *Ramanella minor* Rao with *Uperodon anamalaiensis*.

Key words: Amphibians, bioacoustics, endemism, mitochondrial DNA, natural history, neotype, lectotype, new species, tadpoles, Western Ghats-Sri Lanka biodiversity hotspot

Introduction

The genus *Uperodon* Duméril and Bibron is classified in subfamily Microhylinae of the narrow-mouthed frog family Microhylidae. This genus was originally described to accommodate *Engystoma marmoratum* Guérin-Méneville, subsequently considered as a junior subjective synonym of *Rana systoma* Schneider, which was among the first frog species described from India. Another species, *Cacopus globulosus* Günther was transferred to *Uperodon* and the genus continued to comprise of two species—*Uperodon systoma* and *Uperodon globulosus*, until

recently. A molecular study by Peloso *et al*. (2016) revised the contents of this genus mainly to resolve the paraphyly of genus *Kaloula* Gray that resulted from the phylogenetic position of *Kaloula taprobanica* Parker as being sister to the clade containing *Ramanella* Rao and Ramanna (currently unrecognized) + *Uperodon sensu stricto* (e.g., Van Bocxlaer *et al*. 2006; Pyron & Wiens 2011). As a result, all the members of genus *Ramanella* (= *Uperodon*) and *Kaloula taprobanica* (= *Uperodon taprobanicus*) are now included in genus *Uperodon* (*sensu lato*), which together comprises of 12 recognised species (Frost 2017).

Originally, *Ramanella* was diagnosed as a distinct genus on the basis of external and internal morphological characters (Rao & Ramanna 1925; Parker 1934), and *Uperodon taprobanicus* (Parker 1934) was described as a subspecies—*Kaloula pulchra taprobanica*. There are two notable studies concerning the morphological relationship between the three 'genera'—*Kaloula*, *Ramanella* and *Uperodon* (*sensu stricto*). Parker's monograph of the family Microhylidae (1934) discussed various morphological similarities and dissimilarities useful for genus-level diagnosis. He also transferred four species—*Uperodon montanus* Jerdon, *U. obscurus* Günther, *U. triangularis* Günther and *U. variegatus* Stoliczka—originally described in other genera to *Ramanella*. Ramaswami (1936), however, considered *Ramanella* not to be distinct from *Kaloula* (Peloso *et al*. 2016). Nevertheless, subsequent authors continued to recognize *Ramanella*, and several new species were added to this genus (Parker 1934; Rao 1937; Manamendra-Arachchi & Pethiyagoda 2001).

Over the years, considerable natural history information has accumulated for various *Uperodon* species (see 'results' for detailed discussion). However, several members of the genus are still poorly studied and known either only from their original descriptions and type localities, or from invalidated reports (e.g., *U. anamalaiensis* Rao, *U. montanus*, *U. minor* Rao, *U. nagaoi* Manamendra-Arachchi and Pethiyagoda, *U. palmatus* Parker). Another species, *U. mormorata* Rao was only recently rediscovered (Das & Whitaker 1997). Although numerous additional distribution records are available for *Uperodon* species in literature (see Supplementary Table S1), many lack vouchers or photographs, and therefore require further confirmation. This is also one of the major problems currently plaguing the genus since identities of many *Uperodon* species remain obscure in the absence of type material. The type specimens of species described by Rao (1937) are considered lost (Dubois 1984; Biju 2001) resulting in several uncertainties concerning species identity. Two species, *U. anamalaiensis* and *U. minor*, had not been reported for several decades since their original description. While the rediscovery of *U. anamalaiensis* from its type locality was also recently announced by Vijaykumar *et al*. (2011), no voucher-based observations have been made for *U. minor*. Further, there are several available names currently in the synonymy of *U. variegatus*, of which *Hylaedactylus carnaticus* Jerdon is suggested to be a senior synonym (Parker 1934) but the type material for this species is also reported to be lost (Jerdon 1870). Another taxon, *Ramanella triangularis rufeventris* Rao, currently in the synonymy of *Uperodon triangularis*, was described as a subspecies (Rao 1937) but its type is considered lost (Dubois 1984; Biju 2001). The type locality of *Uperodon triangularis* itself has been noted to be imprecise (Biju 2001). With such essential information currently unavailable for various nominal species, the taxonomy of *Uperodon* is in need of a comprehensive revision to ensure proper species identification, which is also necessary for any meaningful studies on this group. Additionally, several known taxa require designation of neotypes and lectotypes in order to establish nomenclatural stability.

In this work, we studied over 70 *Uperodon* populations from across their range in India and Sri Lanka to understand the existing diversity, variations, geographical ranges and distribution patterns, by integrating evidence from genetics and morphology. For the first time, we present a comprehensive taxonomic revision of all known members of the genus *Uperodon*, along with the description of a new species. Additional information on tadpole morphology, advertisement call structure, breeding ecology, and natural history is summarized with previously available knowledge of various members. Morphological comparisons and affinities are also provided for all the species to facilitate a better working taxonomy for this group.

Materials and methods

Field surveys and specimen collection. Field surveys were conducted in India and Sri Lanka between 2002 and 2015. A total of 44 localities were surveyed in India (33) and Sri Lanka (11) (Table 1). Our sampling effort was focused largely on the Western Ghats–Sri Lanka biodiversity hotspot because of the high diversity and endemism of *Uperodon* frogs in this region. Sampling was usually done through opportunistic searches during both day and

night. Males were also located by their calls after sunset, mostly during the breeding season (June–August in the Western Ghats, October–December in the Eastern Ghats and Sri Lanka) or immediately after sporadic rains. Suitable habitats such as temporary ponds and tree holes were specifically searched for the presence of tadpoles and eggs. Observations on breeding behaviour and ecology were also made during the monsoon seasons in India (June–August/October–November) and Sri Lanka (October–December). Sampled individuals were euthanized in MS-222 (Tricaine methanesulfonate). A portion of the thigh muscle or liver tissue (adult) or tail tissue (tadpole) was taken in absolute ethanol and stored at a temperature of -20°C for molecular studies. Adult specimens were fixed in 4% formalin and preserved in 70% ethanol. Eggs and tadpoles were stored in 3.5% neutral buffered formalin. Type specimens of the new species are deposited in Department of Molecular Biology & Biotechnology, University of Peradeniya (DZ), Sri Lanka; neotypes are deposited in the Zoological Survey of India–Western Ghats Regional Centre (ZSI-WGRC), Calicut, India. Referred specimens are available at Systematics Lab, University of Delhi (SDBDU) and Department of Molecular Biology & Biotechnology, University of Peradeniya (DZ), for the Indian and Sri Lankan species, respectively. All authors were involved in sampling and/or collection of field data.

Molecular study. Genomic DNA was extracted from 67 tissue samples (Table 2) using Qiagen DNeasy blood and tissue kit (Qiagen, Valencia, CA, USA), following the manufacturer's protocol. A fragment of the mitochondrial 16S rRNA gene (≈ 540 bp) was PCR-amplified using the previously published primer set: 16Sar and 16Sbr (Simon *et al*. 1994). Purified PCR products were sequenced on both strands using BigDye Terminator v3.1 Cycle Sequencing Kit on ABI 3730 automated DNA sequencer (Applied Biosystems). DNA sequences were assembled and edited in ChromasPro v1.34 (Technelysium Pty Ltd.). The alignment was created using ClustalW in MEGA 6.0 (Tamura *et al.* 2013) and manually optimized. New sequences are deposited in the GenBank under accession numbers MG557906–MG557972 (Table 2). Uncorrected pairwise genetic distances were computed in PAUP* (Swofford 2002) and intra- and interspecific comparisons between the sequences were made for preliminary genetic delineation of species. SG (Indian material), GS and NW (Sri Lankan material) generated DNA sequences.

Maximum Likelihood (ML) and Bayesian analyses were performed to reconstruct phylogenetic relationships. Ambiguously aligned regions were excluded from the analyses. Trees were rooted using *Kaloula conjuncta*, *K. pulchra* and *K. mediolineata* as outgroups (Van Bocxlaer *et al*. 2006; Pyron & Wiens 2011; Peloso *et al*. 2016). Akaike Information Criteria were implemented in ModelTest 3.4 (Posada & Crandall 1998) to estimate the appropriate model of sequence evolution. Analyses were performed using the best-fit General time reversible model with a proportion of invariant sites and gamma-distributed rate variation among sites (GTR+I+G). Maximum Likelihood searches were executed in PAUP* (Swofford 2002), with all parameters estimated. Bayesian analysis was implemented in MrBayes (Ronquist & Huelsenbeck 2003) using uniform priors and four Metropolis-Coupled Markov Chain Monte Carlo (MCMCMC) chains run for 10 million generations. Trees were sampled every 1000 generations and based on a conservative approach samples from the first five million generations were discarded as burn-in (Huelsenbeck *et al*. 2001). Bayesian posterior probabilities (BPP) for the clades were estimated by summarizing the remaining trees with 50% majority rule in PAUP* (Swofford 2002). Maximum Likelihood clade support (BS) was also assessed by 10,000 rapid bootstrap replicates executed using RAxML 7.3.0 (Stamatakis *et al*. 2008) as implemented in raxmlGUI 1.1 (Silvestro & Michalak 2012). SG and SDB performed the molecular analyses.

TABLE 1. Collection localities for the genetically and/or morphologically studied *Uperodon* samples in the present study.

Locality	Altitude (metres)	Coordinates		Species
		Latitude (°N)	Longitude (°E)	
INDIA				
Tamil Nadu				
Coimbatore district				
Coimbatore	400	11.0825	77.0617	*U. systoma*[1]
Kanchipuram district				

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TABLE 1. (Continued)

Locality	Altitude (metres)	Coordinates		Species
		Latitude (°N)	Longitude (°E)	
Chengalpattu	60	12.6902	80.0258	*U. variegatus*[1]
Kunnapattu	20	12.6303	80.1521	*U. systoma*[1]
Mamallapuram	23	12.7412	80.2372	*U. taprobanicus*[1]
Nilgiris district				
Udhagamandalam (Ooty)	2215	11.4347	76.6692	*U. triangularis*[1]
Tirunelveli district				
Kakkachi	1266	08.5359	77.3952	*U. montanus*[1]
Sengaltheri	1000	08.5371	77.4544	*U. montanus*[2]
Kerala				
Idukki district				
Devikulam	1670	10.0626	77.1040	*U. montanus*[2]
Methooty	446	09.8423	78.8712	*U. anamalaiensis*[1]
Munnar	1410	10.0833	77.1333	*U. montanus*[1]
Upper Manalar, Periyar TR	1564	09.5748	77.3362	*U. montanus*[1]
Kollam district				
Pandimotta, Shendurney WLS	1221	08.8266	77.2122	*U. montanus*[1]
Palakkad district				
Kesavapara, Nelliyampathy	923	10.5243	76.6673	*U. montanus*[1]
Palakkad	86	10.8026	76.6361	*U. variegatus*[1]
Parambikulam TR	544	10.4453	76.8130	*U. anamalaiensis*[1]
Siruvani	880	10.9789	76.6154	*U. montanus*[2]
Thiruvananthapuram district				
Chathankod	140	08.6593	77.1494	*U. anamalaiensis*[1]
Kallar, Ponmudi	180	08.8490	77.1322	*U. anamalaiensis*[1]
Karamama	18	08.4780	76.9683	*U. variegatus*[2]
Makki	227	08.6723	77.1301	*U. anamalaiensis*[2]
Thrissur district				
Mannuthy	40	10.5236	76.2940	*U. taprobanicus*[2]
Meladoor	150	10.3167	76.3500	*U. variegatus*[2]
Wayanad district				
Kalpetta	950	11.6000	76.0833	*U. triangularis*[1], *U. taprobanicus*[2]
Kurichiyarmala	1210	11.6006	75.9664	*U. montanus* [1]
Mananthavady	1100	11.8333	76.0833	*U. triangularis*[1]
Pozhuthana	731	11.5861	76.0309	*U. triangularis*[1]
Settukunnu	823	11.6172	75.9913	*U. montanus*[1]
Suganthagiri	790	11.5407	76.0242	*U. triangularis*[1]
Sulthanbathery	908	11.6642	76.2653	*U. taprobanicus*[1]
Thirunelli	850	11.9106	76.0002	*U. montanus*[1]

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TABLE 1. (Continued)

Locality	Altitude (metres)	Coordinates		Species
		Latitude (°N)	Longitude (°E)	
Karnataka				
Bangalore Urban district				
Bangalore	900	13.064253	77.620233	*U. variegatus*[1], *U. taprobanicus*[1]
Bannerghatta	910	12.7215	77.5680	*U. systoma*[1]
Belgaum district				
Londa	660	15.4433	74.5200	*U. mormorata*[2]
Chikmagalur district				
Bygoor	1042	13.3111	75.6128	*U. mormorata*[1], *U. triangularis*[1]
Mudigere	900	13.1258	75.5979	*U. triangularis*[1]
Hassan district				
Kempholey	649	12.8566	75.6955	*U. anamalaiensis*[2]
Sakleshpur	948	12.9356	75.7697	*U. mormorata*[2*]
Sakleshpur	782	12.8680	75.7029	*U. anamalaiensis*[1]
Kodagu district				
Madikeri	1102	12.4528	75.7027	*U. triangularis*[1]
Wattakolli, Coorg	675	12.1266	75.7860	*U. triangularis*[1]
Shimoga district				
Kachigebailu, Shimoga	639	13.9835	75.1099	*U. mormorata*[1]
Uttara Kannada district				
Castle Rock	622	15.4019	74.3299	*U. mormorata*[1]
Dandeli	494	15.1669	74.6323	*U. mormorata*[1]
Maharashtra				
Kolhapur district				
Amba	590	16.9167	73.7833	*U. mormorata*[1]
Pune district				
Pune	585	18.5641	73.8256	*U. globulosus*[1]
Tamhini Ghat	600	18.5278	73.5744	*U. globulosus*[2]
Sindhudurg district				
Amboli	733	15.9691	73.9882	*U. mormorata*[1]
Goa				
North Goa district				
Anjuna	23	15.5742	73.7482	*U. mormorata*[1]
South Goa district				
Netravali	73	15.0891	74.2331	*U. mormorata*[1]
Gujarat				
Narmada district				
Samot	527	21.6481	73.8566	*U. mormorata*[2]

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TABLE 1. (Continued)

Locality	Altitude (metres)	Coordinates		Species
		Latitude (°N)	Longitude (°E)	
Andhra Pradesh				
West Godavari district				
Ellore (= Eluru)	22	16.7205	81.0903	*U. variegatus*[2*]
Koruturu, Srikakulam	170	17.4297	81.5397	*U. variegatus*[1]
Odisha				
Odisha (unspecified)	–	–	–	*U. systoma*[1], *U. taprobanicus*[1]
Ganjam district				
"Russelconda" (=Bhanjanagar)	83	19.9358	84.5824	*U. globulosus*[2*]
Khurdha district				
Bhubaneswar, Utkal University campus	43	20.3034	85.8401	*U. variegatus*[2]
SRI LANKA				
Ampara district				
Ampara	30	07.3004	81.6688	*U. rohani* **sp. nov.**[2]
Anuradhapura district				
Anuradhapura	90	08.3333	80.4000	*U. rohani* **sp. nov.**[2]
Mihintale	117	08.3549	80.5054	*U. rohani* **sp. nov.**[1]
Nochchiyagama	70	08.2667	80.2167	*U. rohani* **sp. nov.**[2]
Badulla district				
Badulla	830	06.9953	81.0456	*U. rohani* **sp. nov.**[2]
Mahiyanganaya	90	07.3167	80.9833	*U. rohani* **sp. nov.**[2]
Galle district				
Hiyare	125	06.0609	80.3240	*U. nagaoi*[1]
Kanneliya Forest Reserve	150	06.2500	80.3300	*U. nagaoi*[2*]
Hambantota district				
Bundala	8	06.1990	81.2108	*U. rohani* **sp. nov.**[1]
Palatupana, Kirinda	5	06.2667	81.4000	*U. rohani* **sp. nov.**[2]
Kandy district				
Kandy	530	07.2908	80.6369	*U. obscurus*[2]
Panwila	652	07.3726	80.7326	*U. obscurus*[1]
Peradeniya	480	07.2575	80.5963	*U. obscurus*[1]
Pussellawa	900	07.0833	80.5000	*U. obscurus*[2]
Udawatta Kele	465	07.3000	80.5833	*U. obscurus*[2]
Kegalle district				
Babilapitiya estate	120	07.2407	80.2140	*U. obscurus*[2]
Kilinochchi district				
Paranthan, Jaffna	6	09.4333	80.4000	*U. rohani* **sp. nov.**[2]
Kurunegala district				
Karawaddana	114	07.5115	80.4270	*U. rohani* **sp. nov.**[1], *U. taprobanicus*[1]

.....continued on the next page

TABLE 1. (Continued)

Locality	Altitude (metres)	Coordinates		Species
		Latitude (°N)	Longitude (°E)	
Kurunegala 1	230	07.4704	80.3801	*U. rohani* **sp. nov.**[2]
Kurunegala 2	400	07.4448	80.4080	*U. obscurus*[2]
Makandura	25	07.3245	79.9887	*U. rohani* **sp. nov.**[2]
Matale district				
Dambulla	188	07.8601	80.6746	*U. rohani* **sp. nov.**[1], *U. systoma*[1], *U. taprobanicus*[1]
Gammaduwa	1120	07.5885	80.7088	*U. obscurus*[2]
Sigiriya	175	07.9500	80.7500	*U. rohani* **sp. nov.**[2]
Nuwara Eliya district				
Bogawantalawa	1160	06.8250	80.6300	*U. obscurus*[2]
Diyagama estate, Agrapatana	1830	06.8289	80.7797	*U. palmatus*[2]
Laxapana	1220	06.8333	80.5333	*U. obscurus*[2]
Pattipola	1860	06.8500	80.8333	*U. palmatus*[2]
Nuwara-Eliya	1907	06.9717	80.7866	*U. palmatus*[1]
Morey estate	1424	06.7951	80.5240	*U. palmatus*[1]
Polonnaruwa district				
Polonnaruwa	55	07.9333	81.0000	*U. rohani* **sp. nov.**[2]
Ratnapura district				
Koskulana, Panapola, Sinharaja	460	06.4167	80.4500	*U. obscurus*[2]
Morningside, Rakwana	1060	06.4000	80.6333	*U. obscurus*[2]
Colonial locations				
"Base of Anamalai Hills, Coimbatore District", India				*U. anamalaiensis*[*]
"Bangalore (Mysore), S. India"				*U. variegatus*[2*]
"Ceylon" (=Sri Lanka)				*U. obscurus*[2*]
"Gadavery Valey" or "Gadavere", India				*U. variegatus*[2*]
"India orientali"				*U. systoma*[2*]
"Malabar", India				*U. montanus*[2], *U. triangularis*[2*]
"Newera Ellya", Sri Lanka				*U. palmatus*[2*]
"Nilgiri Hills" or "Nilgheries", India				*U. triangularis*[2*]
"Punduloya, Ceylon", Sri Lanka				*U. taprobanicus*[2*]
"the Carnatic", India				*U. variegatus*[*]
"Wynaad", India				*U. montanus*[2*]
"Yellagherry Hills", India				*U. variegatus*[2*]

[1] Genetically and morphologically studied collections from the present study

[2] Other morphologically studied collections and museum specimens

[*] Type locality

External morphology. The new collections were morphologically compared with all the available types and other museum specimens. In cases where the type specimens are either lost or destroyed, morphological identification of species was based on the original descriptions. Gonads were examined by a small lateral or ventral incision to determine the sex and maturity of specimens. Only mature (adult) animals were used for morphological studies. Measurements and associated terminologies follow Biju & Bossuyt (2006) and Biju *et al*. (2014a). The following measurements were taken to the nearest 0.1 mm using a digital vernier caliper or a binocular microscope with an ocular micrometre: SVL (snout-vent length), HW (head width, at the angle of the jaws), HL (head length, from the rear of the mandible to the tip of the snout), MN (distance from the rear of the mandible to the nostril), SL (snout length, from the tip of the snout to the anterior orbital border), EL (eye length, horizontal distance between the bony orbital borders), IUE (inter upper eyelid width, shortest distance between the upper eyelids), UEW (maximum upper eyelid width), IFE (internal front of the eyes, shortest distance between the anterior orbital borders), IBE (internal back of the eyes, shortest distance between the posterior orbital borders), FAL (forearm length, from the flexed elbow to the base of the outer palmar tubercle), HAL (hand length, from the base of the outer palmar tubercle to the tip of the third finger), SHL (shank length), TL (thigh length, from the vent to the knee), FOL (foot length, from the base of the inner metatarsal tubercle to the tip of the fourth toe), FD (disc width of finger), FW (width of finger, measured at the base of the disc), TD (disc width of toe), TW (width of toe, measured at the base of the disc), digit number is represented by roman numerals I–V. All measurements provided in the taxonomy section are in millimetres. Webbing is described as by Biju *et al*. (2014b). Measurements and photographs were taken for the right side of the specimen, except when a character was damaged, in which case the measurement was taken on the left side. SDB and SG performed all the morphological studies.

Principal Component Analyses (PCA) were performed on 17 morphometric variables from adult male and female specimens (separately) of *Uperodon variegatus* and the new species, using the software Statistica v7.1 (StatSoftInc). PCA factor scores for Principal Components (PC) with eigenvalues >1.0 were reported. Factor scores of the first two components were visualized on scatterplots to assess the degree of morphological differentiation between males and females of the two species.

TABLE 2. Samples used for the molecular study.

Species	Collection Locality	Voucher No./Source	Accession No.
Present study			
Uperodon anamalaiensis	India: Karnataka: Sakleshpur	ZSI/WGRC/V/A/957	MG557906
Uperodon anamalaiensis	India: Kerala: Chathankod	SDBDU 2013.2302	MG557907
Uperodon anamalaiensis	India: Kerala: Chathankod	SDBDU 2002.929	MG557908
Uperodon anamalaiensis	India: Kerala: Methooty	SDBDU 2012.1994	MG557909
Uperodon anamalaiensis	India: Kerala: Methooty	SDBDU 2012.1995	MG557910
Uperodon anamalaiensis	India: Kerala: Parambikulam TR	SDBDU 2011.548	MG557911
Uperodon globulosus	India: Maharashtra: Pune	SDBDU 2014.2672	MG557912
Uperodon globulosus	India: Maharashtra: Pune	SDBDU 2014.2682	MG557913
Uperodon globulosus	India: Maharashtra: Pune	SDBDU 2014.2685	MG557914
Uperodon montanus	India: Kerala: Kesavapara	SDBDU 2011.1197	MG557915
Uperodon montanus	India: Kerala: Kurichiyarmala	SDBDU 2006.4877	MG557916
Uperodon montanus	India: Kerala: Munnar	SDBDU 2005.30	MG557917
Uperodon montanus	India: Kerala: Pandimotta	SDBDU 2011.905	MG557918
Uperodon montanus	India: Kerala: Kurichiyarmala	SDBDU 2006.4846	MG557919
Uperodon montanus	India: Kerala: Settukunnu	SDBDU 2011.849	MG557920
Uperodon montanus	India: Kerala: Thirunelli	SDBDU 2011.228	MG557921
Uperodon montanus	India: Tamil Nadu: Kakkachi	SDBDU 2003.40116	MG557922
Uperodon montanus	India: Tamil Nadu: Kakkachi	SDBDU 2002.1925	MG557923
Uperodon montanus	India: Kerala: Upper Manalar	SDBDU 2015.3001	MG557924

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TABLE 2. (Continued)

Species	Collection Locality	Voucher No./Source	Accession No.
Uperodon mormorata	India: Goa: Anjuna	SDBDU 2015.3082	MG557925
Uperodon mormorata	India: Karnataka: Bygoor	SDBDU 2011.507	MG557926
Uperodon mormorata	India: Karnataka: Castle Rock	SDBDU 2011.835	MG557927
Uperodon mormorata	India: Karnataka: Dandeli	SDBDU 2011.1331	MG557928
Uperodon mormorata	India: Karnataka: Shimoga	SDBDU 2012.43	MG557929
Uperodon mormorata	India: Maharashtra: Amba	SDBDU 2005.1763	MG557930
Uperodon mormorata	India: Maharashtra: Amba	SDBDU 2005.2520	MG557931
Uperodon mormorata	India: Maharashtra: Amboli	SDBDU 2004.4513	MG557932
Uperodon mormorata	India: Maharashtra: Amboli	SDBDU 2005.4757	MG557933
Uperodon mormorata	India: Maharashtra: Amboli	SDBDU 2012.2127	MG557934
Uperodon nagaoi	Sri Lanka: Southern: Hiyare	DZ 1356	MG557935
Uperodon nagaoi	Sri Lanka: Southern: Hiyare	DZ 1367	MG557936
Uperodon obscurus	Sri Lanka: Central: Peradeniya	DZ 1364	MG557937
Uperodon obscurus	Sri Lanka: Central: Peradeniya	DZ 1365	MG557938
Uperodon obscurus	Sri Lanka: Central: Panwila	DZ 1408	MG557939
Uperodon palmatus	Sri Lanka: Central: Moray estate	DZ 1275	MG557940
Uperodon palmatus	Sri Lanka: Central: Nuwara-Eliya	DZ 1331	MG557941
Uperodon palmatus	Sri Lanka: Central: Nuwara-Eliya	DZ 1371	MG557942
Uperodon rohani **sp. nov.**	Sri Lanka: North Western: Karawaddana	DZ 1112	MG557943
Uperodon rohani **sp. nov.**	Sri Lanka: Central: Dambulla	DZ 1129	MG557944
Uperodon rohani **sp. nov.**	Sri Lanka: Central: Dambulla	DZ 1130	MG557945
Uperodon rohani **sp. nov.**	Sri Lanka: Southern: Bundala NP	DZ 1336	MG557946
Uperodon rohani **sp. nov.**	Sri Lanka: North Central: Mihintale	DZ 1448	MG557947
Uperodon rohani **sp. nov.**	Sri Lanka: North Central: Mihintale	DZ 1449	MG557948
Uperodon systoma	India: Tamil Nadu: Kunnapattu	SDBDU 2005.4723	MG557949
Uperodon systoma	India: Tamil Nadu: Coimbatore	SDBDU 2005.4750	MG557950
Uperodon systoma	India: Karnataka: Bannerghatta	SDBDU 2014.2522	MG557951
Uperodon systoma	India: Odisha	SDBDU 2002.1151	MG557952
Uperodon systoma	Sri Lanka: Central: Dambulla	DZ 1128	MG557953
Uperodon triangularis	India: Karnataka: Bygoor	SDBDU 2010.332	MG557954
Uperodon triangularis	India: Karnataka: Bygoor	SDBDU 2011.503	MG557955
Uperodon triangularis	India: Karnataka: Madikeri	SDBDU 2012.2220	MG557956
Uperodon triangularis	India: Karnataka: Madikeri	SDBDU 2012.2221	MG557957
Uperodon triangularis	India: Karnataka: Mudigere	ZSI/WGRC/V/A/959	MG557958
Uperodon triangularis	India: Kerala: Kalpetta	SDBDU 2012.2038	MG557959
Uperodon triangularis	India: Kerala: Mananthavady	SDBDU 2003.40240	MG557960
Uperodon triangularis	India: Kerala: Pozhuthana	SDBDU 2014.2627	MG557961
Uperodon triangularis	India: Kerala: Suganthagiri	SDBDU 2014.2595	MG557962
Uperodon variegatus	India: Andhra Pradesh: Srikakulam	SDBDU 2007.4994	MG557963
Uperodon variegatus	India: Karnataka: Bangalore	SDBDU 2002.524	MG557964
Uperodon variegatus	India: Tamil Nadu: Chengalpattu	SDBDU 2005.4727	MG557965
Uperodon taprobanicus	India: Karnataka: Bangalore	SDBDU 2014.2567	MG557966

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TABLE 2. (Continued)

Species	Collection Locality	Voucher No./Source	Accession No.
Uperodon taprobanicus	India: Kerala: Sulthanbathery	SDBDU 2005.4732A	MG557967
Uperodon taprobanicus	India: Odisha	SDBDU 2002.3107	MG557968
Uperodon taprobanicus	India: Tamil Nadu: Mamallapuram	SDBDU 2010.011	MG557969
Uperodon taprobanicus	Sri Lanka	DZ 1157	MG557970
Uperodon taprobanicus	Sri Lanka: Central: Dambulla	DZ 1133	MG557971
Uperodon taprobanicus	Sri Lanka: North Western: Karawaddana	DZ 1110	MG557972
GenBank			
Uperodon mormorata (as *U. montanus*)	–	–	AB612000[1]
Uperodon palmatus (as *U. obscurus*)	Sri Lanka	MM 5980	KC180006[2]
Uperodon systoma	Indian subcontinent	VUB1151	EF017960[3]
Uperodon variegatus	India	VUB1342	EF017963[3]
Uperodon taprobanicus	Sri Lanka	VUB0102	AF249057[4]
Uperodon taprobanicus	Sri Lanka	KUHE: 37252	AB634691[5]
Outgroups			
Kaloula pulchra	China	NMNS 3208	KC822614[6]
Kaloula mediolineata	Thailand: Wang Nam Kieow: Sakaerat	KU 328280	KC822509[6]
Kaloula conjuncta	Philippines: Luzon Island: Palola	ACD 769	KC822537[6]

[1]Kurabayashi *et al*. 2011; [2]de Sá *et al*. 2012; [3]Van Bocxlaer *et al*. 2006; [4]Bossuyt & Milincovitch 2000; [5]Matsui *et al*. 2011; [6]Blackburn *et al*. 2013

Osteology. Adult specimens (N = 3) kept in 10% neutral buffered formalin were cleared and stained using Alcian blue and Alizarin Red following Hanken & Wassersug (1981) and Taylor & Van Dyke (1985). Stained specimens were scored for bone and cartilage within two days of completion of the procedure. Chondrocranial and osteological terminologies follow Cannatella (1999) and Duellman & Trueb (1986), respectively. For comparisons, the term "vomer" (Duellman & Trueb 1986) is used instead of "prevomer" (Trueb 1993), following previous osteological literature on microhylids (e.g., Parker 1934; Ramaswami 1936; Peloso *et al*. 2016). Photographs were taken either using a digital camera or captured with the aid of a QImaging camera mounted on Nikon SMZ 1500 stereomicroscope. GS performed the osteological study.

Larval study. The identity of the tadpoles was confirmed genetically using a 16S rRNA gene fragment. Tadpoles were staged according to Gosner (1960). External morphology of the larvae was described following the terminologies of Altig & McDiarmid (1999a) and Grillitsch *et al*. (1993). Tadpoles were measured to the nearest 0.01 mm using a digital vernier caliper. The following measurements (Altig & McDiarmid 1999a; Bowatte & Meegaskumbura 2012) were taken for each tadpole stage: maximum height of body (bh), maximum width of body (bw), maximum diameter of eye (ed), internarial distance (nn), naro-pupular distance (np), interpupular distance (pp), rostro-narial distance (rn), distance from tip of snout to opening of spiracle (ss), distance from tip of snout to insertion of upper tail fin (su), snout-vent length (svl), total length (tl), distance from vent to tip of tail (vt), maximum height of tail (ht), tail-muscle height (tmh) and tail-muscle width (tmw). SG performed DNA barcoding and GS described the larval morphology.

Bioacoustics. Male calls were recorded for three species using a Marantz PMD620 solid-state digital recorder (44.1 kHz sampling rate, 16-bit resolution) and a Sennheiser ME 66 unidirectional microphone. The gain level of the recorder was set at the beginning of each recording and the microphone was positioned at about 30–50 cm from the calling individual. One specimen from each of the recorded populations was sampled for morphological and genetic identification. Dry and wet bulb air temperatures were noted at each recording site. Five temporal properties (call duration, call rise time, call fall time, number of pulses per call and pulse rate) and one spectral

property (dominant frequency) for a single call of each species were measured using Raven Pro 1.4 (Charif *et al*. 2010). Spectrograms were prepared for graphical representation of the call structure. Terminology and call property definitions follow Bee *et al*. (2013). SG and SDB performed the acoustic study.

Museum and other abbreviations. For museums and frequently used terms, abbreviations are as follows: SDBDU (Systematics Lab, University of Delhi, India), DZ (Department of Molecular Biology & Biotechnology, University of Peradeniya, Sri Lanka), NHM (Natural History Museum, London, United Kingdom) formerly BMNH (British Museum (Natural History), London, United Kingdom), ZSIC (Zoological Survey of India, Kolkata, India), ZSI/WGRC (Zoological Survey of India–Western Ghats Regional Centre, formerly Zoological Survey of India–Western Ghats Field Research Station, Calicut, India), BNHS (Bombay Natural History Society, Mumbai, India), WHT (Wildlife Heritage Trust of Sri Lanka, Colombo), HT (Holotype), NT (Neotype), PT (Paratype), LT (Lectotype), PLT (Paralectotype), ST (Syntype), TT (Topotype), NP (National Park), WLS (Wildlife Sanctuary), TR (Tiger Reserve), SDB (SD Biju), SG (Sonali Garg), MM (Madhava Meegaskumbura), GS (Gayani Senevirathne) and NW (Nayana Wijayathilaka).

Results

DNA analyses. Genetic differentiation among all the *Uperodon* species was assessed based on mitochondrial 16S rRNA gene. The resultant alignment comprised of 511 bp (including gaps) of which 501 unambiguously aligned positions with 108 variable sites and 97 parsimony-informative sites were used for phylogenetic analyses. The ML and Bayesian analyses recovered 12 major lineages with significant support (BPP 0.99–1.0, BS 80–100%) (Fig. 1). These corresponded to 11 previously established *Uperodon* species (except *U. minor*) and one additional divergent lineage. The candidate species from Sri Lanka was delineated based on considerable genetic distance of 2.9% (range 2.4–3.5%) from its closest relative *U. variegatus* known from India (Table 3). This new lineage was highly supported (BPP 1.0, BS 99%). Interspecific uncorrected genetic divergence between the previously known *Uperodon* species ranged from 2.4–9.1% (Table 3), which are consistent or slightly lower than the species-level distances observed in other anuran groups from the region (e.g., Biju *et al*. 2014a; Biju *et al*. 2014b; Garg & Biju 2016; Wijayathilaka *et al*. 2016; Garg *et al*. 2017; Garg & Biju 2017). The observed intraspecific distances reached a maximum of 2.2% and the following major sub-lineages (>1%) were observed: (1) *Uperodon triangularis* comprised of two sub-lineages, one identified as the typical form from the 'Malabar' region of Kerala, and the second with populations from Karnataka that most likely correspond to the subspecies *Ramanella triangularis rufeventris* (for detailed discussion see the taxonomic account for *Uperodon triangularis*); (2) *Uperodon mormorata* also showed two sub-lineages that correspond to populations from two different states, Karnataka (typical) and Maharashtra, respectively; (3) *Uperodon variegatus* populations from the Eastern Ghats (Andhra Pradesh and Tamil Nadu) and Western Ghats (Karnataka and Kerala) formed separate sub-lineages; (4) *Uperodon systoma* sample from Bannerghata (Karnataka) showed a divergence of 2.2% from the other populations; (5) *Uperodon taprobanicus* population from the Eastern Ghats (Odisha) differed genetically from all other Western Ghats and Sri Lankan populations by 1.0–1.2%; and (6) the candidate species also showed intraspecific divergence of up to 1.4% (see taxonomic description of the new species for discussion). In addition, *U. montanus* populations found north and south of the Palghat gap were divergent by up to 1.2%. For *U. anamalaiensis*, a single population from 'Sakleshpur' in Karnataka that is likely to correspond with *U. minor* showed shallow divergence (0.8%) from populations found south of the Palghat gap in Kerala. For intra- and interspecific pairwise comparisons among all the members see Table 3, and for detailed taxonomic notes and implications see the respective species accounts in the 'Taxonomy' section.

Taxonomy

Detailed morphological comparison with available types, museum specimens and original descriptions, shows that the newly identified lineage from Sri Lanka represents a distinct species. This species is formally described as *Uperodon rohani* **sp. nov.** based on molecular and morphological evidence. In anticipation of this outcome, we refer to the species under its new name in the following sections, prior to its formal taxonomic description, which is provided subsequently.

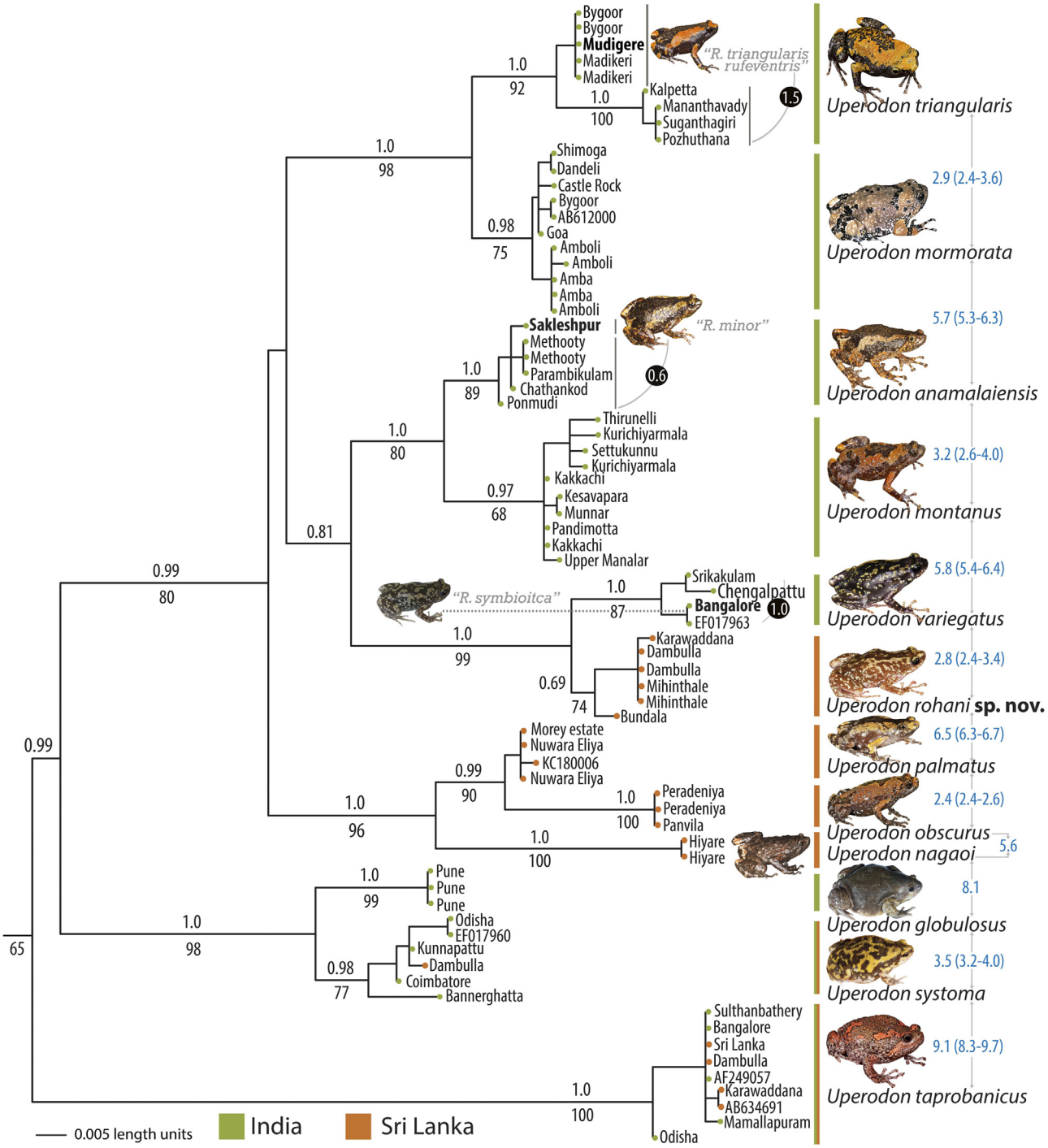

FIGURE 1. Maximum Likelihood phylogram based on 511 bp of mitochondrial 16S rRNA gene sequences from 73 individuals representing all known members of the genus *Uperodon*. Three samples representing taxon under synonymy are shown in quotation marks. Outgroup not shown for graphical purposes. Bayesian Posterior Probabilities and bootstrap values of >50 are shown above and below the branches, respectively. Values towards the species labels represent mean uncorrected genetic distances between the species with range values in parentheses.

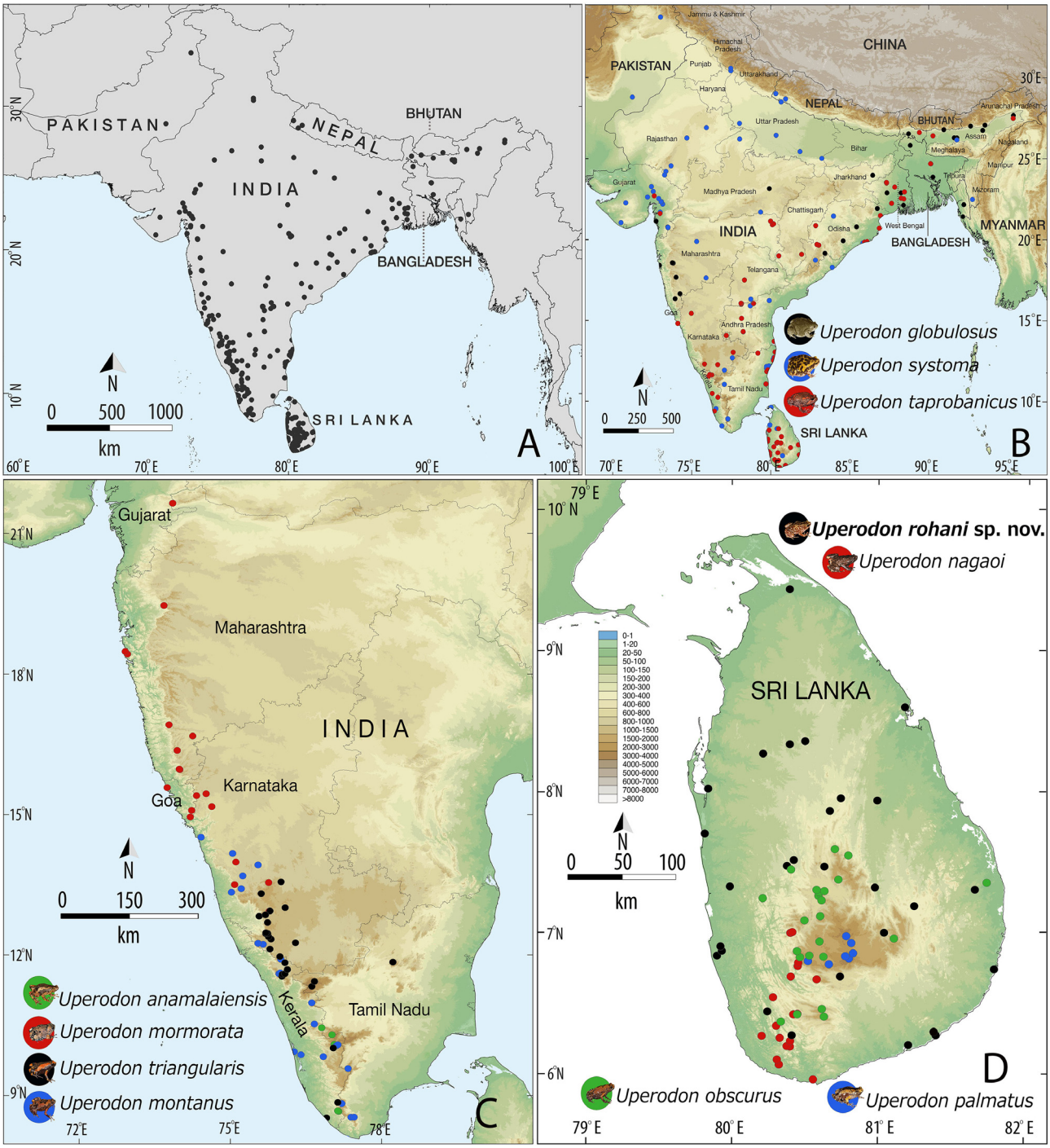

FIGURE 2. A. Geographic distribution of the genus *Uperodon* in Bangladesh, Bhutan, India, Nepal, Pakistan and Sri Lanka; **B.** Distribution of *Uperodon globulosus*, *U. systoma* and *U. taprobanicus*; **C.** Distribution of four endemic *Uperodon* species of the Western Ghats (excluding the widely distributed Indian member *U. variegatus*, shown in Fig. 12A); **D.** Distribution of four endemic *Uperdodon* species of Sri Lanka. Details of localities reported in the present study are provided in Table 1. Records from literature are listed in supplementary Table S1 and indicated here based on approximate coordinates.

Order Anura
Family Microhylidae
Subfamily Microhylinae
Genus *Uperodon*

Type species *Uperodon systoma*

Uperodon Duméril and Bibron, 1841. *Erpétologie Générale ou Histoire Naturelle Complète des Reptiles*. Volume 8. Paris: Librarie Enclyclopedique de Roret. **Type species.** *Engystoma marmoratum* Guérin-Méneville, 1838 (= *Rana systoma* Schneider, 1799) by monotypy.

Hyperodon Agassiz, 1846. *Nomenclator Zoologicus Continens Nomina Systematica Generum Animalium tam Viventium quam Fossilium*. Fasicle 12 (Indicem Universalem). Soloduri: Jent et Gassmann.

Cacopus Günther, 1864 "1863". *The Reptiles of British India*. London: Ray Society by R. Hardwicke.

Ramanella Rao and Ramanna, 1925. On a new genus of the family Engystomatidae. *Proceedings of the Zoological Society of London*, 1925: 587–597.

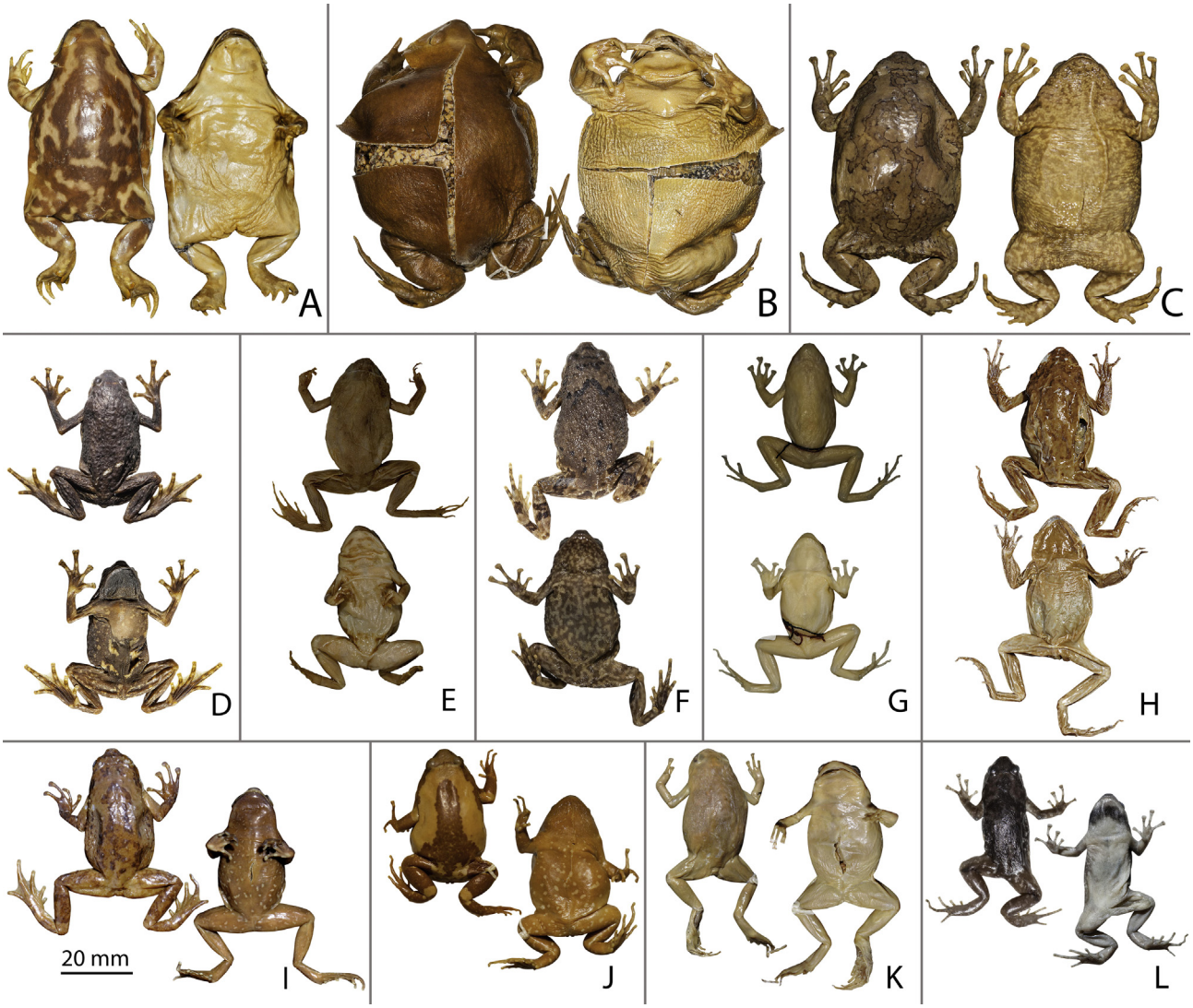

FIGURE 3. Preserved type specimens of *Uperodon* species in dorsal and ventral view. **A.** *Uperodon systoma*, Syntype, ZMB 3551 (female); **B.** *Uperodon globulosus*, Syntype, NHM 62.12.29.4 (ex. BMNH 1947.2.10.97) (female); **C.** *Kaloula pulchra taprobanica*, Holotype, NHM 1905.3.25.138 (ex. BMNH 1947.2.10.62) (female); **D.** *Ramanella anamalaiensis*, Neotype, ZSI/WGRC/V/A/956 (male); **E.** *Hylaedactylus montanus*, Holotype, NHM 72.4.17.212 (ex. BMNH 1947.2.11.19) (female); **F.** *Ramanella mormorata*, Neotype, ZSI/WGRC/V/A/958, (female); **G.** *Ramanella nagaoi*, Holotype, WHT 2826 (male); **H.** *Callula obscura*, Holotype, NHM 58.11.28.42 (ex. BMNH 1947.2.11.20) (female); **I.** *Ramanella palmata*, Holotype, NHM 90.11.8.62 (ex. BMNH 1947.2.11.21); **J.** *Callula triangularis*, Lectotype, NHM 74.4.29.897 (ex. BMNH 1947.2.11.15) (male); **K.** *Hylaedactylus carnaticus*, Lectotype, ZSI 2761 (female); **L.** *Uperodon rohani* **sp. nov.**, Holotype, DZ 1449 (male). (Images: SD Biju and Sonali Garg).

Common name. Globular Frogs (Frank & Ramus 1995)

Diagnosis. Small to large-sized frogs (male SVL 21–56 mm, female SVL 28–72 mm) with globular appearance; head wider than long; pupil oval; skin shagreened to glandular; tympanum hidden; tongue emarginate posteriorly, with or without lingual papillae; fingers free, dermal fringes present, tips of fingers with truncate discs (except in *Uperodon globulosus* and *U. systoma*: rounded, slightly enlarged without discs), without dorsoterminal grooves; webbing between fingers absent; webbing between toes present or absent; prevomers divided or undivided, clavicles absent, and procoracoids rudimentary (Parker 1934; Ramaswami 1936).

Distribution. Genus *Uperodon* is restricted to the Indian subcontinent. It is known to occur widely in India and Sri Lanka, with some reports from adjacent countries, namely, Bangladesh, Bhutan, Nepal and Pakistan. The distribution of the genus extends from 05.9°–33.7° N and 70.5°–95.4° E (Fig. 2). Of the 12 nominal species, eight are restricted to the Western Ghats–Sri Lanka biodiversity hotspot region, with one Indian member (*U. variegatus*) more widely distributed outside the Western Ghats, while three species occur across the entire known range of the genus.

Uperodon systoma (Schneider, 1799)

Marbled Globular Frog

(Figs. 1, 2A–B, 3A, 4A–F, 5A; Tables 1–4)

Original name and description. *Rana systoma* Schneider, 1799. *Historia amphibiorum naturalis et literarariae. Fasciculus primus. Continens Ranas, Calamitas, Bufones, Salamandras et Hydros in genera et species descriptos notisque suis distinctos.* Jena: Friederici Frommanni, 144–146. **Syntype.** ZMB 3551, original description mentions two specimens, one likely to be lost. **Type locality.** "India orientali", India. **Current status of specific name.** Valid name, as *Uperodon systoma* (Schneider, 1799). **Synonyms.** *Engystoma marmoratum* Cuvier, 1829 (Duméril & Bibron 1841; Peters 1864 "1863") and *Systoma leschenaultii* Tschudi, 1838 (Duméril & Bibron 1841).

Note on doubtful synonym. *Pachybatrachus Petersii* Keferstein, 1868 described from "Neu-Süd-Wales" Australia was considered as a synonym of *Uperodon systoma* (Schneider 1799) by Boulenger (1882) and followed by Parker (1934). However, if this taxon was indeed described from Australia (although it might be erroneous according to Frost 2017) it cannot be homogenous with *Uperodon systoma* or any other member of the genus *Uperodon*, which is clearly restricted to South Asia. Although, we could not examine the type of *Pachybatrachus petersii* Keferstein, 1868, its synonymy with *Uperodon systoma* is considered doubtful.

Comments. The original description of *Rana systoma* (Schneider 1799) mentions two specimens (= syntypes) from "India orientali" but the description is likely to have been based on a single specimen (Bauer 1998). Currently a single specimen is available in the ZMB (Berlin) collection (Peters 1864 "1863"; Bauer 1998). We examined the available syntype (an adult female) and found it to clearly match the original description of the species. However, since at least two specimens were originally catalogued for this taxon and the original description was brief, we herein provide a detailed description of the available type specimen, ZMB 3551 (an adult female), as a reference of this species for future taxonomic works.

Comparison. *Uperodon systoma* differs from all other known members of the genus, except *U. globulosus* and *U. taprobanicus*, by its larger snout-vent size, male SVL 51–56 mm, female SVL 47–64 mm (vs. smaller, male SVL 21–40 mm, female SVL 28–43 mm); finger and toe tips rounded, without discs (vs. finger tips enlarged in to discs, except in *U. globulosus*); and presence of two dermal projections on the neopalatinal ridges on posterior side of each choana, widely separated from the vomerine odontophores (vs. prominent dermal projections on the neopalatinal ridges on posterior side of each choana, narrowly separated from the vomerine odontophores in *U. globulosus*; indistinct or weakly to well-developed neopalatinal ridges on posterior side of each choana, fused with the vomerine odontophores in all other species) (Fig. 5A). *Uperodon systoma* differs from *U. globulosus* and *U. taprobanicus* in having divided prevomers, as in the rest of *Uperodon* species (vs. undivided prevomers in *U. globulosus* and *U. taprobanicus*) (Parker 1934); and by its dorsum being light or dark brown with prominent yellow markings (vs. light brown to greyish-brown without any prominent markings in *U. globulosus*; light to dark grey with prominent red or reddish-orange blotches in *U. taprobanicus*). Specifically it also differs from *U. globulosus* by its snout length nearly equal to eye diameter, male EL/SL ratio 95.3–104%, $N = 4$, female EL/SL ratio 98–106%, $N = 1$ (vs. snout nearly twice as long as diameter of eye, male EL/SL ratio 40.5–50.0%, $N = 3$, female EL/SL ratio 44.4–54.8%, $N = 1$) (Table 4).

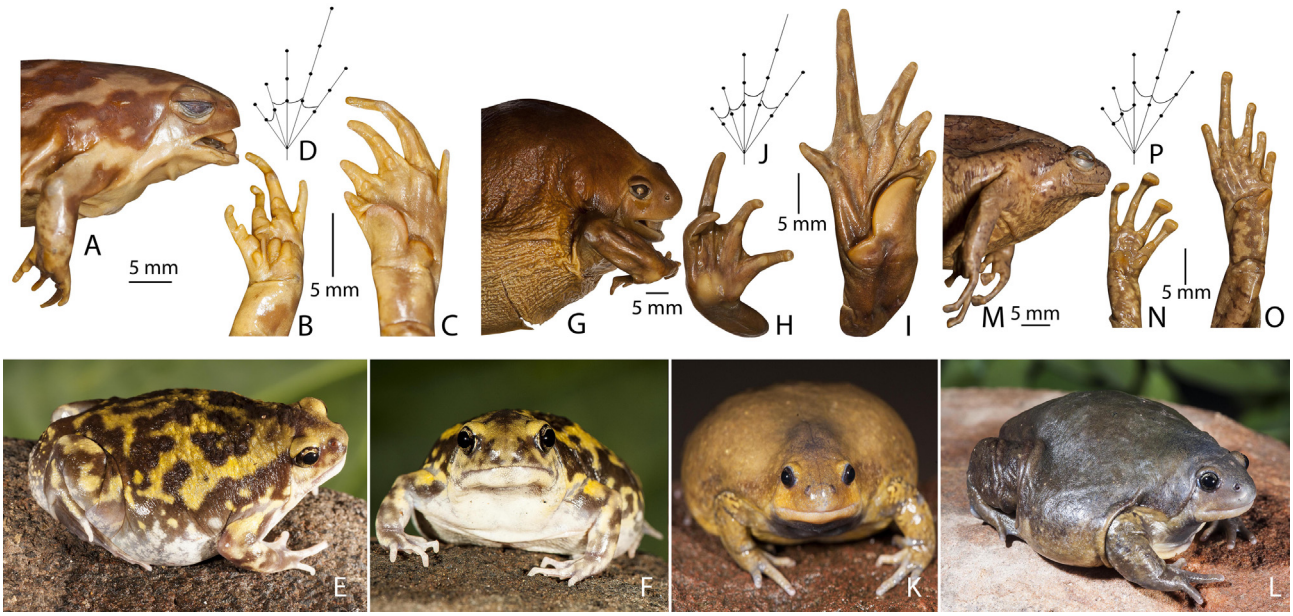

FIGURE 4. A–D. *Uperodon systoma* (Syntype, ZMB 3551) in preservation: **A.** lateral view of head; **B.** ventral view of hand; **C.** ventral view of foot; **D.** schematic illustration of foot webbing; **E–F.** *Uperodon systoma* (SDBDU 2005.2732, female) in life: **E.** dorsolateral view; **F.** anterior view; **G–J.** *Uperodon globulosus* (Syntype, NHM 62.12.29.4 ex. BMNH 1947.2.10.97) in preservation: **G.** lateral view of head; **H.** ventral view of hand; **I.** ventral view of foot; **J.** schematic illustration of foot webbing; **K–L.** *Uperodon globulosus* (SDBDU 2014.2672, male) in life: **K.** anterior view (not preserved); **L.** dorsolateral view; **M–P.** *Uperodon taprobanicus* (Holotype, NHM 1905.3.25.138 ex. BMNH 1947.2.10.62) in preservation: **M.** lateral view of head; **N.** ventral view of hand; **O.** ventral view of foot; **P.** schematic illustration of foot webbing. (Images: SD Biju).

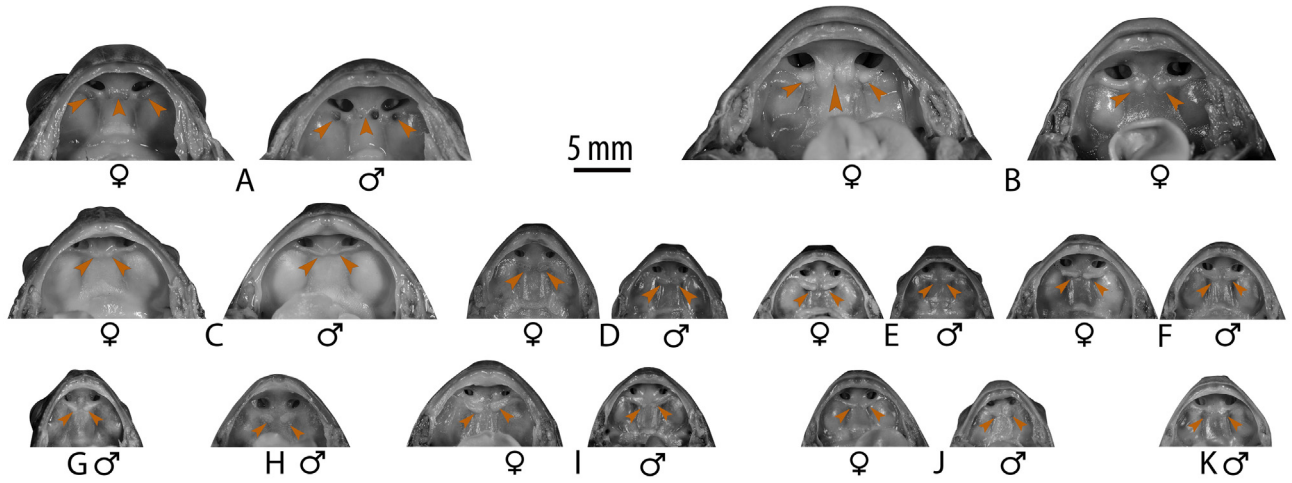

FIGURE 5. Ventral surface of the palate in *Uperodon* species showing vomerine odontophores separated or fused with dermal projections and/or neopalatinal ridges on posterior sides of the choanae (indicated with arrows). **A.** *Uperodon systoma*, SDBDU 2005.2787 (female) and SDBDU 2005.2806 (male); **B.** *Uperodon globulosus*, SDBDU 2014.2673 (female) and SDBDU 2005.4762 (female); **C.** *Uperodon taprobanicus*, SDBDU 2007.6364 (female) and SDBDU 2005.4732A (male); **D.** *Uperodon anamalaiensis*, SDBDU 2013.2302 (female) and SDBDU 2002.3050 (male); **E.** *Uperodon montanus*, SDBDU 2002.24B (female) and SDBDU 2003.40115 (male); **F.** *Uperodon mormorata*, SDBDU 2011.507 (male) and SDBDU 2012.43 (male); **G.** *Uperodon obscurus*, DZ 1366 (male); **H.** *Uperodon palmatus*, DZ 1331 (male); **I.** *Uperodon triangularis*, SDBDU 2007.6400 (female) and ZSI/WGRC/V/A/959 (male); **J.** *Uperodon variegatus*, SDBDU 2005.4726 (female) and SDBDU 2005.4727 (male); **K.** *Uperodon rohani* **sp. nov.**, DZ 1521 (male). (Images: SD Biju).

Genetic divergence. For 16S mitochondrial gene sequences, the sampled populations of *Uperodon systoma* showed an average intraspecific distance of 0.9% (range 0–2.2%, $N = 6$). The sample from Bannerghatta (Karnataka) showed considerable divergence of up to 2.2% from the typical populations in Tamil Nadu, excluding

which, *U. systoma* showed an average intraspecific distance of 0.5% (range 0–0.8%, *N* = 5). Genetically, *U. systoma* is closely related to *U. globulosus*, from which it was found to differ by an average uncorrected genetic distance of 3.5% (range 3.2–4.0%, *N* = 18). For interspecific genetic distances with all other members of the genus, see Table 3.

Description of syntype, ZMB 3551 (measurements in mm) (Figs. 3A, 4A–D). Large-sized (SVL 49.7), globular and robust adult female; head small (HW 11.7, HL 7.9, IFE 6.6, IBE 12.4), less than one-sixth (15.9%) of body length, wider than long (HW/HL ratio 1.5); snout semi-circular to nearly rounded in dorsal and ventral view, rounded in lateral view, its length (SL 4.8) nearly equal to horizontal diameter of eye (EL 4.9); loreal region obtuse with rounded canthus rostralis; interorbital space (IUE 4.8) nearly twice as wide as upper eyelid width (UEW 2.6); nostril oval without lateral flap of skin, nearly equidistant to tip of the snout (NS 1.6) and the eye (EN 1.4); tympanum not visible externally, distinct supratympanic fold extending from posterior corner of upper eyelid near to insertion of forelimb at axilla; eye diameter (EL 4.9); vomerine odontophores present on the palate, prominent, without teeth; presence of two prominent dermal projections on the neopalatinal ridges on posterior side of each choana, widely separated from the vomerine odontophores; tongue moderately large, rounded, shallowly emarginated. Forelimbs moderately short and strong; forearm (FAL 13.2) shorter than hand length (HAL 23.8); finger length formula I<IV<II<III (FI 3.5, FII 5.1, FIII 6.7, FIV 3.6); tips of all fingers rounded, without discs; webbing absent between fingers; subarticular tubercles weakly-developed, oval, all present; two well-developed palmar tubercles (inner, oval, 1.3 mm long; outer, bilobed, 1.7 mm long). Hind limbs relatively short and strong, thigh length (TL 18.3) longer than shank (SHL 15.4) and shorter than foot (FOL 18.6); tips of all toes rounded, without discs; webbing present, small: I2–2II1$^{3}/_{4}$–3III3–4–IV4–2$^{3}/_{4}$V; well-developed dermal fringes present on all toes; subarticular tubercles weakly-developed, oval, all present; two shovel-shaped metatarsal tubercles (inner, 2.3 mm long; outer, 4.3 mm long).

Skin of dorsum, sides of head, and dorsal parts of forelimb, thigh, tibia and tarsus, shagreened (Fig. 3A); posterior parts of thigh, especially cloacal region, granular. Ventral surfaces shagreened and wrinkled (Fig. 3A).

Colouration. *In preservation* (ZMB 3551): Dorsum brown with prominent light grey elongate blotches, flanks lighter in colour than dorsum; forelimbs, dorsal surfaces of thigh, shank and foot, light creamish-brown with darker brown markings; chest, belly, and ventral surfaces of thigh, tibia and foot grey with creamish-brown (Figs. 3A, 4A–D). *In life* (SDBDU 2005.2732): Dorsum brown with prominent yellow blotches, dorsal surface of head yellowish brown, upper eyelids yellow; lateral surfaces of head and flank lighter in colour compared to dorsum; forelimbs, dorsal surfaces of thigh, shank and foot, light brown with yellow blotches; throat, chest, and belly, greyish-white without any marking, ventral surfaces of forelimb, thigh, tibia and foot, white (Figs. 4E–F).

Variations. Morphometric measurements for six specimens are given in Table 4. SDBDU 2005.2806: subarticular tubercles on fingers weakly-developed, throat greyish-white with light brown marbling; SDBDU 2005.2787: Skin of dorsum and limbs coarsely glandular, posterior parts of thigh especially the cloacal region prominently glandular, and throat coarsely granular.

Secondary sexual characters. Male (SDBDU 2005.2787): vocal sac externally visible on the lower jaw; female (SDBDU 2005.2806): ova white, pigmented on pole (diameter 0.9–1.3 mm, *N* = 10).

Geographical distribution and habitat. *Uperodon systoma* is widely distributed in India and Sri Lanka, and also reported from adjoining regions in Nepal and Pakistan (Fig. 2B). In India, it has been reported from the states of Tamil Nadu, Kerala, Karnataka, Maharashtra, Gujarat, Andhra Pradesh, Telangana, Odisha, Madhya Pradesh, Chhattisgarh, Rajasthan, Uttar Pradesh, Himachal Pradesh, West Bengal, Assam and Mizoram. In Sri Lanka, the species is known from Central, Eastern, Northern, North Western, Sabaragamuwa, Southern and Uva Provinces. For detailed list of localities and references thereto see Supplementary Table S1. In the present study, this species was found in Tamil Nadu (Coimbatore and Kunnapattu), Karnataka (Bannerghatta) and Odisha in India, and Dambulla (Central Province) in Sri Lanka (Table 1). Individuals were collected from soil surface close to temporary pools or dry burrows in agricultural fields. See 'Natural history and breeding' observations in the respective section, after the species accounts.

***Uperodon globulosus* (Günther, 1864 "1863")**
Indian Globular Frog (Frank & Ramus 1995)
(Figs. 1, 2A–B, 3B, 4G–L, 5B; Tables 1–4)

Original name and description. *Cacopus globulosus* Günther, 1864 "1863". *The Reptiles of British India.* London: Ray Society by R. Hardwicke, p. 416. **Syntypes.** NHM 62.12.29.4 (ex. BMNH 1947.2.10.97) and NHM 62.12.29.3 (ex. BMNH 1947.2.10.77). **Type locality.** "Russelconda (Madras Presidency)", India. **Current status of specific name.** Valid name, as *Uperodon globulosus* (Günther, 1864 "1863").

Comments. The original description (Günther 1864 "1863") mentions that "two specimens" (= syntypes) from "Russelconda (Madras Presidency)" collected by Dr. Trail were used for the description of this species. We examined the two syntypes available at NHM, London: (1) a gravid female, NHM 62.12.29.4 (ex. BMNH 1947.2.10.97), SVL 67.4 mm, and (2) a sub-adult, NHM 62.12.29.3 (ex. BMNH 1947.2.10.77), SVL 26.9 mm. The female specimen that is also illustrated with the original description (Plate XXVI, Fig. K) was found to be in relatively good condition (Fig. 3B). Since the original description was brief, we herein provide a detailed description of the adult female specimen, NHM 62.12.29.4 (ex. BMNH 1947.2.10.97) that may serve as a reference for *Uperodon globulosus* (Günther, 1864 "1863") in future taxonomic works.

Comparison. *Uperodon globulosus* differs from all other known members of the genus, except *U. systoma* and *U. taprobanicus*, by its larger snout-vent size, male SVL 51–56 mm, female SVL 66–72 mm (vs. smaller, male SVL 21–40 mm, female SVL 28–43 mm); tips of fingers rounded, without discs (vs. finger tips enlarged into discs, except in *U. systoma*); and presence of two prominent dermal projections on the neopalatinal ridges on posterior side of each choana, narrowly separated from the vomerine odontophores (vs. dermal projections widely separated from the vomerine odontophores in *U. systoma*; indistinct or weakly to well-developed neopalatinal ridges on posterior side of each choana, fused with the vomerine odontophores in all other species) (Fig. 5B). *Uperodon globulosus* also differs from all other known *Uperodon* species, except *U. taprobanicus*, in having undivided prevomers (vs. divided prevomers), and differs from *U. taprobanicus* by its dorsum being light brown to greyish-brown without any prominent markings (vs. light to dark grey with prominent red or reddish-orange blotches). For more differences with *U. systoma* see the 'Comparison' section for that species.

Genetic divergence. For 16S mitochondrial gene sequences, intraspecific variation was not observed between the sampled populations of *Uperodon globulosus* (N = 3). Genetically, *U. globulosus* is closely related to *U. systoma*, from which it was found to differ by an average uncorrected genetic distance of 3.5% (range 3.2–4.0%, N = 18). For interspecific genetic distances with all other members of the genus, see Table 3.

Description of syntype, NHM 62.12.29.4 (measurements in mm) (Figs. 3B, 4G–J). Large-sized (SVL 67.4), globular and robust adult female; head small (HW 19.2, HL 13.0, IFE 9.7, IBE 13.9), about one-fifth (19.3%) of body length, wider than long (HW/HL ratio 1.5); snout nearly truncate in dorsal and ventral view, obtuse in lateral view, its length (SL 7.7) more than twice as long as horizontal diameter of eye (EL 3.6); loreal region obtuse, with rounded canthus rostralis; interorbital space over three times wider (IUE 8.8) than upper eyelid width (UEW 2.7); nostril oval without lateral flap of skin, closer to tip of snout (NS 2.8) than to eye (EN 3.3); tympanum not visible externally, distinct supratympanic fold extending from posterior corner of upper eyelid near to insertion of forelimb at axilla; eye diameter (EL 3.6); vomerine odontophores present on the palate, prominent, without teeth; presence of two prominent dermal projections on the neopalatinal ridges on posterior side of each choana, narrowly separated from the vomerine odontophores (Fig. 5B); tongue moderately large, rounded, shallowly emarginated. Forelimbs moderately short and strong, forearm (FAL 14.5) shorter than hand length (HAL 18.0); finger length formula IV<I<II<III; tips of all fingers rounded, without discs; webbing absent between fingers; subarticular tubercles weakly-developed, oval, all present; two well-developed palmar tubercles (inner, oval, 3 mm long; outer, bilobed, 4 mm long). Hind limbs relatively short and strong, thigh length (TL 29.1) longer than shank (SHL 21.7) and foot (FOL 26.5); tips of all toes rounded, without discs; webbing present, small: $I1^{1}/_{2}$–$2^{-}II2^{-}$–$3^{-}III2^{1}/_{2}$–$3^{1}/_{2}IV4^{-}$–$2^{1}/_{2}V$; well-developed dermal fringes present on all toes; subarticular tubercles weakly-developed, oval, all present; two shovel-shaped metatarsal tubercles (inner, 8.6 mm; outer, 4.8 mm).

Skin of dorsum, sides of head, and dorsal parts of forelimb, thigh, tibia and tarsus, shagreened (Fig. 3B); posterior parts of thigh, especially cloacal region, distinctly granular. Ventral surfaces shagreened and wrinkled (Fig. 3B).

Colouration. *In preservation* (NHM 62.12.29.4): Dorsum brown, flanks light greyish-brown; forelimbs, dorsal surfaces of thigh, shank and foot, dark greyish-brown; chest, belly, and ventral surfaces of thigh, tibia and foot, light greyish-brown (Figs. 3B, 4G–I). *In life* (SDBDU 2014.2672): Dorsum greyish-brown, dorsal surface of head grey with bluish tinge, lateral surfaces of head and flank lighter in colour compared to dorsum, with yellow tinge; forelimbs, dorsal surfaces of thigh, shank and foot, greyish-brown with yellow tinge; throat, chest, and belly,

greyish-white without any markings; ventral surfaces of forelimb, thigh, tibia and foot, light grey with cream coloured blotches (Figs. 4K–L).

Variations. Morphometric measurements for five specimens are given in Table 4. SDBDU 2014.2673 (female) has prominent neopalatinal ridges on posterior side of each choana (Fig. 5B).

Secondary sexual characters. Male (SDBDU 2014.2672): single vocal sac externally visible on the lower jaw; female (syntype): ova white, pigmented on pole (diameter 0.9–1.4 mm, $N = 20$).

Tadpole morphology. In dorsal view, tadpoles of *Uperodon globulosus* (Gosner stage 32, $N = 2$) have an elliptical body with narrower and shorter anterior region, wider and longer posterior region; snout appears rounded in dorsal and lateral view (from eyes to base of upper labium); eyes small, bulbous, positioned laterally; umbraculum absent; nasolacrimal duct absent; narial depressions clearly visible in lateral view, located much closer to snout than to eyes, pigmentation not visible around nasal depressions; sinistral spiracle present, opening located at ventral tail-musculature margin; tubular vent tube present posteriorly, with aperture opening medially in line with plane of the ventral fin; tail ends bluntly, composed of bilateral myotomic muscle masses divided by V-shaped septa, with unequal membranes on either side of tail musculature, tail musculature extends up to the end of tail tip; dorsal fins originate after tail-body junction, margin of lower fin not parallel to the margin of tail muscle; mouth (oral disc) absent, keratodonts and jaw sheaths not seen, papillae absent.

Measurements (mm) ($N = 1$): Lateral measurements include, maximum height of body (bh) = 3.66, maximum width of body (bw) = 5.98, maximum diameter of eye (ed) = 0.40, internarial distance (nn) = 2.07, naro-pupular distance (np) = 2.58, rostro-narial distance (rn) = 0.02, interpupular distance (pp) = 5.78, distance from tip of snout to opening of spiracle (ss) = 4.55, distance from tip of snout to insertion of upper tail fin (su) = 6.60, snout-vent length (svl) = 7.74, total length (tl) = 19.15, distance from vent to tip of tail (vt) = 11.60, maximum height of tail (ht) = 4.95, tail muscle height (tmh) = 1.61, tail muscle width (tmw) = 1.35.

Geographical distribution and habitat. *Uperodon globulosus* is widely distributed in India and neighboring regions in Bangladesh, Bhutan and Nepal (Fig. 2B). In India, this species has been reported from the states of Andhra Pradesh, Maharashtra, Gujarat, Odisha, Madhya Pradesh, Chhattisgarh, Uttar Pradesh, Jharkhand, Odisha, West Bengal, Assam and Arunachal Pradesh (for detailed list of localities and references thereto see supplementary Table S1). In the present study, we collected specimens from temporary pools and puddles inside the Pune city (Table 1). At Tamhini Ghats, a large number of males were observed on the road passing through open or agricultural areas, immediately after the first monsoon showers. See 'Natural history and breeding' observations in the respective section, after the species accounts.

***Uperodon taprobanicus* (Parker, 1934)**

Painted Globular Frog

(Figs. 1, 2A–B, 3C, 4M–P, 5C, 6A–C; Tables 1–4)

Original name and description. *Kaloula pulchra taprobanica* Parker, 1934. *A Monograph of the frogs of the family Microhylidae*. London: Trustees of the British Museum, 86–87. **Holotype.** By original designation, NHM 1905.3.25.138 (ex. BMNH 1947.2.10.62), an adult female, SVL 54.9 mm. **Type locality.** "Punduloya", Sri Lanka. **Current status of specific name.** Valid name, as *Uperodon taprobanicus* (Parker, 1934).

Comment. Even though Parker (1934) provided a description for this nominal taxon, considering its recent taxonomic placement in the genus *Uperodon*, here we provide a detailed description of the holotype and comparison of the species with all its presently recognized congeners.

Comparison. *Uperodon taprobanicus* differs from all other known members of the genus by presence of two well-developed neopalatinal ridges on posterior side of each choana, fused with the vomerine odontophores (vs. prominent dermal projections on the neopalatinal ridges on posterior side of each choana, separated from the vomerine odontophores in *U. globulosus* and *U. systoma*; indistinct or weakly-developed neopalatinal ridges in all other species), and its dorsum being light to dark grey with prominent red or reddish-orange blotches (vs. absent). Specifically, it differs from *U. globulosus* and *U. systoma* by its smaller snout-vent size, male SVL 42–52 mm, female SVL 53–55 mm (vs. larger, *U. globulosus*: male SVL 51–56 mm, female SVL 66–72 mm; *U. systoma*: male SVL 51–56 mm, female SVL 47–64 mm), and tips of fingers with discs (vs. rounded, without discs); and from other members of the genus by its larger snout-vent size, male SVL 42–52 mm, female SVL 53–55 mm (vs.

smaller, male SVL 21–40 mm, female SVL 28–43 mm). *Uperodon taprobanicus* also differs from all other known *Uperodon* species, except *U. globulosus*, in having undivided prevomers (vs. divided prevomers).

Genetic divergence. For 16S mitochondrial gene sequences, the sampled populations of *Uperodon taprobanicus* showed an average intraspecific distance of 0.3% (range 0–1.2%, *N* = 9). The sample from Odisha showed a divergence of up to 1.2% from the typical populations. Genetically, *U. taprobanicus* is the most divergent member of the genus and shows high interspecific genetic distances with all the other known members (see Table 3).

Redescription of holotype (measurements in mm) (Figs. 3C, 4M–P). Large-sized (SVL 54.9), globular and robust adult female; head small (HW 16.5, HL 12.4, IFE 8.0, IBE 14.9), less than one-fourth (22.6%) of body length, wider than long (HW/HL ratio 1.3); snout truncate in dorsal and ventral view, vertical in lateral view, its length (SL 5.2) longer than horizontal diameter of eye (EL 4.7); loreal region obtuse with rounded canthus rostralis; interorbital space wider (IUE 5.7) than upper eyelid (UEW 3.8); nostril oval without lateral flap of skin, closer to tip of snout (NS 1.6) than to eye (EN 2.9); tympanum not visible externally, distinct supratympanic fold extending from posterior corner of upper eyelid near to insertion of forelimb at axilla; eye diameter (EL 4.7); vomerine odontophores present on the palate, without teeth; presence of two prominent neopalatinal ridges on posterior side of each choana, fused with the vomerine odontophores (Fig. 5C); tongue moderately large, rounded, shallowly emarginated. Forearms (FAL 16.8) shorter than hand length (HAL 24.5); finger length formula I<II<IV<III; tips of all fingers with truncate discs; webbing absent between fingers; subarticular tubercles rather well-developed, oval, all present; two well-developed palmar tubercles, inner one oval and smaller, and outer one bilobed. Hind limbs relatively short and strong, thigh length (TL 20.8) longer than shank (SHL 17.2) and foot (FOL 19.9); tips of all toes rounded, slightly enlarged, without discs; webbing present, small: I2–2II2^{-}–3III2–3$^{1}/_{3}$IV3$^{1}/_{3}$–2V; weakly-developed dermal fringes present on all toes; subarticular tubercles well-developed, oval, all present; two shovel-shaped metatarsal tubercles (inner, 1.4 mm long; outer, 3.1 mm long).

Skin of dorsum, sides of head, and dorsal parts of forelimb, thigh, tibia and tarsus, shagreened with scattered glandular projections (Figs. 3C, 4M–P); posterior parts of thigh, especially cloacal region, distinctly granular. Ventral surface of throat granular, chest and belly, sparsely granular (Fig. 3C).

Colouration. *In preservation*: Dorsum light brown with large irregular greyish-brown blotches, a dark grey stripe between eyes, flanks and lateral sides of abdomen lighter brown in colour compared to dorsum; chest, belly and ventral surfaces of thigh, tibia and foot, light greyish-brown with dark brown mottling (Fig. 3C). *Colour in life* (SDBDU 2014.2567): Dorsal surface of head, anterior and posterior parts of back, brown and having brick-red blotches with dark brown margins, brick-red stripe with dark brown margin between eyes, lateral surfaces of head light brick-red, and flanks light brown with grey reticulations; forelimbs, dorsal surfaces of thigh, shank and foot, light brown with dark blackish-brown spots and brick red patches; fingers and toes light brown with grey spots; anterior part of thigh and groin brown with light grey reticulations; throat, chest and belly, light reddish-brown with uniform light grey reticulations except on fingers and toes (Figs. 6A–C).

Variations. Morphometric measurements for five specimens, including the holotype, are given in Table 4. SDBDU 2005.3107: dorsal skin sparsely granular; throat prominently granular, chest and belly sparsely granular; anterior parts of thigh prominently granular. SDBDU 2005.4732A: dorsal skin coarsely granular; ventral surface prominently granular, especially throat region; anterior parts of thigh, shank and groin, light greyish-brown with creamy white mottling.

Secondary sexual characters. Male (SDBDU 2005.4732A): vocal sac externally visible on the lower jaw; female (Holotype): ova white, pigmented on pole (diameter 0.8–1.2 mm, *N* = 10).

Geographical distribution and habitat. *Uperodon taprobanicus* is widely distributed in India and Sri Lanka, and also reported from Bangladesh and Nepal (Fig. 2B). In India, it has been reported from the states of Tamil Nadu, Kerala, Karnataka, Maharashtra, Gujarat, Andhra Pradesh, Telangana, Odisha, Madhya Pradesh, Chhattisgarh, West Bengal, Bihar and Assam. In Sri Lanka, it is known from Central, Eastern, North Western, Western, Sabaragamuwa, Southern and Uva Provinces. For detailed list of localities and references thereto see Supplementary Table S1. In the present study, we collected and genetically confirmed the presence of this species in Tamil Nadu (Mamallapuram), Kerala (Mannuthy, Kalpetta and Sulthanbathery), Karnataka (Bangalore) and Odisha in India, and Central (Dambulla) and North Western (Karawaddana) regions of Sri Lanka. It was observed in roadside puddles, wall crevices, cultivated fields and tree holes in both primary and secondary forests, from sea level up to 950 m asl. See 'Natural history and breeding' observations in the respective section, after the species accounts.

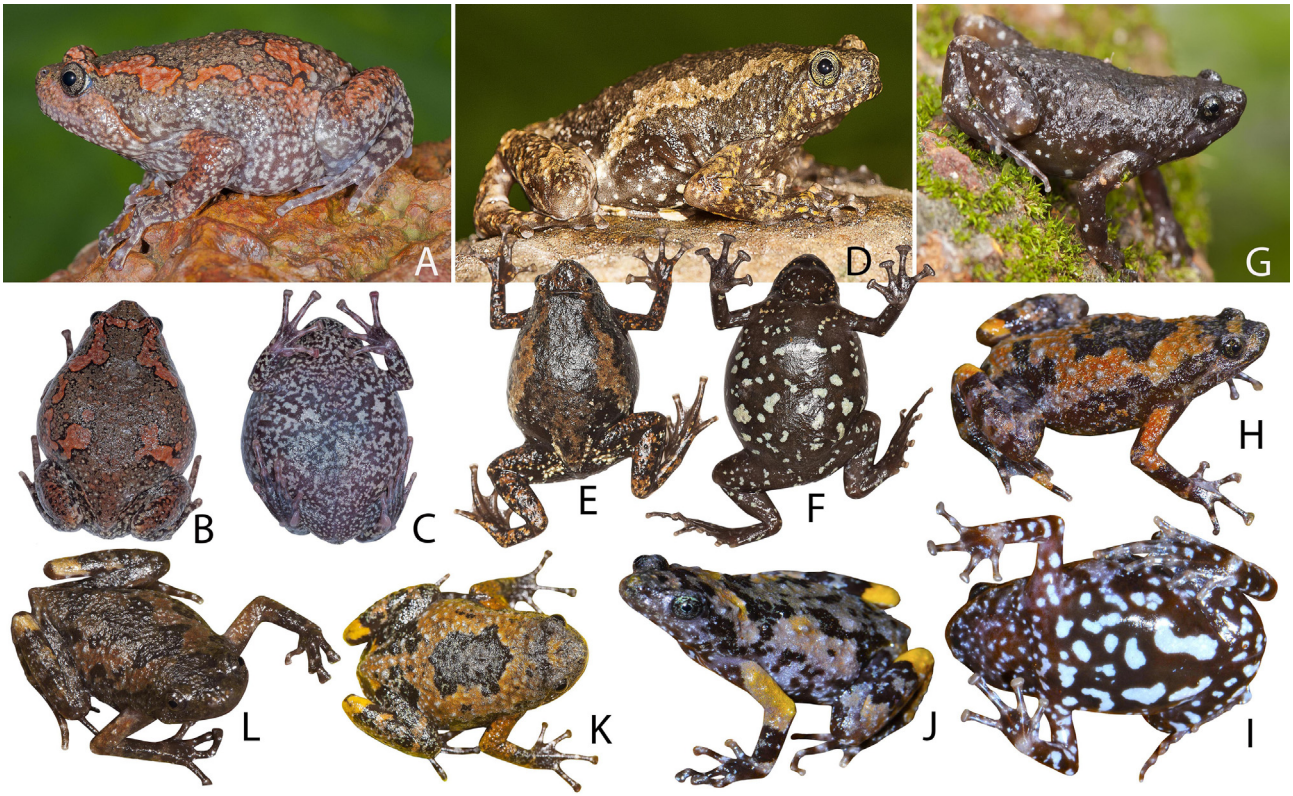

FIGURE 6. *Uperodon taprobanicus*, *U. anamalaiensis* and *U. montanus* in life. **A–C.** *Uperodon taprobanicus* (SDBDU 2014.2567, male): **A.** dorsolateral view; **B.** dorsal view; **C.** ventral view; **D–F.** *Uperodon anamalaiensis*: **D.** dorsolateral view (SDBDU 2013.2302, female); **E.** dorsal view (SDBDU 2017.3507, female); **F.** ventral view (SDBDU 2017.3507, female); **G–L.** *Uperodon montanus*: **G.** dorsolateral view (SDBDU 2011.849, male); **H.** dorsolateral view (SDBDU 2011.1197, male); **I.** ventral view (SDBDU 2002.1925, male); **J.** dorsolateral view (SDBDU 2002.1925, male); **K.** dorsal view (SDBDU 2015.3001, male); **L.** dorsal view (SDBDU 2011.905, male). (Images: SD Biju and Sonali Garg).

***Uperodon anamalaiensis* (Rao, 1937)**
Anamalai Globular Frog
(Figs. 1, 2A, 2C, 3D, 5D, 6D–F, 7A–E, 8A–D; Tables 1–4)

Original name and description. *Ramanella anamalaiensis* Rao, 1937. On some new forms of Batrachia from S. India. *Proceedings of the Indian Academy of Sciences. Section B*, 6: 387–427. **Neotype.** By present designation, ZSI/WGRC/V/A/956, an adult male, SVL 30.9 mm, from Parambikulam, Kerala state, India, collected by SD Biju and team on 15 June 2011. **Type locality.** "Base of Anamalai Hills, Coimbatore District", Tamil Nadu, India. **Current status of specific name.** Valid name, as *Uperodon anamalaiensis* (Rao, 1937). **Synonym.** *Ramanella minor* Rao, 1937 **syn. nov.** [= *Uperodon minor* (Rao, 1937)], Neotype by present designation, ZSI/WGRC/V/A/957, an adult male, from Sakleshpur, Karnataka state, India, collected by SD Biju and team on 29 September 2012.

Neotypification of *Ramanella anamalaiensis* Rao, 1937. This species was described from the "Base of Anamalai Hills, Coimbatore District" based on a single specimen ("total length 28.00 mm"), which was deposited in the Central College, Bangalore (CCB). The original name bearing type for this taxon is considered lost (Dubois 1984; Biju 2001) and the species was known only from its original description, hence also presumed to be "lost", until it was rediscovered recently from the wet evergreen forests of Parambikulam Tiger Reserve (Vijayakumar *et al*. 2011). In the original description, Rao (1937) stated several morphological characters based on which he recognized this taxon to be new, but did not provide any comparison with the other closely known members. Our collections from Parambikulam, which is part of the Anamalai Hills (type locality), are comparable with the original description of *Uperodon anamalaiensis* (Rao 1937) in their general size, morphology, and dorsal and ventral markings. The primary inconsistency between our recent collections and the original description is in the

degree of webbing on foot. Rao (1937) mentions "toes perfectly free" but the accompanying illustration (Rao 1937, plate XXIX, fig. 20) suggests presence of at least small foot webbing. However, since we found variation in foot webbing among the various examined populations of this species, we do not consider this as a reliable character for diagnosing the species. Further, since the taxonomic status of *Ramanella anamalaiensis* Rao, 1937 has remained doubtful (Dutta 1997) primarily due to unavailability of its name bearing type, in accordance with Article 75 of The Code, designation of a neotype is considered necessary for this taxon, in order to clarify its taxonomic status and to define it objectively. Hence, based on diagnostic characters found useful for differentiating *Ramanella anamalaiensis* Rao, 1937 (= *Uperodon anamalaiensis*) from its congeners (as stated in the 'comparison' section below), we herein formally designate ZSI/WGRC/V/A/956, an adult male (SVL 30.9 mm) from Parambikulam, as the neotype of *Ramanella anamalaiensis* Rao, 1937. The neotype description provided subsequently also shows that the neotype is largely consistent with what is known of the former name-bearing type.

Synonymization and neotypification of *Ramanella minor* Rao, 1937. Rao (1937) described another taxon, *Ramanella minor*, from Sakleshpur in Karnataka state along with *Ramanella* (= *Uperodon*) *anamalaiensis*. During our surveys in the Sakleshpur region (type locality) we collected an *Uperodon* specimen that was comparable with Rao's description of *Ramanella minor*. Since the type specimen of this taxon that was originally deposited in the Central College Bangalore (CCB), is also considered lost (Dubois 1984; Biju 2001), a critical study of the original description of *Ramanella minor* Rao suggests that the majority of the mentioned characters are nearly the same as for *Ramanella anamalaiensis* Rao and not helpful in distinguishing them from each other. The major diagnostic characters stated for *Ramanella minor* by Rao (1937), such as 'snout broadly truncated, distance between nostrils equals width of the upper eyelid, interorbital space nearly twice the width of the upper eyelid, no occipital fold,' and the overall colouration, also match with our collections of *Uperodon anamalaiensis*. The major differences between these two taxa as per Rao's descriptions seem to be 'postnarial ridges strongly developed' (vs. 'ridges incompletely developed' in *U. anamalaiensis*), 'diameter of the eye less than the length of the snout' (vs. 'diameter of the eye greater than the length of the snout' in *U. anamalaiensis*), 'canthus rostralis obtuse' (vs. 'rostralis rounded' in *U. anamalaiensis*) and few other minor characters, which are all found to be variable among the various *Uperodon anamalaiensis* populations examined by us (Table 4) and therefore may not be sufficient to distinguish *U. minor* and *U. anamalaiensis* from each other. We also compared the 16S rRNA gene sequences of our collection from Sakleshpur and the *Uperodon anamalaiensis* population from Parambikulam, and found them to show a low genetic difference of 0.8%. Hence, in accordance with Articles 24.2.1 (Statement of the Principle of the First Reviser) and 24.2.2 (Determination of precedence of names or acts by the First Reviser) of The Code, and Recommendation 24A of The Code, we act as the First Revisers and consider *Ramanella minor* Rao, 1937 as a junior subjective synonym of *Ramanella anamalaiensis* Rao, 1937 (= *Uperodon anamalaiensis*). Furthermore, since the taxonomic status of *Ramanella minor* Rao, 1937 **syn. nov.** has been considered doubtful (Dutta 1997) primarily due to unavailability of name bearing types, in accordance with Article 75 of The Code, we herein designate ZSI/WGRC/V/A/957 (an adult male, SVL 31.7 mm, from the original type locality 'Sakleshpur') as the neotype of *Ramanella minor* Rao, 1937, in order to define this taxon objectively and to establish taxonomic stability. The neotype description of *Ramanella minor* Rao, 1937 **syn. nov.** provided along with figures (Figs. S1A–E) in the supplementary file S1, also shows that the neotype is largely consistent with what is known of the former name-bearing type.

Comparison. *Uperodon anamalaiensis* differs from *U. globulosus*, *U. systoma* and *U. taprobanicus* by its smaller snout-vent size, male SVL 25–37 mm, $N = 14$, female SVL 35–39 mm, $N = 4$ (vs. larger, *U. globulosus*: male SVL 51–56 mm, $N = 2$, female SVL 66–72 mm, $N = 3$; *U. systoma*: male SVL 51–56 mm, $N = 2$, female SVL 47–64 mm, $N = 4$; *U. taprobanicus*: male SVL 42–52 mm, $N = 3$, female SVL 53–55 mm, $N = 2$). It also differs from the former two by its finger tips with truncate discs (vs. finger tips rounded without discs), ventral surface with large spots or blotches (vs. without any markings), and presence of two indistinct neopalatinal ridges on posterior side of each choana, fused with the vomerine odontophores (vs. two prominent dermal projections on the neopalatinal ridges on posterior side of each choana, separated from the vomerine odontophores); differs from *U. taprobanicus* by presence of two indistinct neopalatinal ridges on posterior side of each choana, fused with the vomerine odontophores (vs. well-developed neopalatinal ridges). Further, *U. anamalaiensis* differs from *U. nagaoi*, *U. rohani* **sp. nov.** and *U. variegatus* by its ventral surface in having large spots or blotches (vs. absent) and presence of webbing between toes, $I1^{+}$–$2^{-}II1$–$2^{-}III1^{+}$–$2^{-}IV2$–1V (vs. absent). This species could be confused with *U. montanus*, *U. mormorata, U. obscurus, U. palmatus* and *U. triangularis* due to presence of large spots or

blotches on ventral skin. However, *U. anamalaiensis* differs from all these species by presence of continuous broad median band extending from behind the eye up to near the vent (vs. absent or discontinuous patches). Specifically, *U. anamalaiensis* differs from three Indian congeners by the following characters: from *U. montanus* by its relatively larger snout-vent size, male SVL 25–37 mm, *N* = 14, female SVL 35–39 mm, *N* = 4 (vs. relatively smaller, male SVL 21–28 mm, *N* = 12, female SVL 28–34 mm, *N* = 8); shank shorter than thigh, male: SHL/TL ratio 0.8–0.9, *N* = 14, female: SHL/TL ratio 0.9, *N* = 4 (vs. shank equal to thigh, male: SHL/TL ratio 1.0, *N* = 12, female: SHL/TL ratio 1.0, *N* = 8); and thigh almost equal to foot length, male: TL/FOL ratio 1.0–1.1, *N* = 14, female: TL/FOL ratio 1.0, *N* = 4 (vs. thigh shorter than foot, male: TL/FOL ratio 0.8–0.9, *N* = 14, female: TL/FOL ratio 0.8–1.0, *N* = 8) (Table 4). It differs from *U. mormorata* by its relatively smaller snout-vent size, male SVL 25–37 mm, *N* = 14, female SVL 35–39 mm, *N* = 4 (vs. relatively larger, male SVL 31–40 mm, *N* = 9, female SVL 32–43 mm, *N* = 3) and ventral skin surface with scattered spots or blotches (vs. densely marbled); and from *U. triangularis* by presence of webbing between toes (Figs. 7C–E) (vs. absent) and presence of dermal fringes on fingers and toes (vs. absent). Further, *U. anamalaiensis* differs from the Sri Lankan congeners by the following characters: from *U. palmatus* by its snout longer than eye diameter, male: EL/SL ratio 0.5–0.7, *N* = 14, female: EL/SL ratio 0.6–0.8, *N* = 4 (vs. equal, male: EL/SL ratio 1.0, *N* = 4, female: EL/SL ratio 1.0, *N* =2); and from *U. obscurus* by its shank shorter than thigh, male: SHL/TL ratio 0.8–0.9, *N* = 14, female: SHL/TL ratio 0.9, *N* = 4 (vs. nearly equal, male: SHL/TL ratio 0.9–1.0, *N* = 17, female: SHL/TL ratio 0.9–1.1, *N* = 5) (Table 4).

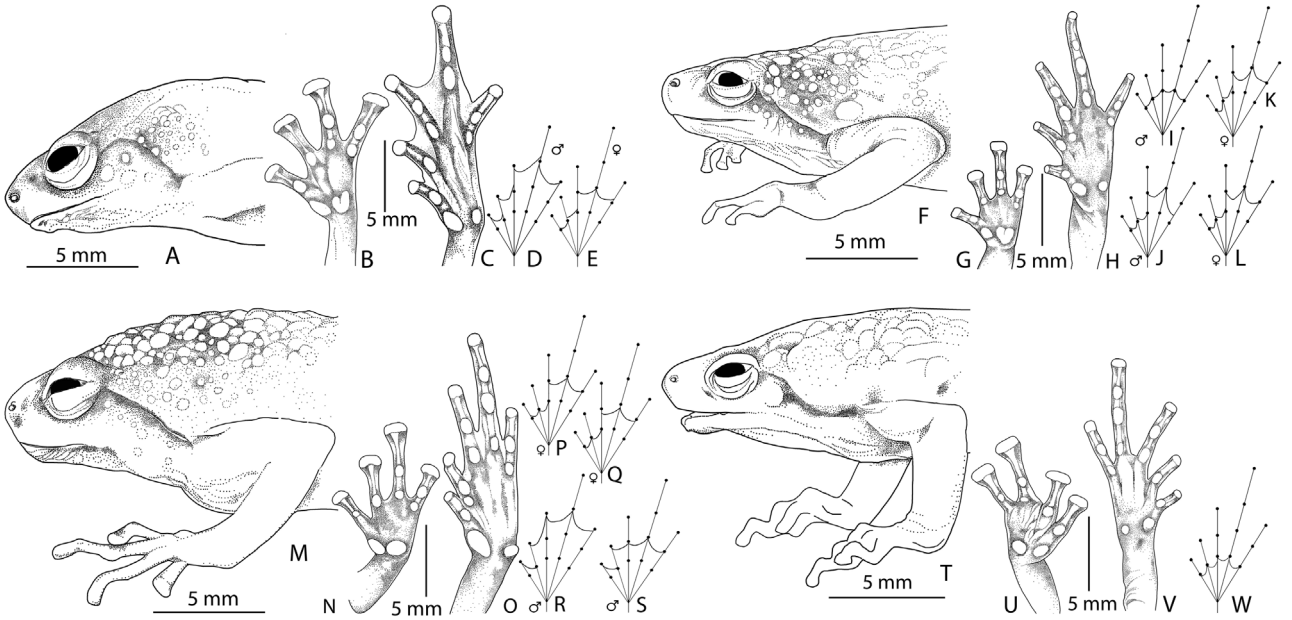

FIGURE 7. Head, hand, foot and foot webbing in *Uperodon anamalaiensis*, *U. montanus*, *U. mormorata* and *U. nagaoi*. **A–E.** *Uperodon anamalaiensis*: **A–D.** Neotype of *Uperodon anamalaiensis* (ZSI/WGRC/V/A/956, male): **A.** lateral view of head; **B.** ventral view of hand; **C.** ventral view of foot; **D.** schematic illustration of foot webbing; **E.** schematic illustration of foot webbing in referred specimen of *U. anamalaiensis* (SDBDU 2013.928, female); **F–L.** *Uperodon montanus*: **F–H.** Topotype of *Uperodon montanus* (SDBDU 2011.849, male): **F.** lateral view of head; **G.** ventral view of hand; **H.** ventral view of foot; **I.** schematic illustration of foot webbing; **J–L.** schematic illustration of foot webbing in referred specimens of *Uperodon montanus*: **J.** SDBDU 2015.3001, male; **K.** SDBDU 2003.40115, female; **L.** SDBDU 2005.30, female; **M–S.** *Uperodon mormorata*: **M–P.** Neotype of *Uperodon mormorata* (ZSI/WGRC/V/A/958, female): **M.** lateral view of head; **N.** ventral view of hand; **O.** ventral view of foot; **P.** schematic illustration of foot webbing; **Q–S.** schematic illustration of foot webbing in referred specimens of *Uperodon mormorata*: **Q.** SDBDU 2002.567, female; **R.** SDBDU 2012.43, male; **S.** SDBDU 2015.3082, male. **T–W.** Holotype of *Uperodon nagaoi* (WHT 2826, male): **T.** lateral view of head; **U.** ventral view of hand; **V.** ventral view of foot; **W.** schematic illustration of foot webbing. (Illustrations: SD Biju).

Genetic divergence. For 16S mitochondrial gene sequences, the sampled populations of *Uperodon anamalaiensis* showed an average intraspecific distance of 0.4% (range 0–0.8%, *N* = 6). Genetically, *U. anamalaiensis* is closely related to *U. montanus*, from which it was found to differ by an average uncorrected genetic distance of 3.2% (range 2.6–4.0%, *N* = 60). For interspecific genetic distances with all other members of the genus, see Table 3.

Description of neotype (measurements in mm) (Figs. 3D, 7A–D). Small-sized (SVL 30.9), slender adult male; head small (HW 8.5, HL 6.3, IFE 3.9, IBE 7.0), about one-fifth (20.3%) of body length, wider than long (HW/HL ratio 1.3); snout truncate in dorsal and ventral view, vertical in lateral view, protruding, its length (SL 3.0) longer than horizontal diameter of eye (EL 2.2); loreal region acute with rounded canthus rostralis; interorbital space about twice as wide (IUE 3.6) as upper eyelid width (UEW 1.7); nostril oval without lateral flap of skin, closer to tip of snout (NS 0.7) than to eye (EN 1.7); tympanum not visible externally, distinct supratympanic fold extending from posterior corner of upper eyelid near to insertion of forelimb at axilla; eye diameter (EL 2.2); vomerine odontophores present on the palate, prominent, with or without teeth; presence of two indistinct neopalatinal ridges on posterior side of each choana, fused with the vomerine odontophores; tongue moderately large, emarginate. Forelimbs moderately long and thin; forearm (FAL 6.9) shorter than hand length (HAL 8.5); finger length formula I<II<IV<III; tips of all fingers with truncate discs, without grooves, moderately wide compared to finger width (FD_I 1.5, FW_I 0.3; FD_{II} 1.5, FW_{II} 0.4; FD_{III} 1.8, FW_{III} 0.5; FD_{IV} 1.5, FW_{IV} 0.4); subarticular tubercles prominent, oval, all present; two well-developed palmar tubercles, inner oval, outer bilobed. Hind limbs relatively long and thin, thigh length (TL 13.9) longer than shank (SHL 12.4) and foot (FOL 13.5); relative digit lengths I<II<V<III<IV; tips of all toes with small truncate to rounded discs, rather wide compared to toe width (TD_I 0.7, TW_I 0.4; TD_{II} 0.9, TW_{II} 0.5; TD_{III} 1.0, TW_{III} 0.5; TD_{IV} 1.1, TW_{IV} 0.5; TD_V 0.8, TW_V 0.4); foot webbing present, moderate: $I1^{+}$–$2^{-}II1$–$2^{-}III1^{+}$–$2^{-}IV2$–1V; well-developed dermal fringes present on all toes; subarticular tubercles prominent, oval, all present; two smooth metatarsal tubercles, oval, outer tubercle slightly larger than the inner.

Skin of snout, between eyes, and sides of head, shagreened to granular; anterior and posterior parts of back, and upper and lower parts of flank, granular (Fig. 3D); dorsal surfaces of forelimb, thigh, tibia and tarsus, shagreened to sparsely granular; throat, chest, abdomen, and ventral surfaces of limbs, shagreened (Fig. 3D).

Colouration. *In preservation*: Dorsum dark greyish-brown with faint dark grey band extending from posterior end of upper eyelid on either side, along the side of dorsum, and approaching the vent; a faint dark grey stripe between eyes; throat, chest and belly, brown with scattered light grey blotches; ventral surfaces of forelimb, thigh, tibia and foot, dark grey with light grey blotches (Fig. 3D). *Colour in life*: Dorsum brown with irregular yellowish-brown spots and prominent yellowish-brown band extending from posterior end of upper eyelid near to vent; yellowish-brown stripe between eyes; lower part of flank brown with yellow speckles; dorsal surfaces of forelimbs, thigh, shank and foot, brown with yellowish-brown cross bands; throat, chest and belly, greyish-brown with scattered light grey blotches; ventral surfaces of forelimb, thigh, tibia and foot, dark grey with light yellow blotches.

Variations. Morphometric measurements for 18 specimens, including the neotype, are given in Table 4. There is not much variation observed in the overall morphology, except for skin colour and markings, sex-based webbing differences (Figs. 7D–E), and presence of vomerine teeth in SDBDU 2013.2302 (Fig. 5D). Dorsal colour and skin granulation varies slightly between individuals even from the same populations. SDBDU 2011.233A, SDBDU 2011.234, SDBDU 2011.548, SDBDU 2012.2000 and SDBDU 2012.1998: dorsum dark grey with a light grey dorsal band extending over the back and a light grey stripe between the eyes, dorsal skin shagreened to sparsely granular, ventral surface (including limbs) uniformly coffee brown with yellowish-grey spots and blotches; SDBDU 2013.2302: anterior parts of thigh sparsely granular with scattered spinular projections; SDBDU 2013.928: dorsum light greyish-brown with a straw coloured band extending over the back, foot webbing I2–$2II2^{-}$–$3^{-}III2$–$3IV3^{-}$–2^{-}V (Fig. 7E); SDBDU 2012.1995: anterior parts of thigh prominently granular with scattered spinular projections.

Secondary sexual characters. Male: vocal sac externally visible on the lower jaw; female (SDBDU 2017.3507): ova white, pigmented on pole (diameter 0.6–0.9 mm, $N = 10$).

Tadpole morphology. In dorsal view, tadpoles of *Uperodon anamalaiensis* (Gosner stage 34, $N = 2$) have an elliptical body with narrower and shorter anterior region, and wider and longer posterior region; snout appears rounded in dorsal view and depressed in lateral view; eyes small, bulbous, positioned laterally; nasolacrimal duct absent; narial depressions visible clearly in lateral view, located much closer to snout than to eyes, pigmentation not visible around nasal depressions; spiracle opens near the vent, flap present; vent tubular, positioned mid-ventrally with aperture opening medially in line with the plane of ventral fin; tail ends with round tip, composed of bilateral myotomic muscle masses divided by V-shaped septa, with unequal membranes on either side of tail musculature; dorsal fins originate after tail-body junction, margin of lower fin not parallel to margin of tail muscle; mouth terminal and appears as a slit opening, keratinized structures absent, papillae absent.

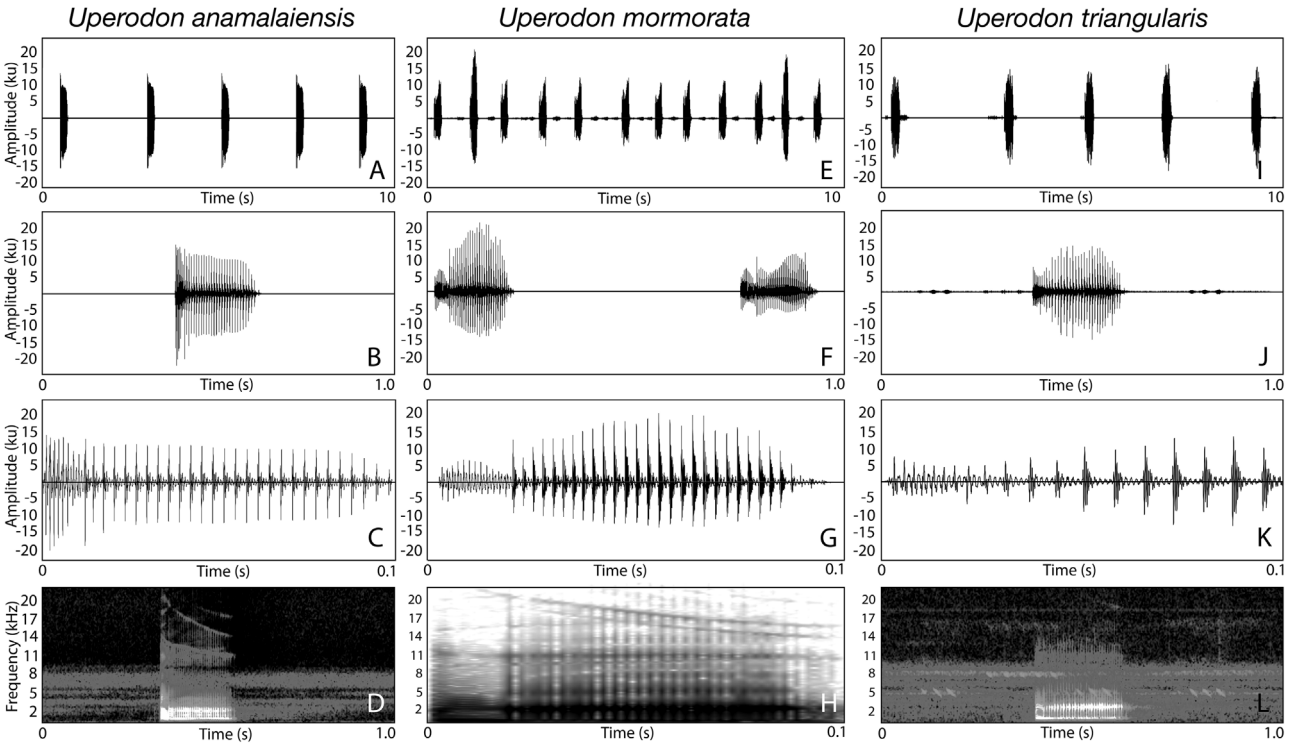

FIGURE 8. Male advertisement calls of *Uperodon anamalaiensis*, *U. mormorata* and *U. triangularis*. **A–D.** *Uperodon anamalaiensis*: **A.** ten second call segment; **B.** one second call segment; **C.** 0.1 second segment showing a single non-pulsatile call; **D.** spectrogram of the call shown in Figure 8B; **E–H.** *Uperodon mormorata*: **E.** ten second call segment; **F.** one second call segment; **G.** 0.1 second segment showing a single non-pulsatile call; **H.** spectrogram of the call shown in Figure 8G; **I–L.** *Uperodon triangularis*: **I.** ten second call segment; **J.** one second call segment; **K.** 0.1 second segment showing a single non-pulsatile call; **L.** spectrogram of the call shown in Figure 8J.

Measurements (mm) (N = 1): Lateral measurements include, maximum height of body (bh) = 3.41, maximum width of body (bw) = 6.87, maximum diameter of eye (ed) = 0.58, internarial distance (nn) = 1.65, naro-pupular distance (np) = 2.86, rostro-narial distance (rn) = 0.02, interpupular distance (pp) = 5.42, distance from tip of snout to opening of spiracle (ss) = 6.44, distance from tip of snout to insertion of upper tail fin (su) = 9.72, snout-vent length (svl) = 8.86, total length (tl) = 21.78, distance from vent to tip of tail (vt) = 13.51, maximum height of tail (ht) = 3.83, tail muscle height (tmh) = 1.97, tail muscle width (tmw) = 1.97.

Vocalization. A male of *Uperodon anamalaiensis* (SDBDU 2012.1994) from Methooty produced a single type of call with pulsatile temporal structure. Calls were not delivered in groups. A typical male call had a duration of 208.9 ms, a short rise time of 4 ms, and fall time of 202.3 ms. The call comprised of 35 pulses that were delivered at a rate of 175.8 pulses/s. Spectrum was characterized by an overall dominant frequency of 1.2 kHz (Figs. 8A–D).

Geographical distribution and habitat. *Uperodon anamalaiensis* was only known from its original description until its recent rediscovery from Parambikulam in the southern Western Ghats of India. The present study provides further morphological and genetically confirmed reports of this species from Kerala (Chathankod and Methooty) and Karnataka (Sakleshpur) (Fig. 2C; Table 1), at elevations between 100–650 m asl. It is also likely to be present in the Anamalai region of Tamil Nadu. Individuals were collected from tree holes, ground puddles and shallow water channels inside disturbed secondary forests (Chathankod and Methooty) as well as primary forest areas, either protected (Parambikulam) or unprotected (Ponmudi and Sakleshpur).

Notes on previous reports. This species was previously misidentified as *Uperodon triangularis* from Ponmudi hills (Inger *et al.* 1984) and Thiruvananthapuram district (Andrew *et al*. 2005) of Kerala state. The report of *U. anamalaiensis* from Munnar in Kerala (Harpalani *et al*. 2015) most likely refers to *U. montanus* (see Supplementary Table S1 for list of localities and references thereto).

***Uperodon montanus* (Jerdon, 1854 "1853")**
Mountain Globular Frog
(Figs. 1, 2A, 2C, 3E, 5E, 6G–L, 7F–L; Tables 1–4)

Original name and description. *Hylaedactylus montanus* Jerdon, 1854 "1853". Catalogue of reptiles inhabiting the Peninsula of India. *Journal of the Asiatic Society of Bengal*, 22:522–534. **Holotype.** By monotypy, NHM 72.4.17.212 (ex. BMNH 1947.2.11.19), an adult female, SVL 28.3 mm. **Type locality.** "Mountain streams in Wynaad", Kerala, India. **Current status of specific name.** Valid name, as *Uperodon montanus* (Jerdon, 1854 "1853").

Comments. The original description by Jerdon (1854 "1853") was brief and subsequently elaborated by Parker (1934). This species is largely known only from its original collection and some scanty reports or checklists (e.g., Dutta 1997; Subramanian *et al*. 2013). Further, considering the recent taxonomic placement of this taxon in genus *Uperodon* and morphological variations observed among populations (particularly in foot webbing), here we provide a detailed redescription of the holotype and comparison of this species with all its presently recognized congeners, to facilitate proper identification.

Comparison. For comparison of *Uperodon montanus* with *U. globulosus*, *U. systoma*, *U. taprobanicus* and *U. anamalaiensis* see 'comparison' section of those species. *Uperodon montanus* differs from *U. nagaoi*, *U. rohani* **sp. nov.** and *U. variegatus* by presence of prominent spots and blotches on its ventral surface (vs. inconspicuous spots and speckles present or absent in *U. nagaoi*, and completely absent in *U. rohani* **sp. nov.** and *U. variegatus*) and relatively smaller snout-vent size, male SVL 21–28 mm, *N* = 12; female SVL 28–34 mm, *N* = 8 (vs. relatively larger, *U. nagaoi*: male SVL 25–32 mm, *N* = 8; *U. rohani* **sp. nov.**: male SVL 26–34 mm, *N* = 16, female SVL 28–35 mm, *N* = 8; *U. variegatus*: male SVL 25–33 mm, *N* = 12, female SVL 29–36 mm, *N* = 7). *Uperodon montanus* could be confused with *U. anamalaiensis, U. mormorata, U. obscurus, U. palmatus* and *U. triangularis* due to presence of prominent spots and blotches on its ventral skin surface. However, *U. montanus* differs from all these species by its relatively smaller snout-vent size, male SVL 21–28 mm, *N* = 12; female SVL 28–34 mm, *N* = 8 (vs. relatively larger, *U. anamalaiensis*: male SVL 25–37 mm, *N* = 14, female SVL 35–39 mm, *N* = 4; *U. mormorata*: male SVL 31–40 mm, *N* = 9, female SVL 32–43 mm, *N* = 3; *U. obscurus*: male SVL 22–31 mm, *N* = 17, female SVL 30–38 mm, *N* = 5; *U. palmatus*: male SVL 27–31 mm, *N* = 4, female SVL 34–36 mm, *N* = 2; *U. triangularis*: male SVL 25–37 mm, *N* = 20, female SVL 33–42 mm, *N* = 4). Specifically, *U. montanus* also differs from *U. mormorata* by its ventral skin being light to dark brown with scattered grey spots or blotches (vs. dark brown with dense marbling); from *U. palmatus* by its snout longer than eye diameter, male: EL/SL ratio 0.6–0.8, *N* = 12, female: EL/SL ratio 0.6–0.8, *N* = 8 (vs. equal, male: EL/SL ratio 1.0, *N* = 4, female: EL/SL ratio 1.0, *N* =2); and from *U. triangularis* by presence of webbing between toes (vs. absent).

Genetic divergence. For 16S mitochondrial gene sequences, the sampled populations of *Uperodon montanus* showed an average intraspecific distance of 0.7% (range 0–1.2%, *N* = 10). Genetically, *U. montanus* is closely related to *U. anamalaiensis*, from which it was found to differ by an average uncorrected genetic distance of 3.2% (range 2.6–4.0%, *N* = 60). For interspecific genetic distances with all other members of the genus, see Table 3.

Redescription of holotype (measurements in mm) (Fig. 3E). Small-sized (SVL 28.3), slender adult female; head small (HW 10.1, HL 7.0, IFE 3.9, IBE 7.5), one-fourth (24.7%) of body length, wider than long (HW/HL ratio 1.4); snout nearly rounded in dorsal and ventral view, nearly acute in lateral view, its length (SL 3.3) longer than horizontal diameter of eye (EL 2.1); loreal region obtuse with rounded canthus rostralis; interorbital space nearly twice as wide (IUE 3.1) as upper eyelid width (UEW 1.6); nostril closer to tip of snout (NS 0.8) than to eye (EN 2.1); supratympanic fold distinct, extending from posterior corner of upper eyelid to insertion of forelimb at axilla; eye diameter (EL 2.1); vomerine odontophores present on the palate; indistinct neopalatinal ridges on posterior side of each choana, appear fused with the vomerine odontophores; tongue moderately large, circular, shallowly emarginated. Forelimbs moderately long and thin; forearm (FAL 6.8) shorter than hand length (HAL 8.7); finger length formula I<II<IV<III. Hind limbs relatively long and thin, thigh length (TL 12.3) shorter than shank (SHL 12.4) and foot (FOL 13.9).

Skin of snout, between eyes, sides of head, and anterior part of dorsum, shagreened to granular; posterior part of back, and upper and lower parts of flank, granular (Figs. 3E); dorsal surfaces of forelimb, thigh, tibia and tarsus, shagreened to sparsely granular; ventral surface uniformly shagreened (Fig. 3E).

Since the hand and foot morphology could not be reliably determined due to poor preservation of the holotype specimen, we are describing these characters based on a topotype specimen (SDBDU 2011.849).

Topotype specimen (SDBDU 2011.849). Hand (Fig. 7G): tips of all fingers with truncate discs, moderately wide compared to finger width (FD_I 0.6, FW_I 0.3; FD_{II} 1.0, FW_{II} 0.7; FD_{III} 1.0, FW_{III} 0.7; FD_{IV} 0.9, FW_{IV} 0.4); well-developed dermal fringes present on all fingers; subarticular tubercles rather prominent, oval, all present; two well-developed palmar tubercles (inner, oval, 0.8 mm; outer, bilobed, 1.1 mm). Foot (Figs. 7H–I): tips of all toes with small rounded discs, rather wide compared to toe width (TD_I 0.5, TW_I 0.4; TD_{II} 0.6, TW_{II} 0.4; TD_{III} 0.6, TW_{III} 0.5; TD_{IV} 0.6, TW_{IV} 0.4; TD_V 0.5, TW_V 0.4); well-developed dermal fringes present on all toes; subarticular tubercles rather prominent, oval; two metatarsal tubercles, oval, outer (0.5 mm long) slightly larger than the inner (0.9 mm long); webbing present, basal: I2–2II2–3III3–4IV4–3V.

Colouration. *In preservation* (SDBDU 2011.849): Dorsum greyish-brown; flanks, forelimbs, dorsal surfaces of thigh, shank and foot, light greyish-brown; chest and belly dark grey with light grey spots and patches, ventral surfaces of thigh, tibia and foot, light grey with lighter grey spots. *Colour in life* (SDBDU 2011.849): Dorsum and lateral sides of head uniformly dark brown with pale brown median patch on the back and few irregular patches near groin and thigh; dorsal surface of limbs dark brown; ventral surface dark brown with irregular white spots and blotches (Fig. 6G).

Variations. Morphometric measurements of 20 specimens, including the holotype, are given in Table 4. Dorsal colouration and webbing is highly variable in this species. Foot webbing: basal in SDBDU 2011.849 (male), I2–2II2–3III3–4IV4–3V; medium in SDBDU 2015.3001 (male), $I2^{-}$–$2II2^{-}$–3III2–3IV3–$2^{1}/_{2}$V; medium in SDBDU 2003.40115 (female), I2–$2II2^{-}$–3^{-}III2–3^{+}IV3^{-}–2V; and medium in SDBDU 2005.30 (female), I2–$2II2^{-}$–3III2–3IV3–2V (Figs. 7I–L). SDBDU 2011.849 (male): Dorsum uniformly brown with faint grey markings; SDBDU 2015.3001 (male): colour in life: dorsum orangish-brown with dark brown median patch on the back and few irregular patches near groin and thigh, forelimbs orangish-brown, and hind limbs orangish-yellow with dark brown cross bands (Fig. 6K); colour in preservation: dorsum grey with brown median patch and irregular brown spots, brown stripe between eyes, posterior part of dorsum (near groin) with two brown blotches on either side, dorsal surface of hand and foot grey with dark brown cross bands; SDBDU 2015.3002 (female): dorsum prominently granular, dorsal markings almost similar to SDBDU 2015.3001.

Note. Parker (1934) illustrated the foot webbing for this species (figure 38, p. 91) and showed relatively more webbing in the male compared to the female. He also stated toes to be "half webbed in males" and "1/3 webbed in females". In our study (N = 20), we found webbing to be highly variable, and since females were also often found to have more extensive webbing than males, this character should not be considered reliable for diagnosing this species.

Secondary sexual characters. Male: Vocal sac externally visible on the lower jaw; female (SDBDU 2002.24B): ova white, pigmented on pole (diameter 0.9–1.5mm, N = 20).

Geographical distribution and habitat. *Uperodon montanus* was originally described from the Wayanad region. In the present study, it is confirmed to occur in the Western Ghats states of Kerala (Devikulam, Munnar, Upper Manalar, Pandimotta, Nelliyampathy, Siruvani, Kurichiyarmala, Settukunnu and Thirunelli) and Tamil Nadu (Kakkachi and Sengaltheri), predominantly from mid to high elevations ranging from 800–1700 m asl (Fig. 2C; Table 1). Individuals were collected either from water-filled tree holes, damp leaf litter on forest floor or ground puddles. This species is likely to be distributed in southern parts of Karnataka. However, reports of *U. montanus* from Gujarat, Maharashtra and northern Karnataka require confirmation and may refer to *U. mormorata* (see Supplementary Table S1 and references thereto).

Uperodon mormorata (Rao, 1937)

Mottled Globular Frog

(Figs. 1, 2A, 2C, 3F, 5F, 7M–S, 8E–H, 9A–D; Tables 1–4)

Original name and description. *Ramanella mormorata* Rao, 1937. On some new forms of Batrachia from S. India. *Proceedings of the Indian Academy of Sciences. Section B*, 6: 387–427. **Neotype.** By present designation, ZSI/WGRC/V/A/958, an adult female, SVL 32.4 mm, from Sakleshpur, Karnataka state, India, collected by SD Biju on 26 June 2003. **Type locality.** "Saklespur (= Sakleshpur), Hassan District, Mysore", India. **Current status of specific name.** Valid name, as *Uperodon mormorata* (Rao, 1937).

Neotypification of *Ramanella mormorata* Rao, 1937. This species was described from "Saklespur" based on

a single specimen "total length 25.00 mm", which was deposited in the Central College, Bangalore. The original name bearing type (or types) of this species are considered lost (Dubois 1984; Das & Whitaker 1997; Biju 2001), and this nominal taxon was also presumed to be "lost" until its rediscovery from "Canacona (15°01'N 74°04'E), adjacent to Cotigao Wildlife Sanctuary (Goa, south-Western India)" based on an available museum specimen from "Malabar" at MCZ, USA (Das & Whitaker 1997). As per the original description, Rao had several available specimens including "young", "immature", "mature males" and "mature females", however, the description was based on a single specimen for which absolute measurements were included. Das & Whitaker (1997) provided a detailed description of this species based on examined specimens, however, without designating a neotype. Our new collection from the type locality Sakleshpur is comparable with the original description of *Ramanella mormorata* Rao, 1937, in overall general morphology, body size and dorsal and ventral markings. Since the original name-bearing type of this species is lost, we consider designation of a neotype necessary to define this nominal taxon objectively for clarification of its taxonomic status and to establish nomenclatural stability. Hence, in accordance with Article 75 of The Code, and based on diagnostic characters found useful for differentiating *Ramanella mormorata* Rao, 1937 (= *Uperodon mormorata*) from its congeners (as stated in the 'comparison' section below), we herein formally designate ZSI/WGRC/V/A/958 (an adult female, SVL 32.4 mm) from the original type locality Sakleshpur as the neotype of *Ramanella mormorata* Rao, 1937. The neotype description provided subsequently also shows that the neotype is largely consistent with what is known of the former name-bearing type.

Comparison. For comparison of *Uperodon mormorata* with *U. globulosus*, *U. systoma*, *U. taprobanicus*, *U. anamalaiensis* and *U. montanus* see 'comparison' section of those species. *Uperodon mormorata* differs from *U. nagaoi*, *U. rohani* **sp. nov.** and *U. variegatus* by its densely mottled ventral surface (vs. inconspicuous spots and speckles present or absent in *U. nagaoi*; and complete absence of spots, blotches or mottling in *U. rohani* **sp. nov.** and *U. variegatus*) and relatively larger snout-vent size, male SVL 31–40 mm, *N* = 9, female SVL 32–43 mm, *N* = 3 (vs. relatively smaller, *U. nagaoi*: male SVL 25–32 mm, *N* = 8; *U. rohani* **sp. nov.**: male SVL 26–34 mm, *N* = 16, female SVL 28–35 mm, *N* = 8; *U. variegatus*: male SVL 25–33 mm, *N* = 12, female SVL 29–36 mm, *N* = 7). This species could be confused with *U. anamalaiensis, U. obscurus, U. palmatus* and *U. triangularis* due to its mottled ventral skin. However, *U. mormorata* differs from all these species by its relatively larger snout-vent size, male SVL 31–40 mm, *N* = 9, female SVL 32–43 mm, *N* = 3 (vs. smaller, *U. obscurus*: male SVL 22–31 mm, *N* = 17, female SVL 30–38 mm, *N* = 5; *U. palmatus*: male SVL 27–31 mm, *N* = 4, female SVL 34–36 mm, *N* = 2; *U. triangularis*: male SVL 25–37 mm, *N* = 20, female SVL 33–42 mm, *N* = 4), its ventral surface (including throat and limbs) being densely marbled (vs. scattered spots or blotches, largely on chest and belly), and shank relatively shorter than thigh, male: SHL/TL ratio 0.8–1.1, *N* = 9, female: SHL/TL ratio 0.8–0.9, *N* = 3 (vs. nearly equal, *U. obscurus*: male: SHL/TL ratio 0.9–1.0, *N* = 17, female: SHL/TL ratio 0.9–1.1, *N* = 5; *U. palmatus*: male: SHL/TL ratio 1.0, *N* = 4, female: SHL/TL ratio 1.0, *N* = 2; *U. triangularis*: male: SHL/TL ratio 0.9–1.1, *N* = 20, female: SHL/TL ratio 0.9–1.0, *N* = 4).

Genetic divergence. For 16S mitochondrial gene sequences, the sampled populations of *Uperodon mormorata* showed an average intraspecific distance of 0.6% (range 0–1.2%, *N* = 11). Populations from Maharashtra and Karnataka were observed to be divergent by up to 1.2%. Genetically, *U. mormorata* is closely related to *U. triangularis*, from which it was found to differ by an average uncorrected genetic distance of 2.9% (range 2.4–3.6%, *N* = 99). For interspecific genetic distances with all other members of the genus, see Table 3.

Description of neotype (measurements in mm) (Figs. 3F, 7M–P). Small-sized (SVL 32.4), relatively robust adult female; head small (HW 9.6, HL 8.8, IFE 4.4, IBE 8.6), less than one-third (27.2%) of body length, wider than long (HW/HL ratio 1.1); snout truncate in dorsal and ventral view, vertical in lateral view, its length (SL 3.1) shorter than horizontal diameter of eye (EL 2.6); loreal region acute with rounded canthus rostralis; interorbital space nearly twice as wide (IUE 3.0) as upper eyelid width (UEW 1.6); nostril closer to tip of snout (NS 0.6) than to eye (EN 1.5); supratympanic fold distinct, extending from posterior corner of upper eyelid to insertion of forelimb at axilla; eye diameter (EL 2.6); vomerine odontophores present on the palate, prominent, without teeth; weakly-developed neopalatinal ridges on posterior side of each choana, appear fused with the vomerine odontophores; tongue moderately large, emarginate. Forelimbs moderately long and thin; forearm (FAL 6.5) shorter than hand length (HAL 9.1); finger length formula I<II<IV<III; tips of all fingers with truncate discs, without grooves, moderately wide compared to finger width (FD_I 1.5, FW_I 0.3; FD_{II} 1.5, FW_{II} 0.4; FD_{III} 1.8, FW_{III} 0.5; FD_{IV} 1.5, FW_{IV} 0.4); subarticular tubercles prominent, oval, all present; two well-developed palmar tubercles

(inner, oval, 1.6 mm long; outer, bilobed, 1.9 mm long). Hind limbs relatively long and thin, thigh length (TL 13.5) longer than shank (SHL 11.1) and foot (FOL 12.9); tips of all toes with small truncate to rounded discs, discs rather wide compared to toe width (TD_I 0.7, TW_I 0.4; TD_{II} 0.8, TW_{II} 0.6; TD_{III} 1.0, TW_{III} 0.7; TD_{IV} 1.0, TW_{IV} 0.6; TD_V 0.8, TW_V 0.5); foot webbing present: $I2^{-}$–2II2–3III2–3IV3–2V; well-developed dermal fringe present on all toes; subarticular tubercles prominent, oval; two smooth metatarsal tubercles, oval, outer slightly longer than the inner.

Skin of snout, between eyes, sides of head, anterior part of the dorsum, posterior parts of back, and upper and lower parts of flank, granular; dorsal surfaces of forelimb, thigh, tibia and tarsus, shagreened to sparsely granular (Figs. 3F, 7M); ventral surfaces shagreened.

Colouration. *In preservation*: Dorsum olive grey with scattered dark brown spots, dark brown inverted 'V' at the level of shoulder (directed downwards), a dark brown line between eyes, another two lines: one on snout, and another between inverted 'V' and line connecting the eyes; dorsal surfaces of forelimb, thigh and shank (including fingers and toes), olive grey with dark brown cross bands; groin and anterior parts of thigh, light grey with light brown mottling, and a light brown patch near cloacal region; throat, chest, belly, and ventral surfaces of forelimbs and hind limbs, light brown with prominent light grey reticulations (Fig. 3F). *Colour in life* (SDBDU 2016.3404): Dorsum dark olive grey with scattered dark brown spots especially on posterior part of dorsum, thigh and shank, faint dark brown inverted 'V' at the level of shoulder (directed downwards); dorsal surfaces of forelimb, thigh and shank (including fingers and toes), olive grey with dark brown cross bands; groin and anterior parts of thigh, light brown with light grey and white mottling; throat, chest, belly, and ventral surfaces of forelimb and hind limb, dark brown with prominent light greyish-blue reticulations (Figs. 9A–C).

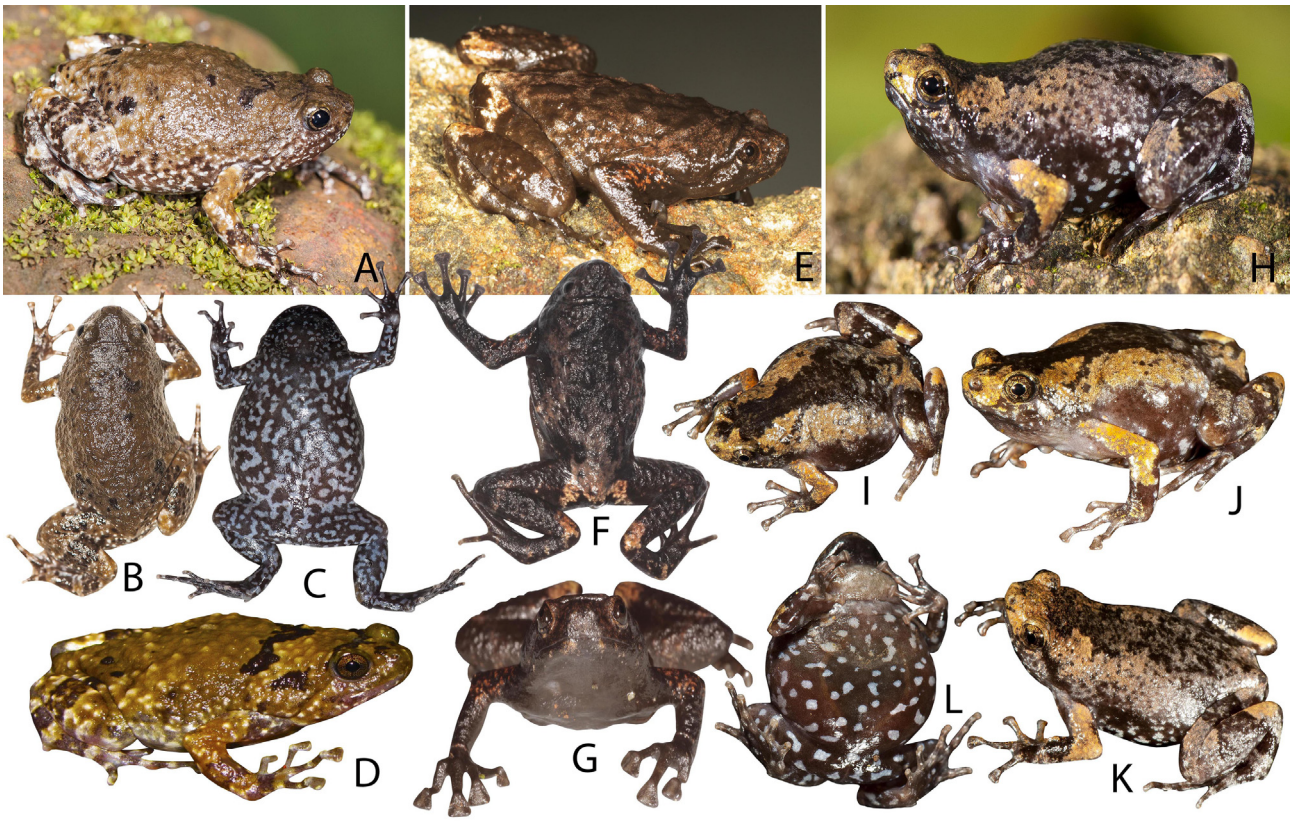

FIGURE 9. *Uperodon mormorata*, *U. nagaoi* and *U. obscurus* in life. **A–C.** *Uperodon mormorata* (SDBDU 2016.3404, male): **A.** Dorsolateral view; **B.** dorsal view; **C.** ventral view; **D.** *Uperodon mormorata* (SDBDU 2011.835, male), dorsolateral view; **E–G.** *Uperodon nagaoi* (DZ 1367, male): **E.** Dorsolateral view; **F.** dorsal view; **G.** frontal view; **H–K.** *Uperodon obscurus*: **H.** Dorsolateral view (DZ 1366, male); **I.** Dorsal view (DZ 1366, male); **J.** dorsolateral view (DZ 1408, male); **K.** dorsolateral view (DZ 1369, male); **L.** ventral view (DZ 1369, male). (Images: SD Biju and E–G Madhava Meegaskumbura).

Variations. Morphometric measurements for 12 specimens, including the holotype, are given in Table 4. Overall, the skin colouration and texture (except markings), are nearly similar in all the examined specimens.

However, webbing between toes is observed to be highly variable, without being consistent even between the same sexes. Foot webbing: SDBDU 2002.567 (female): medium, I2^{-}–2II2–3III2^{+}–3IV3–2V; SDBDU 2012.43 (male): large, I1–2II1–1III1–2IV2–1V; SDBDU 2015.3082 (male): medium, I1–2II1–2III2–3IV3–2V (Figs. 7Q–S). SDBDU 2015.3085: dorsum with more prominent blackish-brown spots.

Note. In the original description, Rao (1937) stated this species to have "No occipital fold". However, Das & Whitaker (1997) discussed its presence based on their observation of occipital folds in both their examined samples of *Uperodon mormorata* (MCZ A. 116283 and MCZ A. 15421). Variable occurrence of occipital fold was earlier also reported by Parker (1934). We closely examined the presence and absence of occipital fold in members of the genus *Uperodon*, and observe that its presence may be an artifact of preservation caused due to stretching of loose skin of the snout towards the head.

Secondary sexual characters. Male (SDBDU 2016.3404): Vocal sac externally visible on the lower jaw; female (ZSI/WGRC/V/A/958) ova white, pigmented on pole (diameter 0.6–0.8 mm, *N* = 20).

Vocalization. Male of *Uperodon mormorata* (SDBDU 2016.3404) from Goa produced a single type of call with pulsatile temporal structure. The calls had uniform intervals and were not delivered in groups. A typical male call had a duration of 182.6 ms, rise time of 108.3 ms, and fall time of 57.4 ms. The call comprised of 28 pulses that were delivered at a rate of 154.7 pulses/s. The spectrum was characterized by single broad peak with mean dominant frequency of 2.6 kHz (Figs. 8E–H).

Geographical distribution and habitat. In the present study, the presence of *Uperodon mormorata* is confirmed in the Western Ghats states of Karnataka, Maharashtra, Goa and Gujarat (Fig. 2C; Tables 1). For additional previous records and references thereto see supplementary Table S1. Report of this species from Assam (Dey 2001) is doubtful. We collected this species predominantly from terrestrial habitats such as rock crevices, fallen logs and under stones, and occasionally from tree barks about two metres above the ground. It was found in and around secondary forest areas (Amba, Amboli, Bygoor, Dandeli, Londa, Netravali, Sakleshpur, Samot and Castle rock), primary forests (Shimoga), as well as marshes (coastal Goa), at elevations from sea level up to 1050 m asl.

Uperodon nagaoi (Manamendra-Arachchi and Pethiyagoda, 2001)

Nagao's Globular Frog
(Figs. 1, 2A, 2D, 3G, 7T–W, 9E–G; Tables 1–4)

Original name and description. *Ramanella nagaoi* Manamendra-Arachchi and Pethiyagoda, 2001. *Ramanella nagaoi*, a new tree-hole frog (Microhylidae) from southern Sri Lanka. *Journal of South Asian Natural History*, 5: 121–133. **Holotype.** WHT 2826, by original designation, an adult male, SVL 25.6 mm. **Type locality.** "Kanneliya Forest Reserve (near Galle), Sri Lanka". **Current status of specific name.** Valid name, as *Uperodon nagaoi* (Manamendra-Arachchi and Pethiyagoda, 2001).

Comparison. For comparison of *Uperodon nagaoi* with *U. globulosus*, *U. systoma*, *U. taprobanicus*, *U. anamalaiensis*, *U. montanus* and *U. mormorata* see 'comparison' section of those species. *Uperodon nagaoi* differs from *U. rohani* **sp. nov.** and *U. variegatus* by its dorsum being light grey to dark brownish-grey without prominent markings (vs. light to dark brown with light grey or olive-markings) and nearly uniform brown ventral skin without or with inconspicuous spots and speckles (vs. uniformly white, without any spots, blotches or mottling). Specifically, it differs from *U. variegatus* by its shank relatively longer than thigh, SHL/TL ratio 1.0–1.2, *N* = 8 (vs. shorter, male: SHL/TL ratio 0.9–1.0, *N* = 16, female: SHL/TL ratio 0.8–0.9, *N* = 7) (Table 4). Further, *U. nagaoi* differs from *U. obscurus* and *U. palmatus* by its shank relatively longer than thigh, male: SHL/TL ratio 1.0–1.2, *N* = 8 (vs. nearly equal, *U. obscurus*: male: SHL/TL ratio 0.9–1.0, *N* = 17, female: SHL/TL ratio 0.9–1.1, *N* = 5; *U. palmatus*: male: SHL/TL ratio 1.0, *N* = 4, female: SHL/TL ratio 1.0, *N* = 2), rudimentary webbing between toes, I1–2II2–3^{+}III3–4IV4^{+}–3V (vs. more, *U. obscurus*: I1–2II1$^{1}/_{2}$–3^{-}III2–3^{+}IV3^{+}–2V; *U. palmatus*: I1–2II1–3^{-}III1–3IV2$^{2}/_{3}$–1V), and ventral skin without or with inconspicuous spots and speckles (vs. prominent spots or blotches). It differs from *U. triangularis* by its dorsal skin in having faint brown to dark brown coloured markings (vs. prominent bright orange coloured markings), ventral skin without or with inconspicuous spots and speckles (vs. prominent spots or blotches), and tadpoles with funnel-shaped mouth and papillae (vs. terminal mouth lacking papillae).

Genetic divergence. For 16S mitochondrial gene sequences, intraspecific variation was not observed between the sampled populations of *Uperodon nagaoi* (*N* = 2). Genetically, *U. nagaoi* is closely related to *U. obscurus* and *U. palmatus*; from these it was found to differ by an average uncorrected genetic distance of 5.6% (*N* = 6) and 4.0% (range 4.0–4.2%, *N* = 8), respectively. For interspecific genetic distances with all other members of the genus, see Table 3.

Description of holotype. A detailed general description was published by Manamendra-Arachchi & Pethiyagoda (2001).

Variations. Morphometric measurements for eight specimens, including the type series, are given in Table 4.

Secondary sexual character. Male (DZ 1367): Vocal sac externally visible on the lower jaw.

Geographical distribution and habitat. This species is endemic to Sri Lanka, where it is known to occur in the Central, Sabaragamuwa, Southern and Western Provinces (Fig. 2D). For list of localities and references thereto see Supplementary Table S1. In the present study, we collected this species from tree holes at Hiyare Forest Reserve (Galle district) from elevation of 125 m asl, in the vicinity of its type locality Kanneliya Forest Reserve. See 'Natural history and breeding' observations in the respective section, after the species accounts.

***Uperodon obscurus* (Günther, 1864 "1863")**
Sri Lankan Globular Frog
(Figs. 1, 2A, 2D, 3H, 5G, 9H–K, 10A–D; Tables 1–4)

Original name and description. *Callula obscura* Günther, 1864 "1863". *The Reptiles of British India*. London: Ray Society by R. Hardwicke: 438. **Holotype.** By monotypy, NHM 58.11.28.42 (ex. BMNH 1947.2.11.20), an adult female, SVL 32.2 mm. **Type locality.** "Ceylon" (Sri Lanka). **Current status of specific name.** Valid name, as *Uperodon obscurus* (Günther, 1864 "1863").

Comparison. For comparison of *Uperodon obscurus* with *U. globulosus*, *U. systoma*, *U. taprobanicus*, *U. anamalaiensis*, *U. montanus*, *U. mormorata* and *U. nagaoi* see 'comparison' section of those species. *Uperodon obscurus* is closely related to *U. palmatus*, both genetically and morphologically. However, it differs from the latter by its snout length longer than horizontal diameter of eye, male: EL/SL ratio 0.6–0.9, *N* = 17; female: EL/SL ratio 0.6–0.9, *N* = 5 (vs. equal, male: EL/SL ratio 1.0, *N* = 4, female: EL/SL ratio 1.0, *N* = 2) (Table 4), snout nearly acute in lateral view (vs. vertical), relatively less webbing, I1–2II1$^{1}/_{2}$–3^{-}III2–3^{+}IV3^{+}–2V (vs. more, I1–2II1–3^{-}III1–3IV2$^{2}/_{3}$–1V) (Fig. 10D), and dorsal skin shagreened to sparsely granular (vs. distinctly granular with warty projections). It differs from *U. triangularis* by its fourth toe webbing extending close up to second subarticular tubercle: I1–2II1$^{1}/_{2}$–3^{-}III2–3^{+}IV3^{+}–2V (vs. toes completely free of webbing). *Uperodon obscurus* cannot be confused with three other species, *U. nagaoi*, *U. rohani* **sp. nov.** and *U. variegatus*, due to its relatively extensive foot webbing, I1–2II1$^{1}/_{2}$–3^{-}III2–3^{+}IV3^{+}–2V (vs. rudimentary or absent), and ventral skin being light to dark brown with distinct blotches or spots (vs. brown without prominent mottling in *U. nagaoi*, and white without any blotches or spots in *U. rohani* **sp. nov.** and *U. variegatus*).

Genetic divergence. For 16S mitochondrial gene sequences, intraspecific variation was not observed between the sampled populations of *Uperodon obscurus* (*N* = 3). Genetically, *U. obscurus* is closely related to *U. palmatus*, from which it was found to differ by an average uncorrected genetic distance of 2.4% (range 2.4–2.6%, *N* = 12). For interspecific genetic distances with all other members of the genus, see Table 3.

Remarks. The original description by Günther (1864 "1863") was very brief. Subsequently Parker (1934) provided a general description based on the types, without a comparison with other closely related members. Hence, a detailed description and comparison of this species with all its congeners is provided here.

Redescription of holotype (measurements in mm) (Figs. 3H, 10A–D). Small-sized (SVL 32.2), slender adult female; head small (HW 9.3, HL 8.8, IFE 4.9, IBE 8.6), less than one-third (27.3%) of body length, wider than long (HW/HL ratio 1.1); snout truncate in dorsal and ventral view, nearly acute in lateral view, its length (SL 4.2) longer than horizontal diameter of eye (EL 3.9); loreal region acute with rounded canthus rostralis; interorbital space more than twice as wide (IUE 3.3) as upper eyelid width (UEW 1.4), and wider than internarial distance (IN 2.7); nostril much closer to tip of snout (NS 0.7) than to eye (EN 2.4); supratympanic fold distinct, extending from posterior corner of upper eyelid to insertion of forelimb at axilla; eye diameter (EL 3.9); vomerine odontophores present on the palate, without teeth; weakly-developed neopalatinal ridges on posterior side of each choana, appear fused with

the vomerine odontophores; tongue moderately large, oval, slightly emarginate. Forelimbs (FAL 8.8) shorter than hand length (HAL 9.5); finger length formula I<II<IV<III, tips of all fingers with oval discs, moderately wide compared to finger width (FD_I 0.8, FW_I 0.4; FD_{II} 1.1, FW_{II} 0.5; FD_{III} 1.0, FW_{III} 0.5; FD_{IV} 0.9, FW_{IV} 0.4); subarticular tubercles prominent, oval, all present; two well-developed palmar tubercles, oval. Hind limbs relatively long and thin, thigh length (TL 13.5) longer than shank (SHL 13.3), and shorter than foot (FOL 14.9); relative digit lengths I<II<V<III<IV, tips of all toes with small truncate to rounded discs, rather wide compared to toe width (TD_I 0.7, TW_I 0.5; TD_{II} 0.8, TW_{II} 0.5; TD_{III} 0.7, TW_{III} 0.5; TD_{IV} 0.7, TW_{IV} 0.5; TD_V 0.5, TW_V 0.5); foot webbing present, I1–2II$1^1/_2$–3^-III2–3^+IV3^+–2V; well-developed dermal fringes present on all toes; subarticular tubercles prominent, oval; two smooth metatarsal tubercles, oval, outer one slightly larger than the inner.

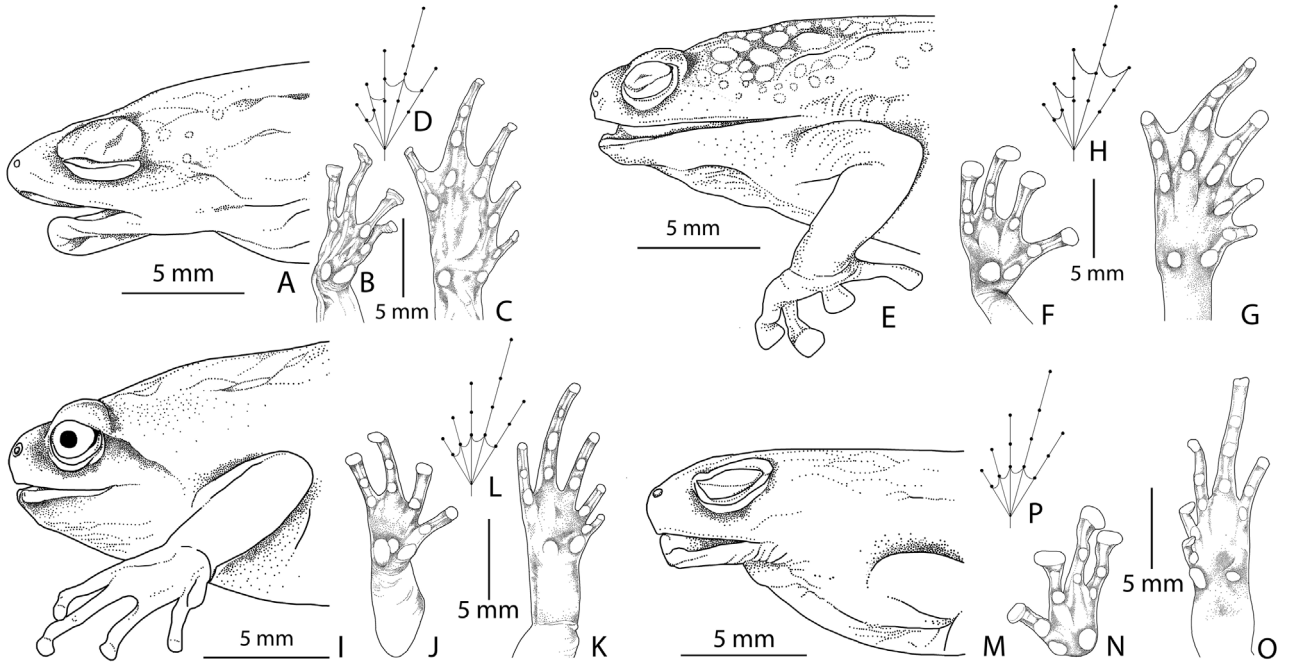

FIGURE 10. Head, hand, foot and foot webbing in *Uperodon obscurus*, *U. palmatus*, *U. triangularis* and *U. variegatus*. **A–D.** Holotype of *Uperodon obscurus* (NHM 58.11.28.42 ex. BMNH 1947.2.11.20, female): **A.** Lateral view of head; **B.** ventral view of hand; **C.** ventral view of foot; **D.** schematic illustration of foot webbing; **E–H.** Holotype of *Uperodon palmatus* (NHM 90.11.8.62 ex. BMNH 1947.2.11.21, female): **E.** Lateral view of head; **F.** ventral view of hand; **G.** ventral view of foot; **H.** schematic illustration of foot webbing; **I–L.** Lectotype of *Uperodon triangularis* (NHM 74.4.29.897 ex. BMNH 1947.2.11.15, male): **I.** Lateral view of head; **J.** ventral view of hand; **K.** ventral view of foot; **L.** schematic illustration of foot webbing; **M.** Lectotype of *Uperodon variegatus* (ZSI 2761, female), lateral view of head; **N–P.** Referred specimen of *Uperodon variegatus* (ZSI 4726, female): **N.** ventral view of hand; **O.** ventral view of foot; **P.** schematic illustration of foot webbing. (Illustrations: SD Biju).

Skin of snout, between eyes, sides of head, and anterior part of dorsum, shagreened to granular; posterior parts of back, and upper and lower parts of flank, granular; dorsal surfaces of forelimb, thigh, tibia and tarsus, shagreened to sparsely granular; throat, chest and abdomen, shagreened; ventral surfaces of forelimb and hind limb, shagreened (Figs. 3H, 10A).

Colouration. *In preservation*: Dorsum greyish-brown with dark brown median patch; flanks light greyish-brown; dorsal surfaces of forelimbs, thigh, shank and foot, light brown; chest and belly, dark grey with faint grey spots; ventral surfaces of thigh, tibia and foot, greyish-brown with faint grey spots (Fig. 3H). *Colour in life* (DZ 1366): Dorsum light orangish-brown with irregular blackish-brown spots, prominent blackish-brown band extending from behind the eye up to vent where it becomes wider; lower parts of flank brown with light bluish-grey spots; dorsal surfaces of forelimb, thigh, shank and foot, orangish-brown with dark brown cross bands; throat light brown; chest greyish-brown; belly and ventral surfaces of forelimb, thigh, tibia and foot, brown with light bluish-grey spots (Figs. 9H–I).

Variations. Morphometric measurements of 17 males and five females, including the holotype, are given in

Table 4. DZ 1408: dorsal skin bright orange and more prominently granular compared to DZ 1366; DZ 1369: dorsum orangish-grey with a dark grey median band, and ventral surfaces coffee brown with light bluish-grey spots, except on the throat.

Secondary sexual characters. Male (DZ 1366): vocal sac externally visible on the lower jaw; female (NHM 1982.1290): ova white, pigmented on pole (diameter 0.7–1.0 mm, $N = 20$).

Geographical distribution and habitat. *Uperodon obscurus* is endemic to Sri Lanka and known to occur in Central, North Western, Sabaragamuwa, Southern and Uva Provinces (Fig. 2D; Tables 1, S1). In the present study, we confirmed the occurrence of this species in Kandy district (Kandy, Peradeniya, Panwila, Pussellawa and Udawatta Kele), Kegalle district (Babilapitiya estate), Kurunegala district (Kurunegala), Matale district (Gammaduwa), Nuwara Eliya district (Bogawantalawa and Laxapana) and Ratnapura district (Sinharaja and Morningside), from elevations of 100 m up to 1220 m asl. It was collected either from tree hollows in disturbed forests adjacent to urban areas (Peradeniya and Panwila), or temporary ponds surrounded with vegetation (Laxapana).

***Uperodon palmatus* (Parker, 1934)**
Parker's Globular Frog
(Figs. 1, 2A, 2D, 3I, 5H, 10E–H, 11A–E; Tables 1–4)

Original name and description. *Ramanella palmata* Parker, 1934. *A Monograph of the Frogs of the Family Microhylidae*. London: Trustees of the British Museum: 93. **Holotype.** NHM 90.11.8.62 (ex. BMNH 1947.2.11.21), by original designation. **Type locality.** "Newera Ellya, Ceylon, 7,000 ft" (= Nuwara-Eliya), Sri Lanka. **Current status of specific name.** Valid name, as *Uperodon palmatus* (Parker, 1934).

Comparison. For comparison of *Uperodon palmatus* with *U. globulosus*, *U. systoma*, *U. taprobanicus*, *U. anamalaiensis*, *U. montanus*, *U. mormorata*, *U. nagaoi* and *U. obscurus* see 'comparison' section of those species. *Uperodon palmatus* differs from *U. triangularis* by presence of webbing between toes, I1–2II1–3–III1–3IV2$^{2}/_{3}$–1V (vs. toes without webbing); and snout equal to eye diameter, male: EL/SL ratio 1.0, $N = 4$, female: EL/SL ratio 1.0, $N = 2$ (vs. longer, male: EL/SL ratio 0.6–0.9, $N = 20$, female: EL/SL ratio 0.7–0.9, $N = 4$) (Table 4). *Uperodon palmatus* cannot be confused with three other species, *U. nagaoi*, *U. rohani* **sp. nov.** and *U. variegatus*, due to presence of more extensive webbing between toes, I1–2II1–3–III1–3IV2$^{2}/_{3}$–1V (vs. rudimentary or absent); and ventral skin light to dark brown with distinct blotches or spots (vs. brown without prominent blotches or spots in *U. nagaoi*, and white without blotches or spots in *U. rohani* **sp. nov.** and *U. variegatus*).

Genetic divergence. For 16S mitochondrial gene sequences, the sampled populations of *Uperodon palmatus* showed an average intraspecific distance of 0.1% (range 0–0.2%, $N = 4$). Genetically, *U. palmatus* is closely related to *U. obscurus*, from which it was found to differ by an average uncorrected genetic distance of 2.4% (range 2.4–2.6%, $N = 12$). For interspecific genetic distances with all other members of the genus, see Table 3.

Remark. A short general description was published by Parker (1934), though without a comparison with other closely related members. Hence, a detailed description and comparison of this species with all its congeners is provided here.

Redescription of holotype (measurements in mm) (Figs. 3I, 10E–H). Small-sized (SVL 34.6), slender adult female; head small (HW 11.8, HL 9.1, IFE 4.8, IBE 9.4), less than one-third (26.3%) of body length, wider than long (HW/HL ratio 1.3); snout truncate in dorsal view, truncate to rounded in ventral view, and vertical in lateral view, its length (SL 3.6) slightly longer than horizontal diameter of eye (EL 3.5); loreal region acute with rounded canthus rostralis; interorbital space twice as wide (IUE 3.8) as upper eyelid width (UEW 1.9), and internarial distance (IN 1.9); nostril much closer to tip of snout (NS 0.5) than to eye (EN 1.9); supratympanic fold distinct, extending from posterior corner of upper eyelid to insertion of forelimb at axilla; eye diameter (EL 3.5); vomerine odontophores present on the palate, without teeth; indistinct neopalatinal ridges on posterior side of each choana, appear fused with the vomerine odontophores; tongue moderately large, oval, slightly emarginate. Forelimbs (FAL 7.4) shorter than hand length (HAL 10.4); finger length formula I<II<IV<III, tips of all fingers with oval discs, moderately wide compared to finger width (FD_{I} 1.0, FW_{I} 0.3; FD_{II} 1.7, FW_{II} 0.5; FD_{III} 1.7, FW_{III} 0.5; FD_{IV} 1.3, FW_{IV} 0.5); subarticular tubercles prominent, oval, all present; two well-developed palmar tubercles. Hind limbs relatively long and thin, thigh length (TL 14.8) longer than shank (SHL 14.6), and shorter than foot (FOL 15.4);

tips of all toes with small truncate to rounded discs, rather wide compared to toe width (TD_I 0.8, TW_I 0.4; TD_{II} 0.8, TW_{II} 0.5; TD_{III} 0.9, TW_{III} 0.5; TD_{IV} 1.1, TW_{IV} 0.5; TD_V 0.8, TW_V 0.4); foot webbing present, I1–2II1–3–III1–3IV2$^{2}/_{3}$–1V; well-developed dermal fringes present on all toes; subarticular tubercles prominent, oval; two oval smooth metatarsal tubercles.

Skin of snout, between eyes, sides of head, anterior part of dorsum, posterior parts of back, and upper and lower parts of flank, granular (Fig. 3I); dorsal surfaces of forelimb, thigh, tibia and tarsus, shagreened to sparsely granular; anterior parts of thigh with spinular projections.

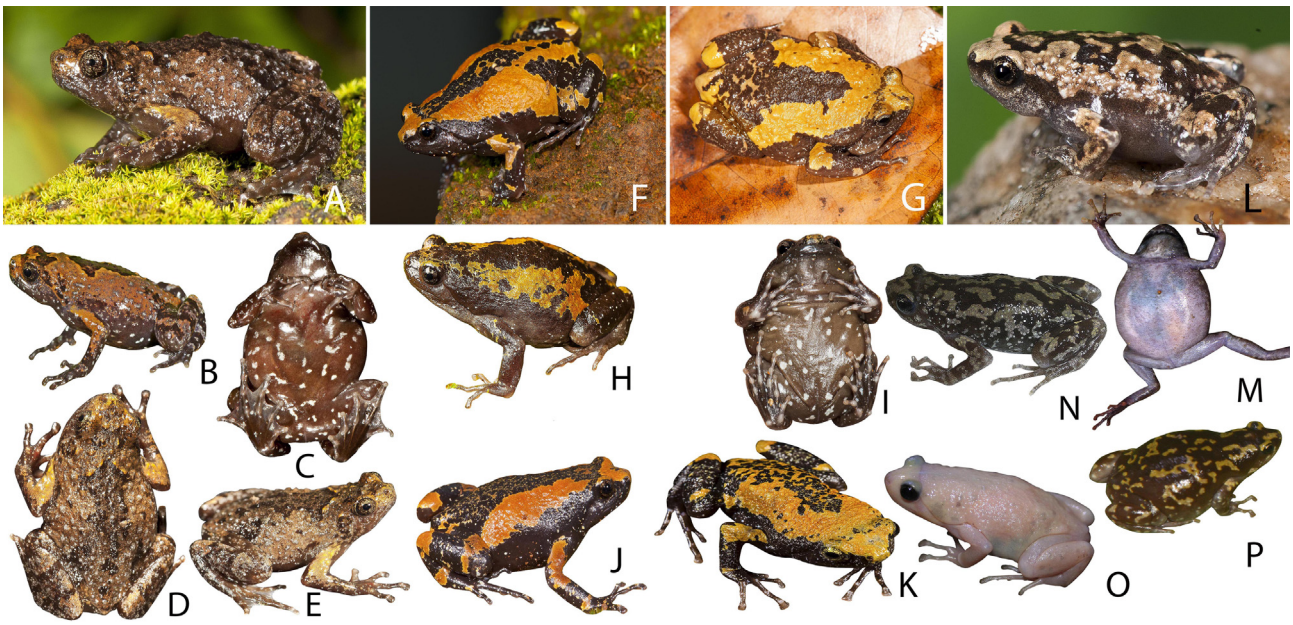

FIGURE 11. *Uperodon palmatus*, *U. triangularis* and *U. variegatus* in life. **A–E.** *Uperodon palmatus*: **A.** Dorsolateral view (DZ 1372, male); **B.** dorsolateral view (DZ 1372, male); **C.** ventral view (DZ 1371, male); **D.** dorsal view (DZ 1331, male); **E.** dorsolateral view (DZ 1331, male); **F–K.** *Uperodon triangularis*: **F.** Dorsolateral view (ZSI/WGRC/V/A/959, male); **G.** dorsal view (SDBDU 2015.2857, male); **H.** ventral view (SDBDU 2015.2857, male); **I.** dorsolateral view (SDBDU 2011.502, male); **J.** dorsolateral view (SDBDU 2012.2200, subadult male); **K.** dorsofrontal view (SDBDU 2012.2038, male); **L–P.** *Uperodon variegatus*: **L.** Dorsolateral view (not preserved); **M.** ventral view (SDBDU 2007.4994, male); **N.** dorsolateral view (not preserved); **O.** dorsolateral view of an albino (or possibly leucistic) form (not preserved); **P.** dorsolateral view (not preserved). (Images: SD Biju, Sonali Garg, N & P - Shyamal L, O - Romulus Whitaker).

Colouration. *In preservation*: Dorsum reddish-brown with light brown spots, prominent light brown median band starting well behind the eye at the level of shoulders and extending up to the vent; flanks light greyish-brown; dorsal surfaces of forelimbs, thigh, shank and foot, light greyish-brown; throat reddish brown; chest light brown; belly light brown with grey spots; ventral surfaces of thigh, tibia and foot, light brown with faint grey spots (Fig. 3I). *Colour in life* (DZ 1372). Dorsum greyish-brown with irregular blackish-brown spots, prominent dark brown band starting well behind the eye at the level of shoulders and extending up to vent; lower parts of flank brown with faint greyish-white spots; dorsal surfaces of forelimb, thigh, shank and foot, greyish-brown with dark brown cross bands; throat light greyish-brown; chest greyish-brown; belly and ventral surfaces of forelimb, thigh, tibia and foot, brown with scattered greyish-white spots (Fig. 11A).

Variations. Morphometric measurements of six specimens, including the holotype, are given in Table 4. DZ 1331: dorsum light greyish-brown with a blackish-brown dorsal band; DZ 1371: dorsum orangish-brown with dark brown dorsal band.

Secondary sexual characters. Male (DZ 1371): vocal sac externally visible on the lower jaw; female (holotype): ova white, pigmented on pole (diameter 0.7–1.0 mm, $N = 10$).

Geographical distribution and habitat. *Uperodon palmatus* is endemic to Sri Lanka with confirmed distribution only in the high elevation regions (1400–2000 m asl) of the Central Province: Agrapatana, Bogawantalawa, Hakgala, Horton plains, Pattipola, Nuwara-Eliya and Morey estate (Fig. 2D; Tables 1, S1). See 'Natural history and breeding' observations in the respective section, after the species accounts.

***Uperodon triangularis* (Günther, 1876 "1875")**
Triangle-spotted Globular Frog
(Figs. 1, 2A, 2C, 3J, 5I, 8I–L, 10I–L, 11F–K; Tables 1–4)

Original name and description. *Callula triangularis* Günther, 1876 "1875". Third report on collections of Indian reptiles obtained by the British Museum. *Proceedings of the Zoological Society of London*, 1875: 567–577. **Syntypes.** NHM 74.4.29.891–900 and NHM 74.4.29.1010, according to Parker (1934). **Type locality.** "Malabar", India. **Current status of specific name.** Valid name, as *Uperodon triangularis* (Günther, 1876 "1875"). **Synonym.** *Ramanella triangularis rufeventris* Rao, 1937 (Dutta 1997), Neotype by present designation, ZSI/WGRC/V/A/959, an adult male, from Mudigere, Karnataka state, India, collected by SD Biju and team on 28 September 2012.

Comments. The original description (Günther, 1876 "1875") mentions 11 syntypes from Malabar, all from Col. Beddome's collection. We examined all the syntypes (nine males and two females) available at NHM, and found NHM 74.4.29.897 (ex. BMNH 1947.2.11.15) to be in agreement with the original description. This specimen was also found to be in well-preserved condition (Fig. 3J). Since the original description for this nominal taxon was brief and based on several specimens from an imprecise locality "Malabar" (Biju 2001), and because this species has often been misidentified by researchers (e.g., Rao 1937; Inger *et al*. 1984), we herein provide a detailed description of an adult male specimen from the type series, NHM 74.4.29.897 (ex. BMNH 1947.2.11.15), that may serve as a reference of this species for future taxonomic works.

Notes on synonymy and neotypification of *Ramanella triangularis rufeventris* Rao, 1937. A new variety of this species was described from "Mudigere, Kadur, Saklespur, Hassan" in Karnataka as *Ramanella triangularis rufeventris* n. var Rao, 1937. This taxon was considered to be a synonym of *Ramanella triangularis* (= *Uperodon triangularis*) by implication (Dutta 1997), however, without any justification or comparison. In order to verify this action, we compared the two taxa based on the original description. While describing *Ramanella triangularis rufeventris*, Rao stated two major differences between the new variety "of the plains" and the typical forms of *Uperodon triangularis* from "Malnad areas" (= Malenadu region of Karnataka): (1) "the snout is pointed, tips obliquely truncated, prominent", and (2) "Tibio-tarsal articulation stands well behind the shoulder", and also included illustrations (Pl. XXIX. Figs. 18 and 18a). Apart from these characters, he used colour and marking differences to distinguish the new variety. During our surveys in regions spanning the type locality of this name bearing taxon ("Mudigere"), we collected *Uperodon* specimens that were comparable with Rao's description of "*Ramanella triangularis rufeventris*" particularly in having a more reddish dorsal colour. Due to unavailability of type specimens, considered lost (Dubois 1984), we relied on the original description to compare our new collections. We found majority of the characters to be same as in *Uperodon triangularis*, with only minor differences in colour and markings that were not reliable for distinguishing the two taxa from each other. Further, since the snout shape mentioned in the original description of *Ramanella triangularis rufeventris* is contradicting, we relied on the illustration that clearly shows the snout as "truncate" and not "pointed", which is also similar to *Uperodon triangularis*. The mitochondrial 16S rRNA gene sequences of our new collections comparable with Rao's new variety, and those of *Uperodon triangularis* from the Malabar region of northern Kerala, were also found to be shallowly divergent (1.5%). Hence, based on findings in this study we confirm *Ramanella triangularis rufeventris* Rao, 1937 to be a junior subjective synonym of *Callula triangularis* Günther, 1876 "1875" [= *Uperodon triangularis* (Günther, 1876 "1875")].

Additionally, since the type material for *Ramanella triangularis rufeventris* Rao, 1937 is lost (Dubois 1984), we herein also designate ZSI/WGRC/V/A/959 (an adult male from Mudigere) as the neotype of *Ramanella triangularis rufeventris* Rao, 1937, in order to define this taxon objectively and to establish taxonomic stability. The description provided along with figures (Figs. S1F–J) in the supplementary file S1 also shows that the neotype is largely consistent with what is known of the former name-bearing type.

Comparison. For comparison of *Uperodon triangularis* with *U. globulosus*, *U. systoma*, *U. taprobanicus*, *U. anamalaiensis*, *U. montanus*, *U. mormorata*, *U. nagaoi*, *U. obscurus* and *U. palmatus* see 'comparison' section of those species. *Uperodon triangularis* cannot be confused with the two other species, *U. rohani* **sp. nov.** and *U. variegatus*, because of its ventral skin being brown to dark blackish-brown with prominent light grey spots and blotches (vs. uniformly white with complete absence of spots and blotches).

Genetic divergence. For 16S mitochondrial gene sequences, the sampled populations of *Uperodon triangularis* showed an average intraspecific distance of 0.9% (range 0–1.6%, $N = 9$). Populations from Karnataka

and Kerala were observed to be divergent by up to 1.6%. Genetically, *U. triangularis* is closely related to *U. mormorata*, from which it was found to differ by an average uncorrected genetic distance of 2.9% (range 2.4–3.6%, *N* = 99). For interspecific genetic distances with all other members of the genus, see Table 3.

Description of syntype, NHM 74.4.29.897 (measurements in mm) (Figs. 3J, 10I–L). Small-sized (SVL 31.6), slender adult female; head small (HW 9.6, HL 7.7, IFE 3.6, IBE 8.4), almost one-fourth (24.4%) of body length, wider than long (HW/HL ratio 1.2); snout rounded to nearly truncate in dorsal and ventral view, nearly acute in lateral view, its length (SL 3.7) longer than horizontal diameter of eye (EL 2.5); loreal region obtuse with rounded canthus rostralis; interorbital space wider (IUE 3.4) than upper eyelid width (UEW 1.9); nostril much closer to tip of snout (NS 0.9) than to eye (EN 2.1); supratympanic fold distinct, extending from posterior corner of upper eyelid to insertion of forelimb at axilla; eye diameter (EL 2.5); vomerine odontophores present on the palate, without teeth; presence of two weakly-developed neopalatinal ridges on posterior side of each choana, fused with the vomerine odontophores; tongue emarginated. Forelimb (FAL 7.1) shorter than hand length (HAL 8.7); finger length formula I<II<IV<III, tips of all fingers with truncate discs, discs moderately wide compared to finger width (FD_{I} 0.8, FW_{I} 0.6; FD_{II} 1.0, FW_{II} 0.7; FD_{III} 0.9, FW_{III} 0.6; FD_{IV} 0.8, FW_{IV} 0.5); subarticular tubercles prominent, oval, all present; two well-developed palmar tubercles (inner, oval, 0.7 mm; outer, shallowly lobed, 1.5 mm). Hind limbs relatively long and thin, thigh length (TL 11.4) longer than shank (SHL 10.9), and shorter than foot (FOL 12.1); tips of all toes with small truncate to rounded discs, discs rather wide compared to toe width; webbing absent between toes; dermal fringes absent on all toes; subarticular tubercles prominent, oval; two smooth metatarsal tubercles, oval, outer one longer (1.6 mm) than the inner (0.9 mm).

Skin of snout, between eyes, sides of head, anterior parts of dorsum, posterior parts of back, and upper and lower parts of flank, shagreened (Fig. 3J); dorsal surfaces of forelimb, thigh, tibia and tarsus, shagreened to sparsely granular; ventral surface uniformly shagreened.

Colouration. *In preservation* (NHM 74.4.29.897): Dorsum orangish-brown with solid darker brown median band on the back starting just above the level of shoulders and extending up to vent, where it becomes wider; brown stripe between eyes; flanks with orangish-brown patches; lateral sides of head brown, anterior and posterior parts orangish-brown; ventral surfaces (including limbs) brown with scattered light brown spots (Fig. 3J). *Colour in life* (SDBDU 2015.2857): Dorsum orange with solid dark brown median band on the back starting just above the level of shoulders and extending close to vent, where it becomes wider; dark brown stripe between eyes and another streak over snout; lateral sides of head and flanks dark brown; dorsal surfaces of limbs (including fingers and toes) dark brown, elbow and knee orange; ventral surfaces (including limbs) dark greyish-brown with scattered light grey spots (Figs. 11F–K).

Variations. Morphometric measurements for 19 males and four females are given in Table 4. Dorsal colouration and markings are highly variable among the examined specimens. SDBDU 2011.503: dorsal skin shagreened to sparsely granular, orange-coloured dorsolateral band discontinuous towards vent; SDBDU 2011.502: dorsal skin shagreened to sparsely granular, orange-coloured dorsolateral band patchy and discontinuous; SDBDU 2012.2038: dorsum largely olive grey in colour with dark brown median patch. SDBDU 2008.409: dorsum light brown with narrow band between upper eyelids.

Secondary sexual characters. Male (SDBDU 2011.504): vocal sac externally visible on the lower jaw; female (SDBDU 2007.6400): ova white, pigmented on pole (diameter 1.3–1.6 mm, *N* = 10).

Tadpole morphology. In dorsal view, tadpoles of *Uperodon triangularis* (Gosner stage 35, *N* = 2) have an elliptical body with narrower anterior region, and wider and longer posterior region; snout appears rounded in dorsal view and depressed in lateral view; eyes small, bulbous, positioned laterally; nasolacrimal duct absent; narial depressions clearly visible in lateral view, located much closer to snout than eyes, pigmentation not visible around nasal depressions; spiracle opens near vent, flap absent; vent tubular, positioned mid-ventrally with aperture opening medially in line with the plane of ventral fin; tail ends bluntly, composed of bilateral myotomic muscle masses divided by V-shaped septa, with unequal membranes on either side of tail musculature; dorsal fins originate after tail-body junction, margin of lower fin not parallel to margin of tail muscle; mouth terminal and appears as slit opening, keratinized structures absent, papillae absent (Figs. 16K–M).

Measurements (mm) (*N* = 1): Lateral measurements include; maximum height of body (*bh*) = 3.14, maximum width of body (*bw*) = 6.67, maximum diameter of eye (*ed*) = 0.56, internarial distance (*nn*) = 1.63, naro-pupular distance (*np*) = 2.78, rostro-narial distance (*rn*) = 0.02, interpupular distance (*pp*) = 5.43, distance from tip of snout to opening of spiracle (ss) = 6.24, distance from tip of snout to insertion of upper tail fin (su) = 9.82, snout-vent

length (svl) = 8.56, total length (tl) = 21.18, distance from vent to tip of tail (vt) = 12.51, maximum height of tail (*ht*) = 3.85, tail muscle height (tmh) = 1.87, and tail muscle width (tmw) = 1.89.

Vocalization. Male of *Uperodon triangularis* (SDBDU 2015.2857) from Suganthagiri produced a single type of call with pulsatile temporal structure. The calls had uniform intervals and were not delivered in groups. A typical male call had a duration of 228.9 ms, rise time of 132.3 ms, and fall time of 97.4 ms. The call comprised of 29 pulses that were delivered at a rate of 133.1 pulses/s. The spectrum was characterized by single broad peak with mean dominant frequency of 2.4 kHz (Figs. 8I–L).

Geographical distribution and habitat. *Uperodon triangularis* is known to occur in the South Indian states of Kerala, Karnataka and Tamil Nadu (Fig. 2C; Tables 1, S1). In the present study, we confirmed the presence of this species in following regions north of Palghat gap in the Western Ghats: Tamil Nadu (Ooty), northern Kerala (Kalpetta, Mananthavady, Pozhuthana and Suganthagiri) and southern Karnataka (Bygoor, Madikeri, Mudigere, and Wattakoli). It is a mid to high elevation species (about 675 m up to 2200 m asl). Individuals were found under fallen logs and stones during the non-breeding season, and observed around temporary puddles and permanent water bodies during the breeding season. At Bygoor, this species was found about four feet above ground on tree bark inside coffee plantations. For misidentified records from south of Palghat gap see 'Notes' under *U. anamalaiensis*.

***Uperodon variegatus* (Stoliczka, 1872)**

Variegated Globular Frog

(Figs. 1, 2A, 3K, 5J, 10M–P, 11L–P, 12A, 13, 14; Tables 1–4)

Original name and description. *Callula variegata* Stoliczka, 1872. Observations on Indian Batrachia. *Proceedings of the Asiatic Society of Bengal*, 1872: 101–113. **Lectotype.** By present designation, ZSI 2761, an adult female, SVL 29.8 mm. **Type locality.** "Ellore" (=Eluru, Andhra Pradesh) India. **Current status of specific name.** Valid name, as *Uperodon variegatus* (Stoliczka, 1872). **Synonyms.** *Hylaedactylus carnaticus* Jerdon, 1854 "1853" (by Parker 1934), *Callula olivacea* Günther, 1876 "1875" (by Boulenger 1890), and *Ramanella symbioitca* Rao and Ramanna, 1925 (by Parker 1934).

Lectotypification of *Callula variegata* Stoliczka, 1872. The original description of this species (Stoliczka 1872) mentions two syntypes from "Ellore". ZSI 2761 was indicated as one of the syntypes (Sclater 1892), and for the second specimen NHMW 4019 and BMNH 74.11.12.2 have been suggested as possible candidates (Tiedemann *et al*. 1994; Dutta & Manamendra-Arachchi 1996; Dutta 1997; Chanda *et al*. 2000). In the present study, the available samples at ZSI, Kolkata (ZSI 2761) and Natural History Museum, London (BMNH 74.11.12.2) were examined. Both these specimens were found to be identical in species status and were in agreement with the original description. However, since this species was described based on two specimens, and there have been confusions related to the status of syntypes (Chanda *et al*. 2000) as well as species identification (e.g., Rao 1937; Günther 1876 "1875"), apart from the availability of several poorly-defined nominal taxa currently in the synonymy of *Uperodon variegatus*, in accordance with Article 74 of The Code, designation of a lectotype from syntypes is advisable for it "to become the unique bearer of the name of a nominal species-group taxon and the standard for its application" in order to clarify the taxonomic status of this species. Hence, based on diagnostic characters found useful for differentiating *Uperodon variegatus* from its congeners (as stated in the 'comparison' section below), we herein designate ZSI 2761 (an adult female, SVL 29.8 mm) from "Ellore", as the lectotype of *Callula variegata* Stoliczka, 1872. The lectotype description provided subsequently is consistent with the original description.

Comparison. *Uperodon variegatus* cannot be confused with any of the known member of this genus, except *Uperodon rohani* **sp. nov.**, because of its dorsal skin that has prominent spots or blotches, and ventral skin white to off-white without any spots, blotches or mottling. *Uperodon variegatus* differs from *Uperodon rohani* **sp. nov.** by a suite of morphological characters (including osteology) and considerable genetic divergence. For comparison with *U. globulosus*, *U. systoma*, *U. taprobanicus*, *U. anamalaiensis*, *U. montanus*, *U. mormorata*, *U. nagaoi*, *U. obscurus*, *U. palmatus, U. triangularis* and *U. rohani* **sp. nov.** see 'comparison' sections of those species.

Genetic divergence. For 16S mitochondrial gene sequences, the sampled populations of *Uperodon variegatus* showed an average intraspecific distance of 0.7% (range 0–1.2%, $N = 4$). The samples from Karnataka and Kerala

(Western Ghats) showed a divergence of up to 1.2% with the populations from Andhra Pradesh and Tamil Nadu (Eastern Ghats). Genetically, *U. variegatus* is closely related to *U. rohani* **sp. nov.**, from which it was found to differ by an average uncorrected genetic distance of 2.8% (range 2.4–3.4%, *N* = 24). For interspecific genetic distances with all other members of the genus, see Table 3.

Description of lectotype (measurements in mm) (Figs. 3K, 10M). Small-sized (SVL 29.8), slender adult female; head small (HW 8.7, HL 7.1, IFE 4.3, IBE 8.3), less than one-fourth (23.8%) of body length, wider than long (HW/HL ratio 1.2); snout rounded to nearly truncate in dorsal and ventral view, acute in lateral view, its length (SL 3.2) longer than horizontal diameter of eye (EL 2.7); loreal region obtuse with rounded canthus rostralis; interorbital space more than twice as wide (IUE 3.6) as upper eyelid (UEW 1.4); nostril closer to tip of snout (NS 0.9) than to eye (EN 1.9); supratympanic fold distinct, extending from posterior corner of upper eyelid to insertion of forelimb at axilla; eye diameter (EL 2.7); vomerine odontophores present on the palate, without teeth; presence of two weakly-developed neopalatinal ridges on posterior side of each choana, fused with the vomerine odontophores; tongue emarginate. Forearm (FAL 5.0) shorter than hand length (HAL 7.8); finger length formula I<II<IV<III, tips of all fingers with truncate discs, discs moderately wide compared to finger width; subarticular tubercles prominent, oval, all present; two well-developed palmar tubercles (inner, oval, 1.1 mm long; outer, shallowly lobed, 1.0 mm long). Hind limbs relatively long, thigh length (TL 11.3) longer than shank (SHL 9.9) and shorter than foot (FOL 12.7); tips of all toes with small truncate to rounded discs; webbing absent between toes; dermal fringes absent on all toes; subarticular tubercles prominent, oval; two smooth metatarsal tubercles, oval, outer one longer (1.3 mm long) than the inner (0.7 mm long).

Skin of snout, between eyes, sides of head, anterior part of dorsum, posterior parts of back, and upper and lower parts of flank, shagreened (Fig. 3K); dorsal surfaces of forelimb, thigh, tibia and tarsus, shagreened to sparsely granular; ventral surfaces shagreened.

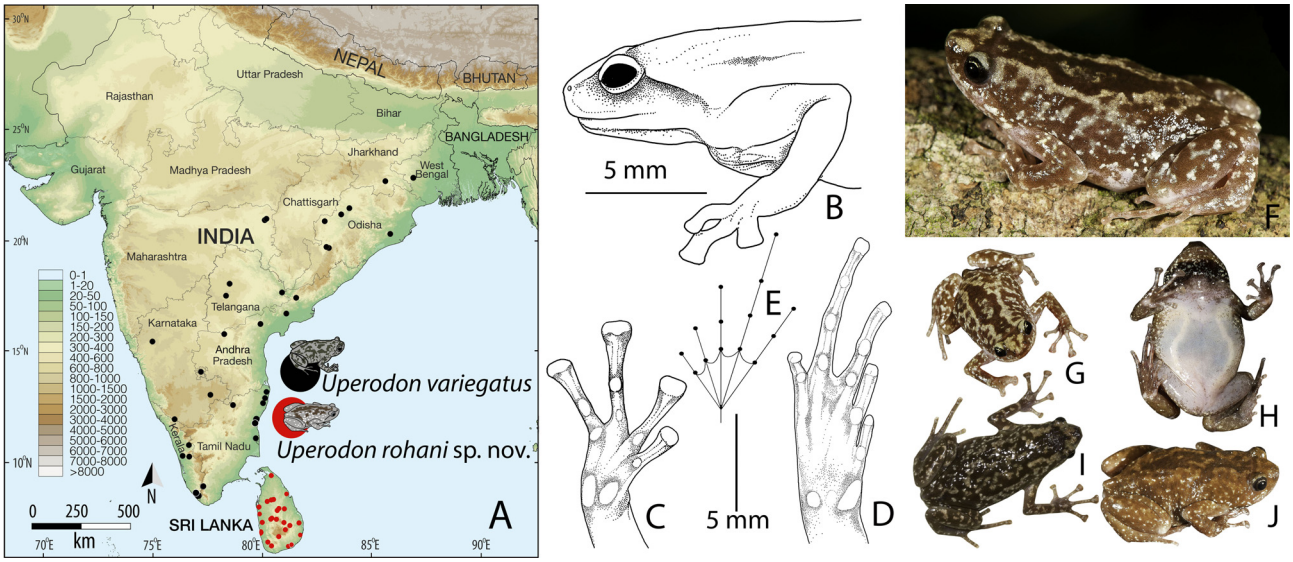

FIGURE 12. A. Distribution of *Uperodon variegatus* and *Uperodon rohani* **sp. nov.** Details of localities reported in the present study are provided in Table 1. Records from literature are listed in supplementary Table S1 and indicated here based on approximate coordinates; **B–E.** Head, hand, foot and schematic illustration of foot webbing in the holotype of *Uperodon rohani* **sp. nov.** (DZ 1449, male): **B.** lateral view of head; **C.** ventral view of hand; **D.** ventral view of foot; **E.** foot webbing; **F–J.** *Uperodon rohani* **sp. nov.** (DZ 1449, male) in life: **F.** dorsolateral view; **G.** dorsal view; **H.** ventral view; **I.** *Uperodon rohani* **sp. nov.** (Paratype, DZ 1485, female), dorsal view; **J.** *Uperodon rohani* **sp. nov.** (DZ 1130, female), dorsolateral view. (Images: SD Biju).

Colouration. *In preservation*: Dorsum uniformly light greyish-brown; flanks greyish-brown; lateral sides of head light brown; ventral surface uniformly light grey (Figs. 3K). *Colour in life* (SDBDU 2007.4994, male). Dorsal surfaces (including limbs) dark brown with scattered olive yellow spots throughout; lateral sides of head dark greyish-brown with scattered olive coloured spots; throat dark grey with calling patch; chest, belly and thigh, flesh-white without markings; ventral surfaces of forelimb, tibia and foot, light grey (Fig. 11L–M).

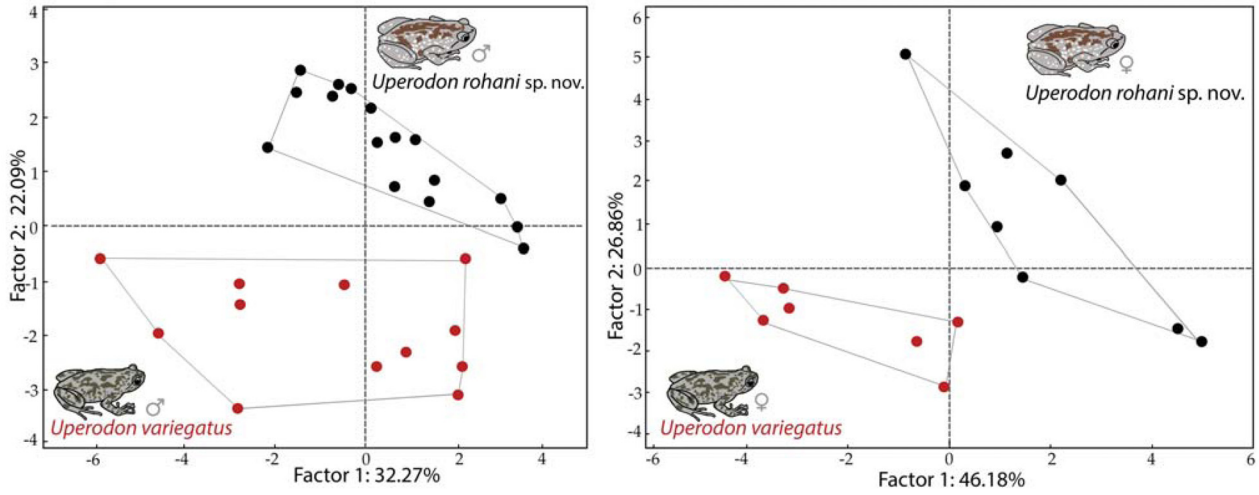

FIGURE 13. Principal Component Analyses showing morphometric differentiation between *Uperodon rohani* **sp. nov.** and *U. variegatus* based on 17 morphological characters. Left: Plot for the first two factor planes explaining 54.4% of the variations among 28 adult male specimens. Right: Plot for the first two factor planes explaining 73% of the variations among 15 adult female specimens. Factor loadings for each component are provided in Table S2.

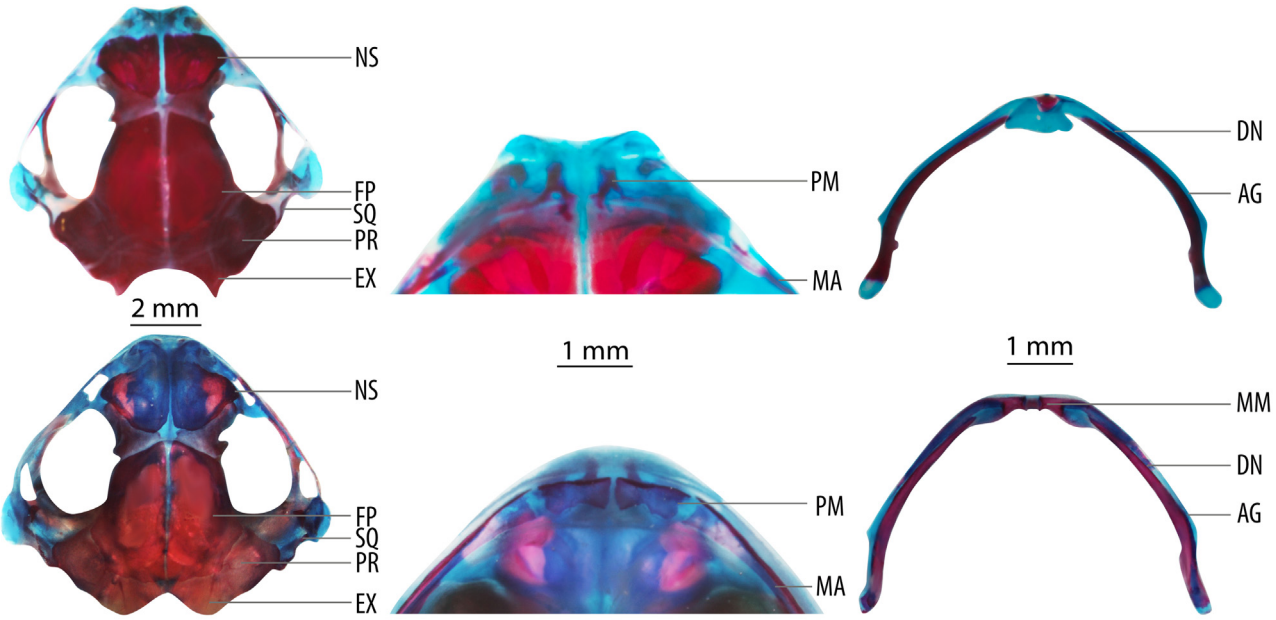

FIGURE 14. Cleared and double stained specimens of ***Uperodon rohani*** **sp. nov.** (above) and *U. variegatus* (below). From left to right: Dorsal view of the crania composed of nasals (NS), frontoparietals (FP), prootics (PR), exoccipitals (EX) and squamosals (SQ); anteroventral view of the crania showing components of the upper jaw, premaxillae (PM) and maxillae (MA); ventral view of the lower jaw comprising of dentaries (DN), angulosplenials (AG) and mentomeckelians (MM). Bones are indicated in red, cartilage in blue. (Images: Gayani Senevirathne).

Variations. Morphometric measurements for 12 males and seven females, including the lectotype, are given in Table 4. Dorsal colouration and markings were highly variable among the examined specimens. SDBDU 2007.6347: dorsum brown with yellowish-grey blotches in life (that turns light brown with grey blotches in preservation); SDBDU 2005.4726: light brown with olive grey blotches in life. Albino (or possibly leucistic) forms of this species are known from Mamallapuram in Tamil Nadu (Fig. 11O).

Secondary sexual characters. Male: vocal sac externally visible on the lower jaw; females (SDBDU 2005.4726): ova white, pigmented on pole (diameter 0.7–1.0 mm, $N = 20$).

Geographical distribution and habitat. *Uperodon variegatus* is a widely distributed species in India. It is

known to occur right from Tamil Nadu and Kerala in the south, northwards up to Karnataka, Andhra Pradesh, Telangana, Odisha, Jharkhand and West Bengal (Fig. 12A; Tables 1, S1). In the present study, genetically identified individuals of this species were largely collected from urban landscapes and disturbed secondary forests (Tamil Nadu: Chengalpattu and Mamallapuram; Kerala: Karamana, Meladoor and Palakkad; Karnataka: Bangalore; and Andhra Pradesh: Srikakulam), from sea level up to 900 m elevations. This species is predominantly found in drier regions towards the eastern coast. At Mamallapuram, it was found in brackish waters, just a few metres away from the seacoast.

***Uperodon rohani* sp. nov.**
Rohan's Globular Frog
(Figs. 1, 2A, 2D, 3L, 5K, 12, 13, 14; Tables 1–4)
http://zoobank.org/urn:lsid:zoobank.org:act:D612A25A-E09E-4193-8B89-3DC62746FB55

Holotype. DZ 1449, an adult male, from Mihintale, Anuradhapura district, Sri Lanka, collected by Madhava Meegaskumbura and team, on 02 October 2014. **Paratypes.** DZ 1448, DZ 1450 and DZ 1374, three adult males, collected along with the holotype; DZ 1336, an adult male, from Bundala NP, Hambantota district, Sri Lanka, collected by MM and team, on 04 November 2013; DZ 1520 and DZ 1521, two adult males, and DZ 1425, an adult female, from Makandura, Kurunegala district, Sri Lanka, collected by MM and team, on 11 September 2014; DZ 1486, an adult male, and DZ 1485, an adult female, from Ampara, Ampara district, Sri Lanka, collected by MM and team, on 10 October 2012; DZ 1129–DZ 1132, four adult females, from Dambulla, Matale district, Sri Lanka, collected by MM and team, on 04 January 2013. **Referred specimens.** NHM 1931.2.1.21, an adult male, from "Ceylon", Sri Lanka, collected by GH Herry; NHM 1973.3015, an adult male, from Kurunegala, "Kurunegala dist.," Sri Lanka, collected by R Sananayake; NMH 1976.264–NHM 1976.265, two adult males, from Badulla, "Hambantota dist.," Sri Lanka, collected by JC Naggs; WHT 5320, an adult male, from Nochchiyagama, Anuradhapura district, Sri Lanka, collected by MM Bahir, C Gans and C Yahalmulla, on 18 November 2000; WHT 01188, an adult male, from Sigiriya, Near Rest house, Matale district, Sri Lanka, collected by D Gabadge, on 08 February 1996; WHT 1749, an adult male, from Polonnaruwa, Polonnaruwa district, Sri Lanka, collected by A Nollert, on 28 July 1997; WHT 01189, an adult male, from Anuradhapura, Anuradhapura district, Sri Lanka, collected by D Gabadage and MM Bahir, on 11 August 1995; NHM 1973.3014, an adult female, from Kurunegala: Ceylon, "Kurunegala dist.," Sri Lanka, collected by R Sananayake; WHT 01191, an adult female, from Palatupana, Kirinda, Hambantota district, Sri Lanka, collected by U. Premachandra, in August 1995.

Etymology. This species is named after Rohan Pethiyagoda, in recognition of his contribution to biodiversity studies in India and Sri Lanka, especially on frogs and fishes. The species epithet is formed as a noun in the genitive case.

Comparison. *Uperodon rohani* **sp. nov.** cannot be confused with *U. globulosus*, *U. systoma* and *U. taprobanicus* due to its smaller snout-vent size, male SVL 26–34 mm, $N = 16$, female SVL 28–35 mm, $N = 8$ (vs. larger, *U. globulosus* male SVL 51–56 mm, $N = 2$, female SVL 66–72 mm, $N = 3$; *U. systoma* male SVL 51–56 mm, $N = 2$, female SVL 47–64 mm, $N = 4$; and *U. taprobanicus* male SVL 42–52 mm, $N = 3$, female SVL 53–55 mm, $N = 2$). *Uperodon rohani* **sp. nov.** specifically also differs from the former two by its finger tips having truncate discs (vs. rounded without discs), and presence of two weakly-developed neopalatinal ridges on posterior side of each choana, fused with the vomerine odontophores (vs. two prominent dermal projections on the neopalatinal ridges on posterior side of each choana, separated from the vomerine odontophores); and from *U. taprobanicus* by presence of two weakly-developed neopalatinal ridges on posterior side of each choana, fused with the vomerine odontophores (vs. well-developed neopalatinal ridges). Further, *U. rohani* **sp. nov.** differs from *U. anamalaiensis*, *U. montanus*, *U. obscurus* and *U. palmatus* by its ventral skin being white to off-white in life (that turns greyish-white in preservation) without any spots or blotches (vs. light or dark brown with prominent spots or blotches), and absence of webbing between toes in both the sexes (vs. present). *Uperodon rohani* **sp. nov.** differs from *U. nagaoi* by its ventral skin being white to off-white in life (that turns greyish-white in preservation) without any spots or speckles (vs. brown to dark brown in life that turns brown or dark greyish-brown in preservation, with or without inconspicuous spots or speckles). For detailed comparison of *U. rohani* **sp. nov.** with *U. globulosus*, *U. systoma*, *U. taprobanicus*, *U. anamalaiensis*, *U. montanus*, *U. mormorata*, *U. nagaoi*, *U. obscurus*, *U. palmatus* and *U.*

triangularis see 'comparison' section of those species. *Uperodon rohani* **sp. nov.** is morphologically and genetically close to *U. variegatus*, from which it differs by its snout nearly equal to eye diameter, male SL/EL ratio 1.0–1.2, *N* = 16, female SL/EL ratio 0.8–1.0, *N* = 8 (vs. snout relatively longer than eye, male SL/EL ratio 1.2–1.6, *N* = 12, female SL/EL ratio 1.2–1.4, *N* = 7); head relatively narrower, male HW/HL 1.0–1.1, *N* = 16, female HW/HL 1.0–1.2, *N* = 8 (vs. head relatively wider, male HW/HL 1.1–1.4, *N* = 12, female HW/HL 1.1–1.4, *N* = 7); and shank relatively longer than thigh, male SHL/TL ratio 1.0–1.1, *N* = 8, female SHL/TL ratio 1.1, *N* = 8 (vs. relatively shorter, male SHL/TL ratio 0.9–1.0, *N* = 12, female SHL/TL ratio 0.8–0.9, *N* = 7) (Table 4).

The new species cannot be confused with previously available names, *Engystoma marmoratum* Cuvier, 1829 and *Systoma leschenaultii* Tschudi, 1838, currently under the synonymy of *Uperodon systoma* Schneider, 1799. The former was described from "l'Inde" (= India) and as stated by Peters (1864 "1863")—"bereits richtig erkannt batten = *Uperodon marmoratum* D. B. und miifste daher den Species namen "systoma" behalten", was already correctly recognized as *Uperodon marmoratum* (= *Uperodon systoma*) by Duméril and Bibron (1841). The latter, also stated by Duméril and Bibron (1841)—"peut-être de la même espèce que notre Upérodonte marbré", is perhaps the same as *Uperodon systoma*, from which the new species cannot be confused based on several morphological characters such as smaller body size (vs. larger), finger tips with truncate discs (vs. rounded without discs) and vomerine odontophores fused with neopalatinal ridges (vs. separated). Furthermore, three other names—*Hylaedactylus carnaticus* Jerdon, 1854 "1853", *Callula olivacea* Günther, 1876 "1875" and *Ramanella symbioitca* Rao and Ramanna, 1925, currently under the synonymy of *Uperodon variegatus* Stoliczka, 1872, were also described from regions in India ("Carnatic", "Yellagherry hills" and "Ellore", respectively), while the distribution of *U. rohani* **sp. nov.** is restricted to Sri Lanka. For specific differences with *U. systoma* and *U. variegatus*, see the detailed comparison with those species.

Morphometric differentiation. *Uperodon rohani* **sp. nov.** showed morphological differentiation from its closely related species, *U. variegatus*. Principal Component Analysis (PCA) for the adult male specimens (*U. rohani* **sp. nov.**: *N* = 12; *U. variegatus*: *N* = 16) recovered five Principal Components (PC) with eigenvalues >1.0 that accounted for 77.2% of the total variance; PC 1 explained 32.3% of the variations, with highest loadings for SVL, HW, IUE, IFE, MN, HAL and TL; PC 2 explained 22.1% of the variations, with highest loadings for SL, IBE, EN, SHL and FOL; PC 3 explained 10% of the variations, with highest loadings for UEW and NS; PC 4 explained 6.9% of the variations, with highest loadings for EL; PC 5 explained 6% of the variations; and the remaining factors altogether explained 22.8% of the variations (Table S2). Principal Component Analysis (PCA) for the adult female specimens (*U. rohani* **sp. nov.**: *N* = 7; *U. variegatus*: *N* = 8) recovered three Principal Components (PC) with eigenvalues >1.0 that accounted for 82.3% of the total variance; PC 1 explained 46.2% of the variations, with highest loadings for SVL, HW, SL, IUE, UEW, IFE, IBE, MN, EN and TL; PC 2 explained 26.9% of the variations, with highest loadings for HL, FAL, HAL and SHL; PC3 explained 9.2% of the variations, with highest loadings for EN; and the remaining factors altogether explained 17.7% of the variations (Table S2). Projections of factor planes 1 and 2 showed distinct clusters for the two species (Fig. 13).

Osteological comparison. *Uperodon rohani* **sp. nov.** and its closely related species, *U. variegatus*, have the following skeletal features: Anteriorly slender, basally wider crania, with widest at anterior margins of tympanic annulus in both species. Cranium length is 93% of its width in *U. rohani* **sp. nov.** and 84.2% in *U. variegatus*. Frontoparietals are largest, covering more than half of crania, slender and quadrangular shaped in both species. Nasals, lying dorsal to nasal capsules, triangular-shaped, medial edge 20.6% of the mid-cranial width in *U. variegatus* and 20.9% in *U. rohani* **sp. nov.** Posterolateral margins of frontoparietals slightly overlay anterolateral margins of prootics. Major differences between the two species concentrate mainly on three bones of the lower and upper jaws—premaxillae, mentomeckelians and dentaries. Premaxillae usually composed of alary, dentary and maxillary processes. In both species, premaxillae are edentate. However, shape of dentary process differs immensely, wherein *U. rohani* **sp. nov.** has well-bifurcated dentary process with 74.9% height compared to width of premaxillae. Comparatively, dentary process of *U. variegatus* is rectangular in shape, with a slight median depression, and 27.4% height compared to premaxillary width. Mentomeckelians are observed as cylindrical endochondral elements, anterior to the anterior ends of Meckel's cartilages, only in *U. variegatus*. Mentomeckelians are absent in *U. rohani* **sp. nov.**; however, the infrarostrals, which are the precursors of Mentomeckelians are still present and can be seen clearly (Fig. 14). Development of dentaries also shows differences between the two species. Dentaries are well-developed, extend for about one-third and two-third of the length of the mandible arc in *U. rohani* **sp. nov.** and *U. variegatus*, respectively (Fig. 14).

Genetic divergence. For 16S mitochondrial gene sequences, the sampled populations of *Uperodon rohani* **sp. nov.** showed an average intraspecific distance of 0.5% (range 0–1.4%, *N* = 6). The sample from Bundala showed a divergence of up to 1.4% from other populations. Genetically, *U. rohani* **sp. nov.** is closely related to *U. variegatus*, from which it was found to differ by an average uncorrected genetic distance of 2.8% (range 2.4–3.4%, *N* = 24). For interspecific genetic distances with all other members of the genus, see Table 3.

Description of holotype (measurements in mm) (3L, 5K, 12B–J). Small-sized (SVL 26.0), relatively slender adult male; head small (HW 6.7, HL 6.2, IFE 3.5, IBE 5.5), less than one-fourth (23.4%) of body length, wider than long (HW/HL ratio 1.1); snout subovoid in dorsal, subovoid to nearly truncate in ventral view, rounded in lateral view, its length (SL 2.6) slightly longer than horizontal diameter of eye (EL 2.5); loreal region rounded with vertical canthus rostralis; interorbital space wider (IUE 2.9) than upper eyelid (UEW 1.6) and internarial distance (IN 1.9); nostril closer to tip of snout (NS 0.7) than to eye (EN 1.4); supratympanic fold distinct, extending from posterior corner of upper eyelid near to insertion of forelimb at axilla; eye diameter (EL 2.5); vomerine odontophores present on the palate, without teeth; presence of two weakly-developed neopalatinal ridges on posterior side of each choana, fused with the vomerine odontophores; tongue emarginate. Forelimbs moderately long and thin; forearm (FAL 5.2) shorter than hand length (HAL 7.2); finger length formula I<II<IV<III, tips of all fingers with oval discs, discs moderately wide compared to finger width (FD_I 0.9, FW_I 0.4; FD_{II} 1.3, FW_{II} 0.4; FD_{III} 1.2, FW_{III} 0.4; FD_{IV} 1.2, FW_{IV} 0.5); subarticular tubercles prominent, oval, all present; two well-developed palmar tubercles, oval. Hind limbs relatively long and thin, thigh length (TL 9.2) slightly shorter than shank (SHL 9.4) and shorter than foot (FOL 11.1); relative digit lengths I<II<V<III<IV; tips of all toes slightly enlarged with truncate to rounded discs, discs rather wide compared to toe width (TD_I 0.7, TW_I 0.6; TD_{II} 0.8, TW_{II} 0.6; TD_{III} 0.7, TW_{III} 0.5; TD_{IV} 0.7, TW_{IV} 0.5; TD_V 0.5, TW_V 0.5); foot webbing absent; subarticular tubercles prominent, oval; two smooth metatarsal tubercles, oval, outer one slightly longer than the inner.

Skin of dorsum, snout, and between eyes, shagreened; sides of head, posterior part of back, and upper and lower parts of flank, smooth; dorsal surfaces of forelimb, thigh, tibia and tarsus, smooth to shagreened; ventral surfaces smooth.

Colouration. *In preservation*: Dorsum dark brown with irregular olive grey coloured blotches, pair of faint and irregular olive grey longitudinal streaks extending from upper eyelids up to vent; dorsal surfaces of forelimbs and hind limbs lighter in colour compared to dorsum and with faint yellowish-grey spots or blotches; sides of head brown; ventral surfaces (including limbs) greyish-white, throat with blackish-brown calling patch (Fig. 3L). *Colour in life*: Dorsum reddish brown with pair of irregular olive yellow coloured longitudinal streaks extending from upper eyelids up to vent, scattered olive yellow coloured spots and blotches especially towards dorsolateral surfaces and posterior part of back, larger olive yellow blotch in center of dorsum, few scattered spots on head, olive yellow patch between nostrils and upper eyelids; lateral sides of head brown with scattered olive yellow spots near margins of mouth; anterior and posterior parts of groin light brown; dorsal surfaces of limbs brown to light brown with scattered olive yellow spots; throat light brown with bluish-black calling patch and irregular light grey speckles; chest, belly and thighs, greyish-white with light brown margins; limbs light brown with irregular light grey speckles (Figs. 12F–J).

Variations. Morphometric measurements for 16 males and eight females, including the type series, are given in Table 4. DZ 1374 and DZ 1336: dorsal skin smooth; DZ 1129: lateral surfaces slightly granular; DZ 1374: lateral surfaces of head slightly granular. DZ 1374: dorsum coffee brown in colour with prominent irregular olive grey spots or patches; DZ 1521: dorsum dark brown with olive grey blotches; DZ 1425: dorsum dark brown with small olive grey spots scattered throughout, scattered spots also seen on surfaces of hand, foot, sides of head and groin; DZ 1485: dorsum darker brown with fewer blotches.

Secondary sexual characters. Male (DZ 1449): vocal sac externally visible on the lower jaw; female (DZ 1425): ova white, pigmented on poles (diameter 0.6–1.0 mm).

Geographical distribution and habitat. *Uperodon rohani* **sp. nov.** is endemic to Sri Lanka, where it is widely distributed throughout the island (Fig. 2D). In the present study, we genetically and/or morphologically confirmed the occurrence of this species at several localities in the Central, Eastern, Northern, North Central, North Western, Southern, and Uva provinces (Table 1). Previous records of *U. variegatus* from Sri Lanka refer to this species (see supplementary Table S1 and references thereto).

Comment. This species was historically considered to be conspecific with the Indian species *Uperodon variegatus* and widely reported as *Ramanella variegata* (see Table 1 and supplementary Table S1).

Natural history and reproductive behaviour

Like most microhylids, *Uperodon* are explosive breeders (e.g., Altig & McDiarmid 1999b; Manamendra-Arachchi & Pethiyagoda 2001). Nevertheless, an extraordinary diversity has been observed within the genus in terms of reproductive behaviour, breeding ecology and larval development. The Sri Lankan species *U. nagaoi*, *U. obscurus* and *U. palmatus* are reported to be phytotelm breeders (Meegaskumbura 1999; Meegaskumbura 2001; Manamendra-Arachchi & Pethiyagoda 2001; Chandrasegaran & Ranawana 2002; Karunarathna & Amarasinghe 2009; Bowatte & Meegaskumbura 2012). Of these three species, *U. nagaoi* is suggested to obligately inhabit tree holes, making it ecologically specialized (Manamendra-Arachchi & Pethiyagoda 2001). We observed a female of *U. nagaoi* submerged in a water-filled tree hole with a clutch of gel-encapsulated eggs adhered to the inner walls (about 4 to 5 cm above the water level) at Hiyare forest reserve in Sri Lanka (Figs. 15I–J), suggesting that this species might exhibit parental care behavior, similar to that observed in some tree hole breeding frog species (e.g., Biju *et al*. 2016). On the other hand, *U. obscurus* and *U. palmatus* are more adaptive, commonly found on forest floor, and also breed in small terrestrial ponds, rock pools and puddles (Meegaskumbura 1999; Meegaskumbura 2001; Manamendra-Arachchi & Pethiyagoda 2001; Ukuwela *et al*. 2010; Janzen & Bopage 2011). Chandrasegaran & Ranawana (2002) noticed various-staged tadpoles of *U. obscurus* inside a tree hole at the same time and pointed out that this species may breed multiples times in a season. Conversely, this also suggests the possibility of sharing of phytotelm by multiple females during a single season.

As for the Indian members, *Uperodon montanus* is known to inhabit and breed inside tree holes (e.g., Krishna *et al*. 2004; Krishna & Bosch 2007). In this study, we observed *U. montanus* inside a water-filled tree hole about six metres above ground at Kesavapara (Nelliyampathy, Kerala) and a damp tree hole about three metres above ground at Upper Manalar (Kerala). However, at Pandimotta (Shendurney WLS, Kerala) calling males of *U. montanus* were collected from a temporary puddle. We also collected *U. anamalaiensis* from tree holes about 8–10 metres above the ground at Chathankod (Kerala) in the southern Western Ghats. This species, however, was observed to breed in shallow-water channels on the ground immediately after the first rains. At Methooty in Kerala, *U. anamalaiensis* was found breeding in rock puddles on exposed streams during the month of May. Males of this species exhibit a single vocal sac while calling and form axillary amplexus with the females. Pigmented eggs of *U. anamalaiensis*, surrounded with a thick jelly layer, can be found as surface films on the breeding sites. Inger *et al*. (1984) observed microhylid tadpoles inside a tree hole at Ponmudi (Kerala) and suspected them to belong to *U. triangularis*. However, since Inger *et al*.'s (1984) descriptions match closely with *U. anamalaiensis* adult and tadpoles reported in our study (see 'Comparative morphology of tadpoles' section), and the presence of *U. anamalaiensis* at Ponmudi is also genetically confirmed (Fig. 1), we consider their observations to be of this species. Although *U. anamalaiensis* and *U. montanus* are reported from tree holes, these are not necessarily phytotelm inhabitants or breeders, as evident from available information and our observations. *Uperodon triangularis* has occasionally been reported from tree holes (Abraham *et al*. 2001) but all collections of this species in the present study were from the ground, usually around puddles, tree bases or from fallen logs. *Uperodon mormorata* may also occasionally be arboreal (Raju Vyas personal communication). We found this species on a tree trunk at Shimoga (Karnataka) 4–5 metres above ground.

Another species, *Uperodon taprobanicus* is also a semi arboreal species widely reported from tree holes both in India and Sri Lanka (e.g., Daniels 2005; Siliwal & Ravichandran 2008; Ganesh 2012). In the present study, this species was collected from tree holes about 4–5 metres above ground at Kalpetta (Wayanad, Kerala) and Odisha, but also from roads (Bangalore town, Karnataka) and agricultural fields (Wayanad) in India. In West Bengal this species has been found inside tree holes about one and a half metres above the ground, and usually descends from tree holes and hollow trunks climbing down backwards with its legs first (Deuti & Goswami 1995). In Sri Lanka it was observed in several habitats such as coconut trunks at Makandura (1–6 individuals), tree trunks of *Terminalia arjuna* adjacent to permanent water holes at Ampara and Kurunegala, termite mounds at Dambulla and on the roadside at Bundala, Katharagama (Hambanthota district) and Anuradhapura.

The wide-ranging Indian species *Uperodon variegatus* is found closest to human-dominated landscapes such as agricultural fields, wall crevices, and often from damp areas of houses such as bathrooms and water closets. This species was observed to breed in stagnant pools and water tanks. Rao & Ramanna (1925) also reported *U. variegatus* from scorpion burrows. The breeding behavior of the new species *U. rohani* **sp. nov.** is close to its congener *U. variegatus*. Amplexus in *U. rohani* **sp. nov.** is axillary as in the case of most species in this genus.

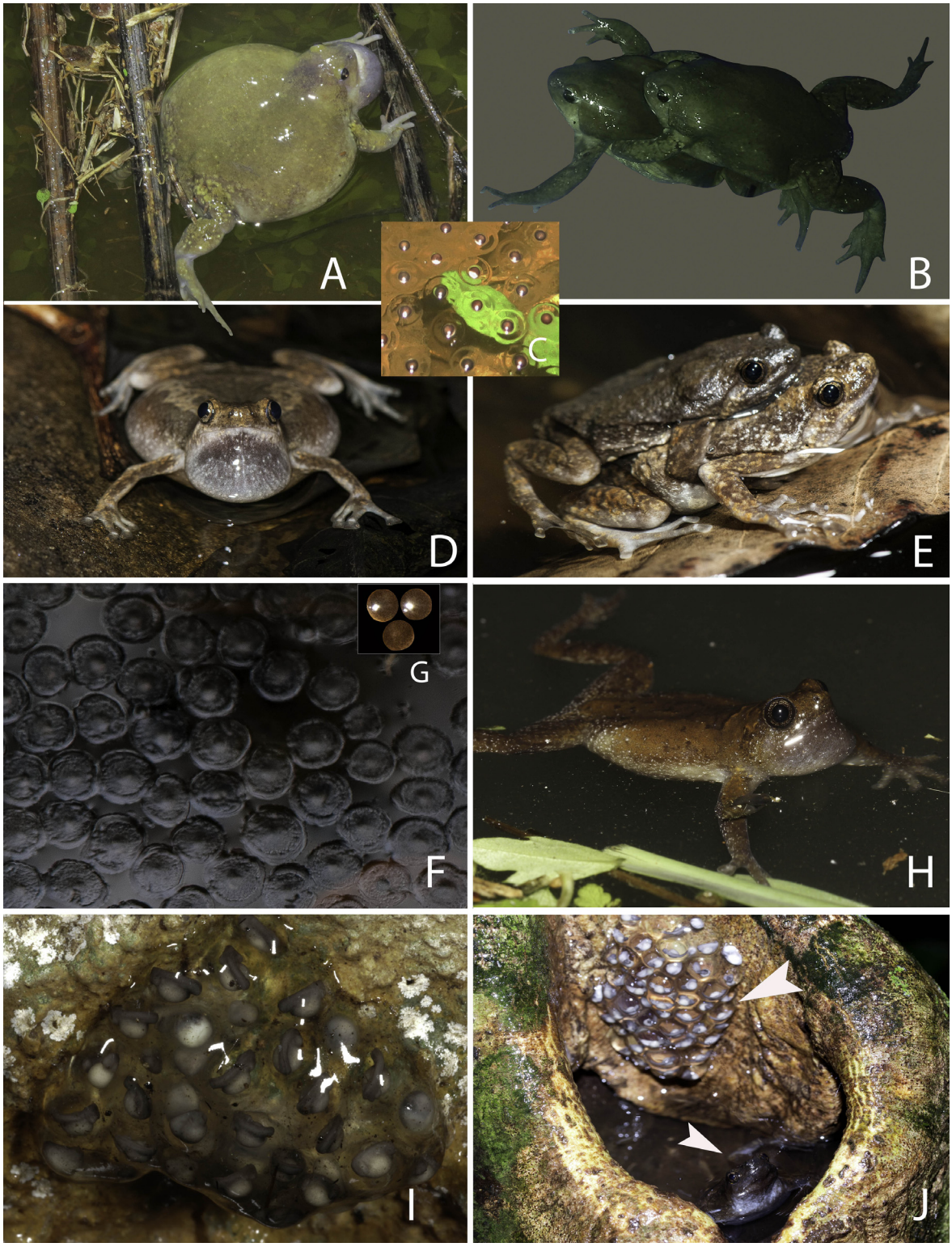

FIGURE 15. Breeding behavior in *Uperodon* species. **A–C.** *Uperodon globulosus*: **A.** Male calling from a temporary water puddle (not preserved); **B.** Male and female in axillary amplexus; **C.** Eggs floating on water surface; **D–G.** *Uperodon anamalaiensis*: **D.** Male calling from a temporary pool of water on a hill stream (SDBDU 2012.1998); **E.** Male and female in axillary amplexus; **F.** jelly-covered eggs floating on water surface; **G.** individual eggs after removal of the jelly layer; **H.** Male of *Uperodon palmatus* calling from a small permanent water pool adjacent to a forest; **I–J.** *Uperodon nagaoi*: **I.** early developmental stages inside a gel-encapsulated egg mass on inner wall of a tree hole; **J.** oviposition site with gel-encapsulated eggs adhered on inner wall of a tree hole (about 4 to 5 cm above the water level on a tree at the edge of a stream in a lowland canopy covered forest) along with an adult male found submerged about 1 cm below the water surface. (Images: A–C. Samadhan Phuge, D–G. SD Biju, H–J. Nayana Wijayathilaka).

Among all the members of this genus, *Uperodon globulosus* and *U. systoma* are unique because of their fossorial habit that also makes it difficult to sight them. In India, our collections of *U. systoma* were made either from small burrows in dry agricultural fields (Coimbatore and Kunnapattu in Tamil Nadu) or tilled soil in uncultivated fields (Bannerghatta, Karnataka). We did not observe the breeding of *U. systoma*, however, though on one occasion erratic calls were heard from the ground adjacent to a temporary pond in Coimbatore town (Tamil Nadu) during the month of October. Individuals were located close to soil burrows. In Sri Lanka, specimens were collected from Makandura (Kurunegala district), Dambulla (Matale district) and Anuradhapura (Anuradhapura district). At Makandura, more than 12 animals were found feeding on termites in and around a termite mound. One of the individuals quickly escaped into a ground burrow upon being disturbed. During a repeat visit to this site, an animal was seen emerging out of the same burrow suggesting that this species may use permanent tunnels. However, so far no information is available on the breeding behavior of these frogs. The second fossorial species, *U. globulosus*, is currently known to occur only in India. In the present study, large aggregations of males were either observed in and around temporary rainwater pools and puddles (Pune, Maharashtra, India; Jaldapara, West Bengal, India) or on roads (Tamhini Ghat, Maharashtra, India) within a few days after the first monsoon showers. Breeding activity was observed between 18:00–02:00 hrs. Male calls are loud and produced by inflating a single gular pouch (Fig. 15A). Calling individuals and amplecting pairs (in axillary amplexus) were found floating inside or at the edges of stagnant water, with the male's head and throat rested over the female's back. During amplexus, a thick cream-coloured sticky substance is observed and it seems to help the pair stick together while mating since pairs were also seen struggling to detach themselves after completion of egg-laying. Before egg laying the female bends its body in the form of an arch. Eggs were seen as surface films in puddles (Fig. 15C). Upon being disturbed, *U. globulosus* frogs are observed to inhale air and swell the two sides of their abdomen like a balloon, while also secreting a sticky white fluid.

The breeding behavior of *U. taprobanicus*, which is also a semi-fossorial species (Dutta & Manamendra-Arachchi 1996), is also likely to be similar to that observed in *U. globulosus*. In India, its breeding activities are usually observed to start with the first rains in June and extend up to the end of July. After a heavy shower, they emerge from their hiding places and mostly breed in pools of dirty water. Males inflate single vocal sacs while calling and use them as floats in water. During amplexus, the mating pairs lay eggs while floating passively in water. At Pondicherry, Tamil Nadu (India), a male and a female of *U. taprobanicus* were found in amplexus while floating in a roadside ditch. Upon handling the pair, we noticed a sticky substance with strong odour over the female's dorsal body surface, especially near the head region, where the male's throat was pressed against the female during axillary amplexus. When disturbed, this species is also reported to exhibit a defense behavior by inhaling air, swelling up like a ball while keeping the head down (Somaweera 2006) and secreting a slimy white fluid through skin pores.

Male advertisement calls have so far been described for *Uperodon taprobanicus* (reported as *'Kaloula pulchra'* from "Ceylon", Nelson 1973), *U. triangularis* (Kuramoto & Dubois 2009), *U. montanus* (reported as *U. 'anamalaiensis'*, Harpalani *et al*. 2015), *U. 'montanus'* (Kadadevaru *et al*. 1998; Krishna & Bosch 2007), *U. variegatus* (Kanamadi *et al*. 1993), *U. nagaoi* (Manamendra-Arachchi & Pethiyagoda 2001), and *U. obscurus* (Nelson 1973). In the present study, we have further described the call structure in *U. anamalaiensis*, *U. mormorata* and *U. triangularis*, based on genetically confirmed identities (see 'Vocalization' sections under the individual species accounts).

Comparative morphology of tadpoles

Free-swimming exotrophic tadpoles (Altig & Johnston 1989) are one of the three developmental modes observed in the family Microhylidae (Parker 1934). Many microhylids are known to be suspension feeders of small particles while swimming (Wells 2007); tadpoles of *Uperodon* also fall under this category. Microhylid tadpoles are also known to exhibit variations in terms of tail morphology and shape of the spiracular opening as well as the location of the mouth and spiracle (Donnelly *et al.* 1990; Bowatte & Meegaskumbura 2012). However, only a few studies are available on tadpole morphology of species in this group (Rao 1918; Kirtisinghe 1958; Ukuwela *et al.* 2010; Manamendra-Arachchi & Pethiyagoda 2001; Bowatte & Meegaskumbura 2012). The location of mouth in *U. montanus* (Parker 1934), *U. triangularis* (Rao 1918; present study), *U. obscurus* (Bowatte & Meegaskumbura 2012),

TABLE 3. Inter and intraspecific uncorrected p-distances (in percent) for the mitochondrial 16S rRNA gene sequences. Values in bold indicate intraspecific distances.

Species	*U. anamalaiensis*	*U. montanus*	*U. mormorata*	*U. nagaoi*	*U. obscurus*	*U. palmatus*	*U. rohani* **sp. nov.**	*U. triangularis*	*U. variegatus*	*U. globulosus*	*U. systoma*	*U. taprobanicus*
U. anamalaiensis	**0.4 (0–0.8)**											
U. montanus	3.2 (2.6–4.0)	**0.7 (0–1.2)**										
U. mormorata	5.7 (5.3–6.3)	5.6 (4.8–6.1)	**0.6 (0–1.2)**									
U. nagaoi	7.3 (7.2–7.4)	6.6 (6.4–6.8)	7.2 (7.0–7.4)	**0**								
U. obscurus	7.8 (7.6–8.0)	6.7 (6.6–7.0)	6.7 (6.3–6.9)	5.6 (5.6–5.6)	**0**							
U. palmatus	6.2 (6.0–6.4)	5.5 (5.4–5.8)	5.8 (5.5–6.1)	4.0 (4.0–4.2)	2.4 (2.4–2.6)	**0.1 (0–0.2)**						
U. rohani **sp. nov.**	5.2 (4.6–5.6)	5.3 (5.0–5.8)	6.6 (6.3–7.1)	7.2 (7.0–7.4)	7.7 (7.5–7.9)	6.5 (6.3–6.7)	**0.5 (0–1.4)**					
U. triangularis	6.6 (6.3–7.1)	5.9 (5.1–6.5)	2.9 (2.4–3.6)	8.0 (7.5–8.5)	6.7 (6.5–6.7)	6.0 (5.7–6.5)	7.3 (6.7–7.9)	**0.9 (0–1.6)**				
U. variegatus	6.3 (5.8–6.7)	5.8 (5.4–6.4)	7.0 (6.5–7.5)	7.1 (7.0–7.4)	7.7 (7.3–8.0)	7.0 (6.9–7.1)	2.8 (2.4–3.4)	7.2 (6.7–7.9)	**0.7 (0–1.2)**			
U. globulosus	8.1 (7.7–8.4)	7.7 (7.2–8.0)	7.7 (7.5–7.9)	8.1 (8.1–8.1)	8.2 (8.2–8.2)	7.6 (7.5–7.7)	8.2 (8.1–8.5)	8.3 (7.9–8.9)	8.8 (8.5–9.1)	**0**		
U. systoma	8.0 (7.5–8.6)	7.5 (6.8–8.4)	7.6 (7.1–8.3)	8.9 (8.8–9.0)	8.4 (8.2–8.8)	8.0 (7.8–8.2)	9.3 (8.9–10.1)	8.2 (7.5–8.9)	9.4 (8.7–9.9)	3.5 (3.2–4.0)	**0.9 (0–2.2)**	
U. taprobanicus	9.6 (9.1–10.3)	9.7 (8.9–10.3)	8.7 (8.1–9.3)	10.8 (10.5–11.1)	10.2 (9.9–10.5)	10.4 (10.1–10.9)	10.1 (9.5–10.7)	8.7 (8.3–9.1)	10.7 (10.5–11.5)	9.9 (9.7–10.1)	9.1 (8.3–9.7)	**0.3 (0–1.2)**

TABLE 4. Morphometric measurements of *Uperodon* species. All measurements are in millimetres (mm). The status of each specimen is given after the museum number: Holotype (HT), Paratype (PT), Neotype (NT), Lectotype (LT), Syntype (ST).

Sex	Locality	Museum Number	SVL	HW	HL	SL	EL	IUE	UEW	IFE	IBE	MN	EN	NS	FAL	HAL	TL	SHL	FOL
			Uperodon systoma (Schneider, 1799)																
F	"India orientali"	ZMB 3551 (ST)	49.7	11.7	7.9	4.8	4.9	4.8	2.6	6.6	12.4	7.1	1.4	1.6	13.2	23.8	18.3	15.4	18.6
F	Kunnapattu	SDBDU 2005.2806	63.3	15.5	10.2	5.0	5.2	6.5	3.3	7.9	14.8	9.3	1.5	1.9	17.1	27.3	23.2	19.4	23.6
F	Kunnapattu	SDBDU 2005.4724	48.2	14.1	8.8	4.5	4.4	5.6	3.1	6.5	13.0	7.4	1.7	2.1	13.9	23.9	19.4	16.4	20.5
F	Coimbatore	SDBDU 2005.2732	47.0	12.5	8.9	4.3	4.1	5.1	2.6	6.8	11.9	7.3	1.9	2.0	13.3	21.3	17.3	15.2	19.0
		Average	**52.1**	**13.5**	**9.0**	**4.7**	**4.7**	**5.5**	**2.9**	**7.0**	**13.0**	**7.8**	**1.6**	**1.9**	**14.4**	**24.1**	**19.6**	**16.6**	**20.4**
		Standard deviation	**7.6**	**1.7**	**0.9**	**0.3**	**0.5**	**0.7**	**0.4**	**0.6**	**1.3**	**1.0**	**0.2**	**0.2**	**1.8**	**2.5**	**2.6**	**1.9**	**2.3**
M	Kunnapattu	SDBDU 2005.2787	55.2	13.6	8.7	5.0	4.9	5.8	3.1	7.3	13.2	8.8	2.0	2.2	15.6	24.5	22.1	17.4	21.1
M	Dambulla	DZ 1128	51.0	14.8	11.5	4.8	5.1	5.8	3.3	6.5	13.1	9.3	1.8	2.1	12.2	20.9	21.6	17.6	22.0
		Average	**53.1**	**14.2**	**10.1**	**4.9**	**5.0**	**5.8**	**3.2**	**6.9**	**13.2**	**9.1**	**1.9**	**2.2**	**13.9**	**22.7**	**21.9**	**17.5**	**21.6**
		Standard deviation	**3.0**	**0.8**	**2.0**	**0.1**	**0.1**	**0.0**	**0.1**	**0.6**	**0.1**	**0.4**	**0.1**	**0.1**	**2.4**	**2.5**	**0.4**	**0.1**	**0.6**
			Uperodon globulosus (Günther, 1864 "1863")																
F	Russelconda	NHH 62.12.29.4 (ex. BMNH 1947.2.10.97) (ST)	67.4	19.2	13.0	7.7	3.6	8.8	2.7	9.7	13.9	10.2	3.3	2.8	14.5	18.0	29.1	21.7	26.5
F	Pune	SDBDU 2014.2673	71.7	18.7	12.7	7.4	3.7	8.7	2.6	9.6	15.3	11.3	3.4	2.9	20.5	32.0	27.4	23.3	28.1
F	Odisha	SDBDU 2005.4762	66.5	17.0	12.0	7.4	3.0	8.1	2.3	9.4	13.8	10.0	3.2	2.8	17.5	28.9	24.0	21.6	25.0
		Average	**68.5**	**18.3**	**12.6**	**7.5**	**3.4**	**8.5**	**2.5**	**9.6**	**14.3**	**10.5**	**3.3**	**2.8**	**17.5**	**26.3**	**26.8**	**22.2**	**26.5**
		Standard deviation	**2.8**	**1.2**	**0.5**	**0.2**	**0.4**	**0.4**	**0.2**	**0.2**	**0.8**	**0.7**	**0.1**	**0.1**	**3.0**	**7.4**	**2.6**	**1.0**	**1.6**
M	Bihar	ZSI A9575	55.9	15.9	10.6	6.3	2.8	6.7	1.5	7.7	11.9	7.8	2.5	2.5	11.3	13.7	21.1	15.6	20.3
M	Dhanbad	ZSI A4478	51.7	14.2	11.8	6.2	3.4	7.5	1.9	8.1	12.9	7.9	2.6	2.4	11.2	14.2	19.1	17.2	21.8
		Average	**53.8**	**15.1**	**11.2**	**6.3**	**3.1**	**7.1**	**1.7**	**7.9**	**12.4**	**7.9**	**2.6**	**2.5**	**11.3**	**14.0**	**20.1**	**16.4**	**21.1**
		Standard deviation	**3.0**	**1.2**	**0.8**	**0.1**	**0.4**	**0.6**	**0.3**	**0.3**	**0.7**	**0.1**	**0.1**	**0.1**	**0.1**	**0.4**	**1.4**	**1.1**	**1.1**
			Uperodon taprobanicus (Parker, 1934)																
F	"Punduloya"	NHM 1905.3.25.138 (ex. 1947.2.10.62) (HT)	54.9	16.5	12.4	5.2	4.7	5.7	3.8	8.0	14.9	9.9	2.9	1.6	16.8	24.5	20.8	17.2	19.9
F	Mannuthy	SDBDU 2007.6364	53.7	16.0	12.1	5.3	4.5	5.2	3.3	7.8	14.2	10.3	2.9	1.5	16.3	26.5	21.1	17.8	20.2
		Average	**54.3**	**16.3**	**12.3**	**5.3**	**4.6**	**5.5**	**3.6**	**7.9**	**14.6**	**10.1**	**2.9**	**1.6**	**16.6**	**25.5**	**21.0**	**17.5**	**20.1**
		Standard deviation	**0.8**	**0.4**	**0.2**	**0.1**	**0.1**	**0.4**	**0.4**	**0.1**	**0.5**	**0.3**	**0.0**	**0.1**	**0.4**	**1.4**	**0.2**	**0.4**	**0.2**
M	Bangalore	SDBDU 2014.2567	42.5	12.7	11.0	4.5	3.7	4.1	2.9	5.7	11.6	9.3	2.5	1.3	12.5	19.0	15.2	12.9	16.7
M	Odisha	SDBDU 2002.3107	51.9	14.4	11.2	5.0	4.2	5.2	3.6	7.6	12.9	9.6	3.0	1.6	14.9	23.9	19.2	16.6	20.2
M	Kalpetta	SDBDU 2005.4732A	51.1	13.8	10.5	4.7	3.8	5.4	2.5	7.3	12.5	8.5	2.8	1.5	15.0	23.6	19.5	16.5	19.4

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TABLE 4. (Continued)

Sex	Locality	Museum Number	SVL	HW	HL	SL	EL	IUE	UEW	IFE	IBE	MN	EN	NS	FAL	HAL	TL	SHL	FOL
		Average	**48.5**	**13.6**	**10.9**	**4.7**	**3.9**	**4.9**	**3.0**	**6.9**	**12.3**	**9.1**	**2.8**	**1.5**	**14.1**	**22.2**	**18.0**	**15.3**	**18.8**
		Standard deviation	**5.2**	**0.9**	**0.4**	**0.3**	**0.3**	**0.7**	**0.6**	**1.0**	**0.7**	**0.6**	**0.3**	**0.2**	**1.4**	**2.7**	**2.4**	**2.1**	**1.8**
		Uperodon anamalaiensis (Rao, 1937)																	
M	Parambikulam	ZSI/WGRC/V/A/956 (NT)	30.9	8.5	6.3	3.0	2.2	3.6	1.7	3.9	7.0	6.2	1.7	0.7	6.9	8.5	13.9	12.4	13.5
M	Parambikulam	SDBDU 2011.233A	36.7	10.2	8.2	4.3	2.3	3.9	1.6	4.3	8.4	6.3	2.3	0.9	7.1	10.4	14.4	12.9	14.6
M	Parambikulam	SDBDU 2011.234	35.2	8.9	6.7	3.4	2.3	3.6	1.7	4.5	8.3	6.7	2.1	0.8	7.5	9.3	14.5	13.1	14.2
M	Parambikulam	SDBDU 2011.548	28.7	8.8	6.5	3.0	2.3	2.7	1.3	3.4	6.2	6.2	1.7	0.5	6.5	8.3	11.2	9.3	10.4
M	Methooty	SDBDU 2012.2000	32.1	9.0	7.5	3.2	2.2	3.6	1.8	4.2	7.8	6.6	2.1	0.9	6.4	8.5	13.3	11.7	13.0
M	Methooty	SDBDU 2012.1994	32.2	9.8	7.6	3.6	2.2	3.5	1.8	4.2	9.1	6.7	2.0	1.0	8.0	10.3	13.1	12.1	13.7
M	Methooty	SDBDU 2012.1998	31.8	8.5	6.2	3.0	2.1	3.2	1.6	3.9	7.4	6.0	2.2	0.8	6.1	8.9	13.1	11.6	12.5
M	Methooty	SDBDU 2012.1996	30.6	8.3	6.9	3.2	2.1	4.1	1.7	3.8	7.7	6.0	1.9	0.8	7.1	8.5	13.0	11.2	12.7
M	Methooty	SDBDU 2012.1999	31.7	9.4	7.2	3.5	2.3	3.3	1.5	4.8	8.2	6.1	2.3	0.8	6.6	9.1	13.0	11.7	13.5
M	Methooty	SDBDU 2011.121	25.4	7.4	6.1	3.1	2.1	2.9	1.2	3.5	6.1	5.4	2.3	0.7	6.1	7.3	10.8	9.1	10.6
M	Ponmudi	SDBDU 2002.929	30.5	8.6	6.4	3.5	2.0	3.7	1.7	4.4	7.5	5.3	1.8	0.9	7.0	8.3	12.1	10.4	12.5
M	Chathankod	SDBDU 2002.3050	31.8	9.3	7.7	3.1	2.2	3.4	1.8	4.4	8.1	6.5	2.0	0.6	6.8	9.1	13.7	12.3	13.5
M	Chathankod	SDBDU 2002.3051	28.9	8.2	6.1	3.0	1.9	3.4	1.5	3.8	8.0	5.8	2.3	0.7	7.1	8.8	12.1	11.3	12.6
M	Sakleshpur	ZSI/WGRC/V/A/957 (NT)	31.7	9.1	7.1	3.1	2.1	3.4	1.3	4.2	7.4	5.9	2.2	0.9	6.2	8.6	13.8	11.8	13.3
		Average	**31.3**	**8.9**	**6.9**	**3.3**	**2.2**	**3.5**	**1.6**	**4.1**	**7.7**	**6.1**	**2.1**	**0.8**	**6.8**	**8.9**	**13.0**	**11.5**	**12.9**
		Standard deviation	**2.7**	**0.7**	**0.7**	**0.4**	**0.1**	**0.4**	**0.2**	**0.4**	**0.8**	**0.4**	**0.2**	**0.1**	**0.5**	**0.8**	**1.1**	**1.2**	**1.2**
F	Chathankod	SDBDU 2013.2302	38.6	10.6	8.6	3.7	2.3	4.4	1.9	4.7	8.3	7.7	2.4	0.9	9.2	11.9	15.4	14.2	15.7
F	Chathankod	SDBDU 2013.928	38.5	10.6	8.6	3.2	2.6	3.7	1.7	5.3	8.4	7.5	2.3	0.9	8.4	10.0	14.9	13.1	15.2
F	Methooty	SDBDU 2012.1995	37.4	9.8	8.2	3.9	2.9	4.3	1.7	4.9	9.2	6.4	2.2	1.0	8.2	10.7	15.0	12.8	15.7
F	Chathankod	SDBDU 2017.3507	35.3	8.9	6.8	3.3	2.8	3.3	1.7	4.7	7.6	6.3	1.9	0.9	6.9	10.0	14.9	12.9	14.3
		Average	**37.5**	**10.0**	**8.1**	**3.5**	**2.7**	**3.9**	**1.8**	**4.9**	**8.4**	**7.0**	**2.2**	**0.9**	**8.2**	**10.7**	**15.1**	**13.3**	**15.2**
		Standard deviation	**1.5**	**0.8**	**0.9**	**0.3**	**0.3**	**0.5**	**0.1**	**0.3**	**0.7**	**0.7**	**0.2**	**0.1**	**1.0**	**0.9**	**0.2**	**0.6**	**0.7**
		Uperodon montanus (Jerdon, 1854 "1853")																	
M	Settukunnu	SDBDU 2011.849	27.1	8.1	6.9	2.9	1.9	3.1	1.0	3.6	6.6	5.8	1.6	1.1	5.6	7.2	11.1	11.2	12.4
M	Pandimotta	SDBDU 2011.905	25.6	7.6	6.6	2.7	2.0	3.0	1.1	4.1	5.6	5.1	1.4	0.8	5.6	7.4	11.1	11.1	12.5
M	Pandimotta	SDBDU 2011.906	22.5	7.5	6.0	2.8	2.0	3.1	1.1	4.0	6.1	5.5	1.9	0.8	4.9	6.5	10.5	10.6	11.6
M	Kesavapara	SDBDU 2011.1197	23.6	8.0	6.3	2.6	1.6	2.6	1.3	3.4	5.8	5.1	2.0	0.7	5.5	6.6	10.1	10.2	11.7
M	Kakkachi	SDBDU 2003.40116	22.1	6.7	5.8	2.8	1.9	2.9	1.1	3.1	6.0	5.1	1.4	0.7	5.4	6.1	9.8	9.4	11.2
M	Sengaltheri	SDBDU 2002.24A	21.2	6.5	5.5	2.8	2.0	3.1	1.0	3.3	6.3	4.8	1.6	0.6	5.1	6.4	9.2	9.1	10.1
M	Kakkachi	SDBDU 2002.1925	22.2	7.1	5.6	2.7	1.8	3.2	1.2	3.1	6.0	4.1	1.7	0.6	5.7	6.1	9.5	9.2	10.1

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TABLE 4. (Continued)

Sex	Locality	Museum Number	SVL	HW	HL	SL	EL	IUE	UEW	IFE	IBE	MN	EN	NS	FAL	HAL	TL	SHL	FOL
M	Upper Manalar	SDBDU 2015.3001	25.2	7.2	6.4	2.8	2.1	2.7	1.2	3.9	6.9	4.9	1.4	0.7	5.4	6.7	10.8	10.7	11.7
M	"Malabar"	NHM 74.4.29.999	26.6	7.9	6.5	2.8	1.9	3.1	1.2	4.3	6.3	5.6	1.8	0.7	5.7	7.2	11.1	11.1	12.0
M	"Malabar"	NHM 74.4.29.1000	22.4	7.1	6.0	2.8	2.1	3.1	1.1	4.0	6.1	5.2	1.7	0.8	5.7	7.3	9.1	9.3	11.4
M	"Malabar"	NHM 74.4.29.1002	23.4	7.6	5.9	2.7	2.2	3.0	1.2	3.5	6.2	5.7	1.4	0.6	5.6	7.2	10.1	10.4	11.2
M	Devikulam	NHM 97.10.1.35	22.7	7.2	5.6	2.6	1.8	3.0	1.2	3.5	6.0	4.9	1.6	0.6	5.7	6.8	9.8	10.1	11.2
		Average	**23.7**	**7.4**	**6.1**	**2.8**	**1.9**	**3.0**	**1.1**	**3.7**	**6.2**	**5.2**	**1.6**	**0.7**	**5.5**	**6.8**	**10.2**	**10.2**	**11.4**
		Standard deviation	**1.9**	**0.5**	**0.4**	**0.1**	**0.2**	**0.2**	**0.1**	**0.4**	**0.3**	**0.5**	**0.2**	**0.1**	**0.3**	**0.5**	**0.7**	**0.8**	**0.8**
F	"Wynad"	NHM 72.4.17.212 (ex. 1947.2.11.19) (HT)	28.3	10.1	7.0	3.3	2.1	3.1	1.6	3.9	7.5	5.9	2.1	0.8	6.8	8.7	12.3	12.4	13.9
F	Kakkachi	SDBDU 2003.40115	28.1	8.9	7.2	3.1	2.3	3.2	1.4	3.8	7.2	5.7	1.7	0.5	6.6	8.4	12.0	12.2	13.8
F	Sengaltheri	SDBDU 2002.24B	31.2	10.9	8.5	3.2	2.2	4.3	1.6	4.8	8.3	6.5	1.9	0.8	7.5	9.1	13.8	13.9	14.5
F	Upper Manalar	SDBDU 2015.3002	31.8	11.0	8.1	3.5	2.4	3.5	1.7	4.6	8.0	6.2	2.0	0.9	7.2	9.5	13.7	13.9	15.2
F	Munnar	SDBDU 2005.30	29.8	10.5	7.0	3.2	2.0	3.0	1.7	4.0	7.5	6.0	1.9	0.9	7.0	8.8	12.2	12.4	14.0
F	Malabar	NHM 74.4.29.993	33.6	11.1	8.1	3.5	2.6	3.6	1.7	4.8	8.6	7.1	2.6	1.1	7.9	9.8	13.9	13.9	14.9
F	Devikulam	NHM 97.10.1.34	30.2	10.0	7.1	3.3	2.5	3.1	1.6	4.7	7.9	6.9	2.5	1.0	7.8	9.1	13.1	13.3	14.9
F	Devikulam	NHM 97.10.1.37	30.0	10.0	7.0	3.2	2.1	3.2	1.5	4.5	8.1	6.9	2.6	1.0	7.8	9.2	13.0	13.1	14.3
		Average	**30.4**	**10.3**	**7.5**	**3.3**	**2.3**	**3.4**	**1.6**	**4.4**	**7.9**	**6.4**	**2.2**	**0.9**	**7.3**	**9.1**	**13.0**	**13.1**	**14.4**
		Standard deviation	**1.8**	**0.7**	**0.6**	**0.1**	**0.2**	**0.4**	**0.1**	**0.4**	**0.5**	**0.5**	**0.4**	**0.2**	**0.5**	**0.4**	**0.8**	**0.7**	**0.5**
		Uperodon mormorata (Rao, 1937)																	
M	Shimoga	SDBDU 2012.43	31.2	9.9	8.0	2.6	2.0	3.9	1.5	4.5	7.9	7.2	2.5	0.7	6.2	8.9	12.4	11.1	13.1
M	Bygoor	SDBDU 2011.507	38.9	11.5	9.2	3.3	2.7	4.5	2.0	6.0	8.8	7.6	2.0	1.1	8.6	10.5	15.5	13.3	15.4
M	Castle Rock	SDBDU 2011.835	37.2	11.4	9.5	2.2	2.9	3.7	1.7	5.3	8.7	7.3	2.3	1.1	7.9	10.2	15.5	12.6	15.7
M	Castle Rock	SDBDU 2003.40197	35.9	10.5	7.1	3.2	2.9	3.9	1.9	5.1	9.3	7.3	1.9	0.8	7.3	10	14.9	12.5	14.3
M	Amboli	SDBDU 2002.2018B	33.2	10.5	7.3	3.4	2.7	3.7	1.9	5.1	8.6	7.0	2.1	1.0	7.0	9.0	12.7	11.9	13.6
M	Amboli	SDBDU 2002.2017	38.3	12.2	7.6	3.6	3.4	4.7	1.9	5.0	9.4	7.4	1.8	1.0	9.1	10.3	13.0	14	15.3
M	Amboli	SDBDU 2002.2018A	39.3	12.9	9.6	3.0	3.4	4.7	2.1	6.2	9.7	9.5	2.2	1.4	8.7	10.5	15.2	14.1	15.5
M	Goa	SDBDU 2015.3082	32.8	10.1	8.4	3.5	3.0	3.8	1.7	4.2	8.2	7.5	2.0	0.7	6.6	9.2	13.4	12.2	13.9
M	Netravali	SDBDU 2016.3404	34.2	11.0	9.1	3.6	2.5	4.0	1.7	5.0	9.0	7.8	1.8	1.0	7.3	9.3	13.0	12.0	14.1
		Average	**35.7**	**11.1**	**8.4**	**3.2**	**2.8**	**4.1**	**1.8**	**5.2**	**8.8**	**7.6**	**2.1**	**1.0**	**7.6**	**9.8**	**14.0**	**12.6**	**14.5**
		Standard deviation	**2.9**	**1.0**	**1.0**	**0.5**	**0.4**	**0.4**	**0.2**	**0.6**	**0.6**	**0.7**	**0.2**	**0.2**	**1.0**	**0.7**	**1.3**	**1.0**	**0.9**
F	Sakleshpur	ZSI/WGRC/V/A/958 (NT)	32.4	9.6	8.8	3.1	2.6	3.0	1.6	4.4	8.6	6.8	1.5	0.6	6.5	9.1	13.5	11.1	12.9
F	Samot	SDBDU 2002.567	38.6	11.8	9.8	3.1	2.8	3.9	1.5	5.3	8.9	8.6	2.8	1.1	7.7	9.6	14.3	12.9	14.7
F	Amboli	SDBDU 2015.3085	42.5	13.2	9.8	4.1	2.7	4.6	2.4	5.2	10.4	8.3	2.2	1.2	8.9	11.5	16.4	14.5	16.7

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TABLE 4. (Continued)

Sex	Locality	Museum Number	SVL	HW	HL	SL	EL	IUE	UEW	IFE	IBE	MN	EN	NS	FAL	HAL	TL	SHL	FOL
		Average	**37.8**	**11.5**	**9.5**	**3.4**	**2.7**	**3.8**	**1.8**	**5.0**	**9.3**	**7.9**	**2.2**	**1.0**	**7.7**	**10.1**	**14.7**	**12.8**	**14.8**
		Standard deviation	**5.1**	**1.8**	**0.6**	**0.6**	**0.1**	**0.8**	**0.5**	**0.5**	**1.0**	**1.0**	**0.7**	**0.3**	**1.2**	**1.3**	**1.5**	**1.7**	**1.9**
		Uperodon nagaoi (Manamendra-Arachchi and Pethiyagoda, 2001)																	
M	Kanneliya FR	WHT 2826 (HT)	25.6	6.8	6.0	3.3	2.0	2.9	1.3	4.2	6.5	4.7	1.6	0.9	6.2	6.5	11.5	11	11.2
M	Kanneliya FR	WHT 2867 (PT)	27.4	8.5	7.1	3.5	2.2	3.2	1.4	4.2	7.9	4.5	2.0	0.7	6.4	8.0	10.7	12.6	12.7
M	Kanneliya FR	WHT 2865 (PT)	27.3	7.4	6.7	3.2	2.1	3.2	1.5	3.7	6.9	4.8	1.6	0.7	6.2	8.1	11.7	12.3	12.3
M	Kanneliya FR	WHT 2868 (PT)	26.5	7.8	6.9	3.3	2.0	3.1	1.6	4.6	6.7	5.1	1.7	0.7	6.6	7.8	10.5	11.3	12.5
M	Kanneliya FR	WHT 2866 (PT)	27.7	7.4	6.5	3.4	2.1	3.3	1.7	4.0	6.7	4.3	1.6	0.6	7.5	7.6	10.8	12.3	12.4
M	Kanneliya FR	WHT 2863 (PT)	27.2	7.6	6.8	3.3	2.1	3.4	1.3	4.0	6.7	4.5	1.7	0.7	6.5	7.4	10.4	12.1	12.2
M	Kanneliya FR	WHT 2864 (PT)	26.7	8.2	7.2	3.5	2.1	2.8	1.7	3.9	6.9	4.4	1.6	0.7	6.2	7.8	11.0	11.7	11.8
M	Hiyare	DZ 1367	30.1	8.1	7.1	3.6	2.3	3.7	1.4	4.4	7.0	5.9	2.0	0.8	7.4	8.0	12.4	13.4	13.3
		Average	**27.3**	**7.7**	**6.8**	**3.4**	**2.1**	**3.2**	**1.5**	**4.1**	**6.9**	**4.8**	**1.7**	**0.7**	**6.6**	**7.7**	**11.1**	**12.1**	**12.3**
		Standard deviation	**1.3**	**0.5**	**0.4**	**0.1**	**0.1**	**0.3**	**0.2**	**0.3**	**0.4**	**0.5**	**0.2**	**0.1**	**0.5**	**0.5**	**0.7**	**0.8**	**0.6**
		Uperodon obscurus (Günther, 1864 "1863")																	
M	Morning side SL	WHT 3510	25.4	7.9	6.9	2.8	2.1	3.2	1.5	4.0	6.6	5.7	1.3	0.4	5.6	6.5	11.1	10.9	11.1
M	Laxapana, SL	WHT 7500	27.8	8.7	6.8	3.0	2.1	2.8	1.7	3.8	6.9	6.1	1.5	0.5	5.5	7.4	10.5	10.3	11.8
M	Pussellawa, SL	WHT 07697	26.2	7.7	6.5	2.7	2.2	2.4	1.6	3.6	7.2	5.6	1.3	0.6	5.8	7.5	12.0	12.1	11.1
M	Udawattekelle SL	WHT 00463A	22.8	6.9	6.5	2.3	2.1	2.7	1.7	3.5	6.3	4.4	1.4	0.4	5.1	6.2	9.9	10	9.9
M	Koskulana	WHT 1194	24.5	7.6	6.7	2.5	1.8	3.0	1.2	3.7	6.3	5.7	1.5	0.6	5.4	7.1	11.5	10.6	10.4
M	Paradeniya Campus	DZ 1369	26.3	7.7	6.9	2.8	1.8	3.6	1.3	4.2	6.8	6.2	1.7	0.6	5.9	7.0	10.4	10.6	10.3
M	Paradeniya Campus	DZ 1370	24.9	7.4	6.6	2.5	2.0	3.0	1.5	4.1	6.7	6.1	1.5	0.5	5.5	7.0	10	10.0	9.5
M	Paradeniya Campus	DZ 1366	24.2	7.5	6.8	2.6	2.0	3.2	1.7	4.1	7	5.9	1.5	0.5	5.9	7.2	10.9	11.0	12.7
M	Panwila, SL	DZ 1408	24.8	7.6	6.8	2.8	2.0	3.3	1.7	3.7	6.5	5.5	1.8	0.5	5.5	7.2	10.2	9.9	10.9
M	Paradeniya Campus	DZ 1365	27.8	8.0	7.2	3.1	2.1	3.6	1.6	4.3	6.9	5.9	1.8	0.7	6.4	7.3	10.9	11.1	11.1
M	Kandy: Sri Lanka	NHM 1982.1291	24.5	7.7	6.8	2.7	2.0	3.1	1,4	3.9	7	5.8	1.9	0.6	6.3	6.7	10.2	10.6	10.8
M	Kandy: Sri Lanka	NHM 1982.1292	25.9	7.7	5.9	2.7	2.1	3.0	1.3	3.9	6.6	5.2	2.4	0.4	4.6	7.6	10.1	10.6	12.0
M	Babilapitiya Estate	NHM 1973.3308	23.5	7.5	6.5	2.6	2.1	2.8	1.6	3.7	6.8	6.1	1.7	0.6	4.5	5.7	10.4	10.0	9.5
M	Babilapitiya Estate	NHM 1973.3309	22.7	7.9	6.6	2.4	1.7	3.1	1.7	3.4	7.0	6.1	2.0	0.6	5.2	6.3	10.4	10.2	9.7
M	Bogawantalowa	NHM 1973.3010	21.9	8.6	7.3	2.2	1.6	3.2	1.2	3.8	7.0	6.4	1.9	0.7	5.5	7.0	10.6	10.5	10.4
M	Krunegala: Ceylon	NHM 1973.3012	30.1	8.9	7.8	3.3	2.6	2.8	1.9	4.5	7.8	6.7	1.3	0.6	7.6	8.1	12.4	12.1	13.4
M	Krunegala: Ceylon	NHM 1973.3013	30.1	8.7	7.6	3.3	2.5	3.1	1.5	4.4	8.0	7.1	1.7	0.6	7.2	7.3	12.7	12.7	13.8

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TABLE 4. (Continued)

Sex	Locality	Museum Number	SVL	HW	HL	SL	EL	IUE	UEW	IFE	IBE	MN	EN	NS	FAL	HAL	TL	SHL	FOL
		Average	**25.5**	**7.9**	**6.8**	**2.7**	**2.0**	**3.1**	**1.5**	**3.9**	**6.9**	**5.9**	**1.7**	**0.6**	**5.7**	**7.0**	**10.8**	**10.8**	**11.1**
		Standard deviation	**2.4**	**0.5**	**0.4**	**0.3**	**0.3**	**0.3**	**0.2**	**0.3**	**0.5**	**0.6**	**0.3**	**0.1**	**0.8**	**0.6**	**0.8**	**0.8**	**1.3**
F	"Ceylon"	NHM 58.11.28.42 (ex. 1947.2.11.20) (HT)	32.2	9.3	8.8	4.2	3.9	3.3	1.4	4.9	8.6	6.5	2.4	0.7	8.8	9.5	13.5	13.3	14.9
F	Kandy: Sri Lanka	NHM 1982.1290	32.3	8.5	7.4	3.6	2.1	3.4	1.7	4.5	7.7	6	1.9	0.7	6.1	9.3	11.7	12.7	13.3
F	Gammaduwa	NHM 1955.1.10.77	30.1	8.9	7.7	3.5	2.1	3.6	2.1	4.7	8.5	6.5	1.9	0.7	7.1	6.9	12.6	13.3	12.6
F	Morning side, SL	WHT 05982	30.9	9.9	8.9	3.4	2.1	4	2	4.1	8.6	7.2	1.9	0.7	7.1	8.6	14.3	13.1	14.8
F	Morning side, SL	WHT 5980	37.1	10.4	9.1	3.9	3.1	4	1.9	4.5	8.7	7.4	2.2	1.0	8.5	9.7	15.4	14.9	15.6
		Average	**32.5**	**9.4**	**8.4**	**3.7**	**2.7**	**3.7**	**1.8**	**4.5**	**8.4**	**6.7**	**2.1**	**0.8**	**7.5**	**8.8**	**13.5**	**13.5**	**14.2**
		Standard deviation	**2.7**	**0.8**	**0.8**	**0.3**	**0.8**	**0.3**	**0.3**	**0.3**	**0.4**	**0.6**	**0.2**	**0.1**	**1.1**	**1.1**	**1.4**	**0.8**	**1.2**
		Uperodon palmatus (Parker, 1934)																	
M	"Newera Ellya"	NHM 90.11.8.63 (ex. 1947.2.11.22)	27.9	8.5	7	2.5	2.4	3.1	1.7	4.2	7.5	6.4	1.7	0.4	7.4	7.9	11.2	11.5	12.4
M	Nuwara Eliya	DZ 1371	28.9	7.9	6.9	2.8	2.7	3.1	1.6	4.1	7.4	6.9	1.3	0.8	7.1	8.5	11.4	11.3	13.2
M	Nuwara Eliya	DZ 1331	30.7	8.8	7.4	2.7	2.8	2.8	1.9	4.5	8.0	7.5	1.7	1.0	7.6	9.0	12.1	12.2	14.5
M	Nuwara Eliya	DZ 1372	30.5	8.7	7.6	2.7	2.8	3.4	2	4.4	8.4	7.2	1.8	0.6	7.7	8.9	12.4	12.4	14.1
		Average	**29.5**	**8.5**	**7.2**	**2.7**	**2.7**	**3.1**	**1.8**	**4.3**	**7.8**	**7.0**	**1.6**	**0.7**	**7.5**	**8.6**	**11.8**	**11.9**	**13.6**
		Standard deviation	**1.3**	**0.4**	**0.3**	**0.1**	**0.3**	**0.2**	**0.2**	**0.2**	**0.5**	**0.5**	**0.2**	**0.3**	**0.3**	**0.5**	**0.6**	**0.5**	**0.9**
F	"Newera Ellya"	NHM 90.11.8.62 (ex. 1947.2.11.21) (HT)	34.6	11.8	9.1	3.6	3.5	3.8	1.9	4.8	9.4	5.7	1.9	0.5	7.4	10.4	14.8	14.6	15.4
F	Diyagama estate	WHT 5424	35.3	10.1	8.5	3.3	3.4	3.5	2.2	4.5	8.3	6.8	1.9	0.8	8.2	9.7	13.5	13.6	15.6
		Average	**35.0**	**11.0**	**8.8**	**3.5**	**3.5**	**3.7**	**2.1**	**4.7**	**8.9**	**6.3**	**1.9**	**0.7**	**7.8**	**10.1**	**14.2**	**14.1**	**15.5**
		Standard deviation	**0.5**	**1.2**	**0.4**	**0.2**	**0.1**	**0.2**	**0.2**	**0.2**	**0.8**	**0.8**	**0**	**0.2**	**0.6**	**0.5**	**0.9**	**0.7**	**0.1**
		Uperodon triangularis (Günther, 1876)																	
M	"Malabar"	NHM 74.4.29.897 (ex. 1947.2.11.15) (ST)	31.6	9.6	7.7	3.7	2.5	3.4	1.9	3.6	8.4	5.7	2.1	0.9	7.1	8.7	11.4	10.9	12.1
M	"Malabar"	NMH 74.4.29.892 (ex. 1947.2.11.10)	32.3	10.7	8.3	3.3	2.9	2.1	1.9	4.9	9.4	6.8	1.9	1.7	7.7	9.5	13.1	12.0	13.8
M	"Malabar"	NHM 74.4.29.894 (ex. 1947.2.11.12)	32.2	2.0	10	3.8	2.8	3.5	2.0	5	9.4	8	1.7	0.8	7.3	9.8	11.8	12.9	14.8
M	"Malabar"	NHM 74.4.29.895 (ex. 1947.2.11.13)	32.7	9.3	9.4	3.6	2.3	3.9	1.8	4.7	8.7	8.1	1.9	1.1	6.8	8.6	11.2	11.3	13.3
M	"Malabar"	NHM 74.4.29.896 (ex. 1947.2.11.14)	31.9	10	7.7	3.6	2.7	3.4	2.0	4.4	9.2	6.1	2.0	0.7	5.6	8.9	12.4	11.5	13.3

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TABLE 4. (Continued)

Sex	Locality	Museum Number	SVL	HW	HL	SL	EL	IUE	UEW	IFE	IBE	MN	EN	NS	FAL	HAL	TL	SHL	FOL
M	"Malabar"	NHM 74.4.29.898 (ex. 1947.2.11.16)	30.5	9.1	7.2	3.6	2.5	2.9	1.7	4.1	8.9	5.7	2.0	1.0	6.5	9	11.4	11.6	11.5
M	"Malabar"	NHM 74.4.29.899 (ex. 1947.2.11.17)	29.5	9.3	7.4	3.0	2.6	4.1	1.7	4.0	8.4	6.1	1.9	0.9	6.9	8.9	12.2	11.7	13.7
M	"Malabar"	NHM 74.4.29.900 (ex. 1947.2.11.18)	25.6	7.8	5.8	3.0	2.4	2.5	1.5	3.6	7.2	6.5	1.6	0.9	5.8	6.9	8.8	10.0	10.5
M	Nilgheries	NHM 87.8.26.2	29.4	8.9	6.9	3.6	2.3	2.7	1.7	3.9	8.1	6	1.6	0.9	6.1	8.2	11.7	10.3	12.6
M	Bygoor	SDBDU 2011.504	32.7	10.3	8.2	3.5	2.8	3.6	2.0	4.3	8.7	6.8	1.6	0.9	6.5	8.8	12.4	11.9	13.0
M	Kalpetta	SDBDU 2012.2038	27.2	8.9	7.8	2.9	2.4	3.5	1.4	4.2	7.9	6.6	1.4	0.9	6.4	8.2	11.1	11.0	12.3
M	Bygoor	SDBDU 2011.503	36.0	11.1	8.6	3.4	2.4	3.9	2.1	5.1	8.9	6.9	1.9	0.9	8.0	10.3	13.2	12.6	14.6
M	Bygoor	SDBDU 2010.332	35.2	10.7	7.3	3.6	2.7	3.7	2.0	5.3	9.6	6.5	2.2	0.8	8.1	10.1	13.7	12.7	13.9
M	Kalpetta	SDBDU 2008.409	28.8	9.6	7.3	3.3	2.2	3.1	2.1	4.9	8.4	6.4	1.8	0.9	6.9	8.6	12.9	11.0	12.5
M	Bygoor	SDBDU 2011.502	34.2	10.1	7.6	3.8	2.4	3.9	2.1	4.9	8.8	6.3	1.8	0.9	7.4	9.7	12.6	12.7	13.4
M	Bygoor	SDBDU 2011.506	36.8	10.7	7.9	3.6	2.9	3.1	2.2	4.2	9.1	6.7	2.1	0.9	6.4	9.3	13.6	12.9	13.1
M	Mudigere	ZSI/WGRC/V/A/959 (NT)	29.7	9.4	6.7	2.7	2.2	3.0	1.9	4.0	7.9	6.0	1.6	0.9	6.0	8.8	11.0	10.1	12.4
M	Kalpetta	SDBDU 2007.6358	28.9	9.3	7.1	2.9	2.5	3.1	2.1	3.7	8.5	6.0	1.8	0.9	6.2	8.1	11.1	11.4	12.6
M	Suganthagiri	SDBDU 2015.2857	31.0	10.7	8.2	3.5	2.6	3.2	2.1	4.5	8.8	6.3	1.8	0.9	7.0	9.1	11.8	11.8	13.5
		Average	**31.4**	**9.3**	**7.7**	**3.4**	**2.5**	**3.3**	**1.9**	**4.4**	**8.6**	**6.5**	**1.8**	**0.9**	**6.8**	**8.9**	**12.0**	**11.6**	**13.0**
		Standard deviation	**2.9**	**2.0**	**0.9**	**0.3**	**0.2**	**0.5**	**0.2**	**0.5**	**0.6**	**0.7**	**0.2**	**0.2**	**0.7**	**0.8**	**1.2**	**0.9**	**1.0**
F	Ooty	SDBDU 2007.6400	40.8	11.5	8.4	3.7	2.7	4.6	2	4.9	9.5	8.1	2.1	1.1	8.1	10.8	13.8	14.1	14.2
F	Kalpetta	SDBDU 2003.40240	33.0	9.4	8	3.5	2.5	3.7	2	4.1	8.5	6.4	2	1.2	7.3	9	12.9	11.5	13.4
F	"Malabar"	NHM 74.4.29.891 (ex. 1947.2.11.9)	35.8	11.1	9.3	3.3	2.9	3.5	1.7	5.7	9.9	7.1	1.6	1	7.8	9.8	13.9	12.9	14.2
F	"Malabar"	NHM 74.4.29.893 (ex. 1947.2.11.11)	41.1	12.6	9.2	3.4	3	4.9	1.6	5.2	10.1	8.9	1.9	0.9	7.9	11.4	15.4	14.2	15.7
		Average	**37.7**	**11.2**	**8.7**	**3.5**	**2.8**	**4.2**	**1.8**	**5.0**	**9.5**	**7.6**	**1.9**	**1.1**	**7.8**	**10.3**	**14.0**	**13.2**	**14.4**
		Standard deviation	**4.0**	**1.3**	**0.6**	**0.2**	**0.2**	**0.7**	**0.2**	**0.7**	**0.7**	**1.1**	**0.2**	**0.1**	**0.3**	**1.1**	**1.0**	**1.3**	**1.0**
		Uperodon variegatus (Stoliczka, 1872)																	
M	Yellagherry Hills	NHM 72.4.29.1351 (ex. 1947.2.11.23)	26.8	7.4	6.2	3.1	2.4	3.1	1.4	3.9	6.6	5.9	1.6	0.8	5.8	7.5	10.6	9.8	11.5
M	Yellagherry Hills	NHM 72.4.29.1352 (ex. 1947.2.11.24)	25.6	7.0	6.3	3.2	2.6	2.9	1.3	3.4	6.5	5.3	1.6	0.8	5.6	7.1	10.2	9.9	11.0
M	Bangalore	NHM 1925.9.18.1 (ex. 1947.2.11.35)	30.1	8.8	7.3	3.4	2.4	3.3	1.3	4.1	6.9	6.2	1.7	0.6	5.6	7.4	10.8	9.9	10.8

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TABLE 4. (Continued)

Sex	Locality	Museum Number	SVL	HW	HL	SL	EL	IUE	UEW	IFE	IBE	MN	EN	NS	FAL	HAL	TL	SHL	FOL
M	Koruturu	SDBDU 2007.4994	32.1	8.9	6.5	3.3	2.6	3.3	1.4	4.2	7.5	6.3	1.6	0.8	5.7	8.8	11.1	9.5	12.1
M	Karamana	SDBDU 2007.6348	28.8	8.4	7.2	3.0	2.3	4.0	1.5	4.3	7.4	7.0	1.8	0.9	6.2	8.5	10.5	9.8	12.4
M	Palakkad	SDBDU 2002.524	29.8	8.5	6.8	3.2	2.4	3.6	1.6	4.2	7.2	6.2	1.3	0.7	6.0	7.1	11.0	9.4	10.4
M	Palakkad	SDBDU 2002.523	27.7	7.1	6.6	3.0	2.4	3.2	1.3	3.5	6.5	5.9	1.5	0.9	4.9	7.0	9.6	8.8	10.2
M	Meladoor	SDBDU 2003.40222	27.5	7.9	6.7	3.2	2.6	2.9	1.3	3.5	6.7	5.0	1.0	0.9	5.5	7.5	9.5	8.9	10.3
M	Chengalpattu	SDBDU 2005.4727	28.9	7.8	6.7	3.4	2.2	3.4	1.5	3.8	7.0	6.0	1.7	0.7	5.6	7.8	10.9	9.8	12.6
M	Utkal Uni. Campus	NHM 1984.132	27.4	6.9	6.3	3.3	2.1	3.2	1.4	3.7	6.7	5.8	1.5	0.8	5.5	7.3	9.5	9.1	10.3
M	Utkal Uni. Campus	NHM 1984.133	28.8	7.5	6.3	3.5	2.5	3.4	1.5	3.9	6.8	5.2	1.6	0.8	5.6	7.2	9.8	9.6	10.4
M	RR Lab area	NHM 1984.135	26.9	7.8	6.3	3.4	2.6	3.2	1.4	3.6	6.8	4.8	1.5	0.7	5.1	7.1	9.9	9.0	10.1
		Average	**28.4**	**7.8**	**6.6**	**3.3**	**2.4**	**3.3**	**1.4**	**3.8**	**6.9**	**5.8**	**1.5**	**0.9**	**5.6**	**7.5**	**10.3**	**9.5**	**11.0**
		Standard deviation	**1.8**	**0.7**	**0.4**	**0.2**	**0.2**	**0.3**	**0.2**	**0.3**	**0.3**	**0.6**	**0.2**	**0.2**	**0.3**	**0.6**	**0.6**	**0.4**	**0.9**
F	Ellore	ZSI 2761 (LT)	29.8	8.7	7.1	3.2	2.7	3.6	1.4	4.3	8.3	6.2	1.9	0.9	5.0	7.8	11.3	9.9	12.7
F	Gadavery Valey	NHM 1908.1.29.26	30.6	8.9	7.4	3.3	2.6	3.9	1.5	4.0	8.2	6.1	1.9	0.9	6.1	8.0	11.3	10.1	12.9
F	Gadavere	NHM 77.8.6.12	34.2	9.6	7.4	3.8	2.9	4.1	1.6	4.6	8.1	6.9	1.8	0.8	6.3	8.2	12.1	9.9	12.8
F	Bangalore	NHM1925.9.18.1 (ex. 1947.2.11.34)	35.6	9.9	7.7	3.8	2.8	3.8	1.8	4.7	8.3	7.3	1.9	0.8	6.4	8.3	12.9	10.5	13.1
F	Chengalpattu	SDBDU 2005.4726	33.8	9.6	7.1	3.4	2.9	3.8	1.7	4.5	8.0	7.0	1.8	0.9	6.3	8.6	12.1	10.4	13.1
F	Karamana	SDBDU 2007.6347	32.9	9.5	7.4	3.4	2.5	4.0	1.6	4.5	8.1	7.2	1.7	0.9	5.8	8.9	12.1	10.6	13.9
F	RR Lab area	NHM 1984.134	30.7	8.0	7.1	3.3	2.6	3.6	1.6	4.2	7.7	6.2	1.9	0.6	6.0	8.4	11.9	9.9	12.7
		Average	**32.5**	**9.2**	**7.3**	**3.5**	**2.7**	**3.8**	**1.7**	**4.4**	**8.1**	**6.7**	**1.9**	**0.8**	**6.0**	**8.3**	**12.0**	**10.2**	**13.0**
		Standard deviation	**2.2**	**0.7**	**0.2**	**0.2**	**0.2**	**0.2**	**0.2**	**0.2**	**0.2**	**0.5**	**0.1**	**0.1**	**0.5**	**0.4**	**0.6**	**0.3**	**0.4**
								***Uperodon rohani* sp. nov.**										
M	Mihintale	DZ 1449 (HT)	26.0	6.7	6.2	2.6	2.5	2.9	1.6	3.5	5.5	5.2	1.4	0.7	5.2	7.2	9.2	9.4	11.1
M	Mihintale	DZ 1448 (PT)	28.0	7.4	7.2	2.7	2.6	3.0	1.4	3.4	5.9	6.4	1.9	0.9	6.0	7.7	9.4	9.9	12.4
M	Mihintale	DZ 1450 (PT)	30.7	7.8	7.1	2.8	2.4	3.6	1.5	3.6	6.2	5.8	1.9	0.9	5.6	8.0	10.0	10.4	12.1
M	Mihintale	DZ 1374 (PT)	26.8	7.3	7.0	2.8	2.6	3.2	1.5	3.5	5.4	5.3	1.7	1.1	5.7	7.7	9.9	10.3	11.8
M	Bundala NP	DZ 1336 (PT)	26.4	7.4	7.0	2.6	2.4	2.9	1.5	3.9	6.1	5.8	1.8	0.5	5.7	7.5	9.3	9.6	11.3
M	Makandura	DZ 1520 (PT)	26.2	6.6	6.3	2.6	2.5	3.1	1.2	3.8	5.4	5.2	1.6	0.8	4.8	7.2	9.9	10.2	11.1
M	Makandura	DZ 1521 (PT)	28.9	7.7	7.2	2.8	2.4	2.8	1.5	3.7	5.7	5.8	1.9	0.9	5.8	7.7	11.0	10.9	12.2
M	Ampara	DZ 1486 (PT)	33.1	7.2	7.0	2.4	2.3	3.3	1.4	3.5	5.8	5.3	1.8	0.9	6.0	8.0	10.0	10.4	12.6
M	Ceylon	NHM 1931.2.1.21	28.6	7.5	7.0	2.6	2.4	3.2	1.2	3.3	6.6	5.7	1.8	0.9	6.1	7.9	10.1	10.7	11.6
M	Kurunegala: Ceylon	NHM 1973.3015	27.6	7.2	6.8	2.8	2.5	2.9	1.2	3.6	6.3	5.5	1.7	0.8	5.9	7.2	9.7	10.3	10.2

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TABLE 4. (Continued)

Sex	Locality	Museum Number	SVL	HW	HL	SL	EL	IUE	UEW	IFE	IBE	MN	EN	NS	FAL	HAL	TL	SHL	FOL
M	Badulla, Sri Lanka	NMH 1976.264	26.3	7.0	6.7	2.7	2.5	3.0	1.3	3.7	6.3	5.9	1.8	0.6	6.4	7.5	10.0	11.0	11.6
M	Badulla, Sri Lanka	NHM 1976.265	27.4	7.1	6.9	2.8	2.5	2.9	1.2	3.7	6.1	5.8	1.9	0.6	5.6	7.1	9.9	10.5	11.2
M	Nachchiyagama	WHT 5320	30.1	8.0	7.7	2.6	2.4	2.9	1.1	3.4	6.5	5.8	1.6	0.6	5.6	7.4	10.2	10.6	12.5
M	Sigiriya, Near RH	WHT 01188	28.0	7.8	7.3	2.6	2.6	3.0	1.2	3.5	6.6	5.9	1.7	0.5	5.6	7.6	10.0	10.5	10.9
M	Polonnaruwa	WHT 1749	26.3	6.6	6.4	2.9	2.6	2.7	1.2	3.5	6.2	5.2	1.5	0.6	5.7	7.5	9.4	9.8	10.1
M	Anuradhapura	WHT 01189	27.7	7.6	7.1	2.7	2.3	2.9	1.3	3.5	6.3	5.5	1.5	0.6	5.4	7.1	9.6	9.9	11.2
		Average	**28.0**	**7.3**	**6.9**	**2.7**	**2.5**	**3.0**	**1.3**	**3.6**	**6.1**	**5.6**	**1.7**	**0.7**	**5.7**	**7.5**	**9.9**	**10.3**	**11.5**
		Standard deviation	**1.9**	**0.4**	**0.4**	**0.1**	**0.1**	**0.2**	**0.2**	**0.2**	**0.4**	**0.3**	**0.2**	**0.2**	**0.4**	**0.3**	**0.4**	**0.5**	**0.8**
F	Kurunegala: Ceylon	NHM 1973.3014	28.7	7.4	6.8	2.6	2.7	3.4	1.3	3.5	6.3	5.1	2.0	0.6	5.9	7.8	10.3	11.4	11.0
F	Palatupana, Kirinda	WHT 01191	30.0	7.6	6.8	2.4	2.6	3.5	1.5	3.4	6.7	5.4	2.1	0.5	6.1	7.9	9.9	10.9	11.2
F	Dambulla	DZ 1129 (PT)	34.5	9.1	8.8	2.5	2.6	3.7	1.5	4.5	6.8	6.4	2.0	0.6	7.8	10.0	11.9	12.9	14.4
F	Dambulla	DZ 1130 (PT)	33.3	8.6	7.9	2.7	2.6	3.6	1.3	4.2	6.6	6.4	2.0	0.5	6.9	9.0	11.0	12.2	13.8
F	Dambulla	DZ 1132 (PT)	34.2	8.5	7.2	2.8	2.7	3.6	1.4	4.5	7.1	6.2	2.1	0.6	6.6	8.4	12.0	13.1	13.9
F	Dambulla	DZ 1131 (PT)	31.9	8.3	7.3	2.5	2.5	3.4	1.3	4.1	6.7	6.4	2.1	0.6	6.9	8.8	11.2	12.4	13.3
F	Makandura	DZ 1425 (PT)	31.1	8.4	7.8	2.6	2.7	3.5	1.6	4.1	6.8	6.9	2.3	0.9	6.3	7.3	10.8	11.8	12.1
F	Ampara	DZ 1485 (PT)	31.3	8.3	7.4	2.4	2.9	3.6	1.4	4.5	7.0	6.7	2.3	0.9	6.5	8.8	11.1	12.1	12.7
		Average	**31.9**	**8.3**	**7.5**	**2.6**	**2.7**	**3.5**	**1.4**	**4.1**	**6.8**	**6.2**	**2.0**	**0.7**	**6.6**	**8.5**	**11.0**	**12.1**	**12.8**
		Standard deviation	**2.0**	**0.5**	**0.7**	**0.1**	**0.1**	**0.1**	**0.1**	**0.4**	**0.2**	**0.6**	**0.2**	**0.2**	**0.6**	**0.8**	**0.7**	**0.7**	**1.3**

U. anamalaiensis (present study), *U. variegatus* (Rao 1918), *U. systoma* (Kirtisinghe 1957), and *U. globulosus* (present study) is terminal, whereas *U. palmatus* has a dorsoterminal mouth (Kirtisinghe 1958) and *U. nagaoi* has a funnel-shaped mouth (Manamendra-Arachchi & Pethiyagoda 2001). Tail morphology does not differ substantially among these species and almost all are known to have rounded tail tips as studied in *U. palmatus* (Kirtisinghe 1958), *U. triangularis, U. variegatus* (Rao 1918), *U. obscurus* (Bowatte & Meegaskumbura 2012) and *U. nagaoi* (Manamendra-Arachchi & Pethiyagoda 2001). Location of spiracle tends to show variation among the studied species, with spiracles in *U. variegatus, U. triangularis* (Rao 1918), *U. anamalaiensis* and *U. globulosus* (present study) located ventral to the gut; spiracle openings in *U. palmatus* (Kirtisinghe 1958) and *U. montanus* (Parker 1934) near tubular vent; and the opening slightly beyond posterior end of body in *U. obscurus* and *U. nagaoi* (Manamendra-Arachchi & Pethiyagoda 2001; Bowatte & Meegaskumbura 2012) (Fig. 16).

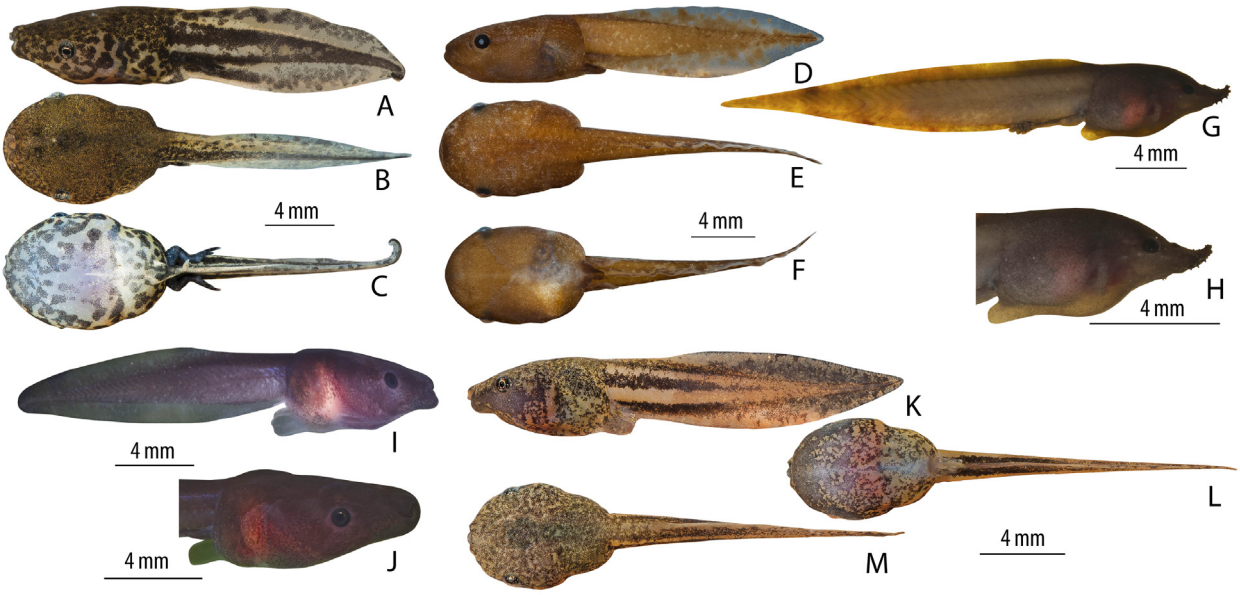

FIGURE 16. Tadpoles of *Uperodon globulosus*, *U. anamalaiensis*, *U. nagaoi*, *U. obscurus* and *U. triangularis*. **A–C.** *Uperodon globulosus* in life, Gosner stage 32: **A.** Lateral view; **B.** dorsal view; **C.** ventral view; **D–F.** *Uperodon anamalaiensis* in preservation, Gosner stage 34; **D.** Lateral view; **E.** dorsal view; **F.** ventral view; **G–H.** *Uperodon nagaoi* in preservation, Gosner stage 37: **G.** Lateral view; **H.** lateral view of head; **I–J.** *Uperodon obscurus* in life: **I.** Lateral view, Gosner stage 30; **J.** Lateral view of head, Gosner stage 38; **K–M.** *Uperodon triangularis* in life, Gosner stage 35: **K.** Lateral view; **L.** ventral view; **M.** dorsal view. (Images: SD Biju, I–J & G–H. Madhava Meegaskumbura).

Discussion

The genus *Uperodon* is morphologically one of the most diverse anuran groups of the Western Ghats–Sri Lanka biodiversity hotspot. Its members exhibit immense variations with respect to body shape (slender vs. robust and globular), body size (21–72 mm), lifestyle (burrowing vs. arboreal), reproductive behaviour (arboreal vs. terrestrial), and tadpole morphology. Species within the group also form three highly divergent evolutionary lineages, which along with striking phenotypic differences could be the major reason for acceptance of the previous generic-level classification despite the advent of molecular systematics (e.g., Van Bocxlaer *et al*. 2006; Pyron & Wiens 2011). Recently, based on molecular evidence and earlier observations of Ramaswami (1936), Peloso *et al*. (2016) considered the synonymy of *Ramanella* (*sensu stricto*) and *Kaloula pulchra taprobanica* with *Uperodon* (*sensu stricto*) as the most parsimonious option for stabilizing the taxonomy of this group. Our taxonomic revision using an integrative approach, which includes all members of this morphologically variable group, will aid future studies on *Uperodon* (*sensu lato*) frogs. Furthermore, this study delineates the geographical ranges of all known *Uperodon* species, clarifying their patterns of distribution. Of the 12 nominal species, eight are restricted to the Western Ghats–Sri Lanka biodiversity hotspot (*U. anamalaiensis*, *U. montanus*, *U. mormorata*, *U. nagaoi*, *U. obscurus*, *U. palmatus*, *U. rohani* **sp. nov.** and *U. triangularis*), accounting for 67% endemism at the species level. Among these species, four each are endemic to the Western Ghats and Sri Lanka, respectively. The remaining

species—*U. globulosus*, *U. systoma*, *U. taprobanicus* and *U. variegatus*, are more widely distributed outside the Western Ghats–Sri Lanka hotspot region, with distributions of the former three extending up to adjoining countries such as Bangladesh, Bhutan, Nepal and Pakistan (Fig. 2A; Tables 1, S1).

Although knowledge on the natural history of *Uperodon* species is sparse, some interesting insights can be gained regarding the reproductive requirements of these frogs. Several species are known to be arboreal and may therefore possess dilated finger and toe tips as an adaptation for climbing (Blackburn *et al*. 2013). The non-dilated digit tips in some members (*U. globulosus* and *U. systoma*), however, are suggestive of terrestrial lifestyles. Further, only a few species breed inside tree holes; most others are opportunistic, breeding in ground puddles. It would thus be interesting to investigate the various reproductive modes in *Uperodon* frogs, how they have evolved to utilize different niches, and the possible factors responsible for diversification. In the future, based on comprehensive phylogenies, morphological and ecological traits can be analyzed to address various evolutionary questions. Such studies could also shed light on the adaptability of *Uperodon* frogs, especially in the absence of suitable habitats such as tree holes, which is likely to be their most immediate threat with increasing habitat destruction and degradation in the Western Ghats–Sri Lanka biodiversity hotspot.

Acknowledgements

We are grateful to Rohan Pethiyagoda and Mark D Scherz for their valuable comments and suggestions that were helpful in improving the earlier draft of this paper; Robin Suyesh for help in the acoustic and statistical analyses; Mahadev Mathpati for support in compilation and preparation of Table S1; K Jayaram for field and logistic support to SDB and SG in Tamil Nadu; Aravind Madhyasthya, KV Gururaja and KP Dinesh for field support to SDB and SG in Karnataka; Past members of the Systematics Lab (University of Delhi) for field support; Romulus Whitaker and Janaki Lenin for logistic support to SDB and SG during fieldwork at Mamallapuram (Tamil Nadu) and for permission to use their photographs of *Uperodon variegatus*; L. Shyamal for permission to use the image of *Uperodon variegatus*; Mark-Oliver Rödel and Frank Tillack (ZMB, Berlin) for providing access to specimens in their care and their hospitality to SDB and SG; Kailash Chandra and G Maheswaran (ZSI, Kolkata), PM Sureshan (ZSI, Calicut) and Rahul Khot (BNHS, Mumbai), Manori Goonatilake and Chandrika Munasinghe (NHM, Colombo) for access to specimens in their care and museum support to SDB and SG; Barry Clarke and David Gower (NHM, London) for access to specimens in their care and museum support to SDB; the state forest departments in India (Kerala, Karnataka, Tamil Nadu, Maharashtra) for study permits and field support; the Department of Wildlife Conservation and Forest Department of Sri Lanka for research permits. We also thank the editor (Miguel Vences) and the two reviewers (Mark D Scherz and KV Gururaja) for valuable suggestions. This study was partially supported by the following grants to SDB: Critical Ecosystem Partnership Fund, Conservation International, USA (Project 55918/ 2009); University of Delhi Research and Development Grants 2013–14 and 2015–16; DST Purse Grant Phase I (2009–2013) and Phase II (2015–16), Department of Science and Technology, Ministry of Science and Technology, Government of India. SG received research fellowships from University of Delhi, University Teaching Assistantship Scheme (2010/56562), and Council for Scientific and Industrial Research (CSIR No. 9/45(1381)/2015-EMR-I). GS received a Rufford Small Grant (No. 192721) and MM received a grant from National Research Council of Sri Lanka (No. 11-124).

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Supplementary Material

An integrative taxonomic review of the South Asian microhylid genus *Uperodon*

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TABLE S1. Distribution of *Uperodon* species. 1. Genetically and morphologically studied collections from the present study, 2. Other morphologically studied collections and museum specimens in the present study, 3. Previously published literature and other available records (including reports that require further confirmation). Asterisk symbol denotes the type locality.

State / Province	Locality	Reference
	Uperodon anamalaiensis	
	INDIA	
Tamil Nadu	"Base of Anamalai Hills, Coimbatore District"*	Rao 1937
Kerala	Parambikulam TR, Palakkad district	Vijaykumar *et al*. 2011[2]; Present Study[1]
	Munnar, Idukki district	Harpalani *et al.* 2015[3]
	Chathankod, Thiruvananthapuram district	Present Study[1]
	Kallar, Ponmudi, Thiruvananthapuram district	Present Study[1]
	Makki, Thiruvananthapuram district	Present Study[2]
	Methooty, Idukki district	Present Study[1]
Karnataka	Kempholey, Hassan district	Present Study[1]
	Sakleshpur, Hassan district	Present Study[1]
	Uperodon globulosus	
	INDIA	
Kerala	Manimala River, Erumely, near Koratty bridge, Kottayam district	George & Alex 1995[3]; Dutta 1997[3]
Karnataka	Khanapur, Belgaum district	Abdulali 1962[3]
	"Mysore"	Dutta 1997[3]
Maharashtra	"Kanheri Caves (*ca.* 1,300 ft.), near Borivli, Salsette Island, Bombay"	Abdulali & Daniel 1954[3]
	Kanheri Caves, Mumbai	Bhaduri & Daniel 1956[3]
	"Bombay"	Daniel 1963a[3]
	Balewadi, Pune district	Padhye *et al.* 2002[3]
	Pashan, Pune district	Padhye *et al.* 2002[3]
	Navegaon National Park, Gondia district	Bhandarkar *et al.* 2012[3]
	Supegaon, Phansad Wildlife Santuary	Katwate *et al.* 2013[3]
	"Satara Tehsil"	Prasad *et al.* 2013[3]
	Radhanagari Wildlife Santuary	Yadav & Yankanchi 2014[3]
	Shivaji University, Kolhapur district	Yadav *et al.* 2014[3]
	Pune, Pune district	Present Study[1]
	Tamhini Ghat, Pune district	Present Study[2]
Andhra Pradesh	Sundipenta/Sikharam, Nallamalai Hills	Rao *et al.* 2005[3]

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TABLE S1. (Continued)

State / Province	Locality	Reference
	Mannanur – Farahabad, Nallamalai Hills	Srinivasulu *et al.* 2006[3]; Srinivasulu *et al.* 2007[3]
	Mukhadwaram – Srisailam, Nallamalai Hills	Srinivasulu *et al*. 2007[3]
	"Nallamala hills"	Srinivasulu & Das 2008[3]
	Seshachalam Biosphere Reserve	Guptha *et al.* 2012[3]
	Thummalapalle uranium mining area, Thummalapalle, YSR Kadapa district	Reddy *et al.* 2013[3]
Gujarat	Ahwa, Dang district	Daniel 1963a[3]
	Waghai, Dang district	Daniel 1963a[3]
	Shoolpaneshwar WLS, Bharuch district	Naik & Vinod 1993[3]; Sarkar & Ray 2000[3]
	Surat Dangs, Narmada district	Dutta 1997[3]
	Vansda National Park	Vyas 2004[3]
Madhya Pradesh	"Jabalpur"	Dutta 1992[3]; Chandra & Gajbe 2005[3]
	"Berar"	Dutta 1997[3]
	Kachpura Ward, Jabalpur	Chandra & Ray 2007[3]
	Tropical Forest Research Institute campus, Jabalpur	Paunikar 2017[3]
Chhattisgarh	"Bastar"	Sarkar 1993[3]; Chanda 1995[3]; Chandra & Gajbe 2005[3]; Dutta 2015[3]
	Indravati Tiger Reserve	Chanda 1995[3]; Chandra & Gajbe 2005[3]
Odisha	"Russelconda"*	Günther, 1864 "1863"[2]
	Sambalpur University Campus, Sambalpur district	Sarkar 1993[3]
	"Dhenkanal"	Dutta 1997[3]
	Bedkot, Karlapat WLS	Deuti & Raha 2010[3]
	Karlapat, Karlapat WLS	Deuti & Raha 2010[3]; Deuti *et al.* 2014
	"Mundguda" (= Mundraguda), Karlapat WLS	Deuti & Raha 2010[3]
	"Rayagada"	Deuti *et al.* 2014[3]
	North Orissa University Campus, Mayurbhanj district	Boruah *et al.* 2016[3]
Jharkhand	Tundi, Dhanbad district	Sarkar 1991[3]
West Bengal	"Calcutta"	Bhaduri 1945[3]
	"Jalpaiguri"	Bhaduri & Basu 1956[3]; Dutta 1997[3]
	24 Pargonas district	Sarkar *et al*. 1992[3]
	Haora (=Howrah) district	Sarkar *et al*. 1992[3]
	Hugli (=Hooghly) district	Sarkar *et al*. 1992[3]
	Dhupguri, Jalpaiguri district	Sarkar *et al*. 1992[3]
	Sulkapara, Jalpaiguri district	Sarkar *et al*. 1992[3]
	Mandalpushkarini, Medinipur district	Sarkar *et al*. 1992[3]
	"40 miles north of Calcutta: Camp Kanchrapara"	Dutta 1997[3]
	Midnapore district	Pratihar & Deuti 2011[3]

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TABLE S1. (Continued)

State / Province	Locality	Reference
	Durgapur city, Paschim Bardhaman district	Pal *et al.* 2012[3]
	Amarabati pond, Durgapur, Paschim Bardhaman district	Dutta & Mukhopadhyay 2013[3]
	Durgapur Government College campus, Paschim Bardhaman district	Dutta & Mukhopadhyay 2013[3]
Uttar Pradesh	Dudhwa National Park, Kamrup district	Hegde 2013[3]
Assam	Kamrup district	Bhaduri & Saha 1980[3]; Dutta 1997[3]
	Mandakata, Kamrup district	Choudhury *et al.* 1999[3]
	Sonitpur district	Choudhury *et al.* 1999[3]
	Dibru Saikhowa National Park	Choudhury *et al.* 2001[3]
	Barak Valley	Dey 2001[3]
	Sivasagar district	Bortamuli & Bordoloi 2008[3]
Arunachal Pradesh	"Pakhui Wildlife Sanctuary, Bhalukpung, Tippi and Near Khari River"	Borah & Bordoloi 2001[3]
	Itanagar, Papumpare	Borah & Bordoloi 2003[3]
	BANGLADESH	
Chittagong	Bandarban Hill district	Reza & Perry 2015[3]
	Kaptai National Park, Rangamati district	Shihan & Kabir 2015[3]
Dhaka	Madhupur National Park, Tangail district	Reza & Perry 2015[3]
	Rasulpur, Madhupur NP, Tangail district	Mahony *et al.* 2009[3]
	Savar, Dhaka district	Mahony *et al.* 2009[3]
	Jahangirnagar University, Dhaka district	Reza & Perry 2015[3]
Rangpur	Berakuthi, Barua, Nilphamari district	Sarker *et al*. 2012[3]
	BHUTAN	
–	Royal Manas National Park	Das *et al.* 2016a[3]
	NEPAL	
	(n.a.)	Shrestha 2001[3]; Anders 2002[3]; Shah & Tiwari 2004[3]; Frost 2017
	Uperodon montanus	
	INDIA	
Colonial location	"Anamallays"	Parker 1934[3]
	"Malabar"	Parker 1934[2]
	"Travancore"	Parker 1934[3]
Tamil Nadu	Kalakkad Mundunthurai Tiger Reserve	Cherian *et al*. 1999[3]; Johnsingh 2001[3]; Vasudevan *et al.* 2001[3]
	Kakkachi, Tirunelveli district	Present Study[1]
	Sengaltheri, Tirunelveli district	Present Study[2]
Kerala	"Wynaad"*	Jerdon 1854 "1853"[2]
	"Devicolum, Travancore (4,000-7,000 ft)"	Parker 1934[3]
	"Trevandrum, Travancore"	Parker 1934[3]
	"Kochi"	Dutta 1997[3]

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TABLE S1. (Continued)

State / Province	Locality	Reference
	Wayanad	Abraham *et al.* 2001[3]
	Amballoore, Chimmini Wildlife Sanctuary	Andrews *et al.* 2005a[3]
	Silent Valley, Poochappara	Andrews *et al.* 2005a[3]
	Thiruvananthapuram district	Andrews *et al.* 2005b[3]
	Devikulam, Idukki district	Present Study[2]
	Kesavapara, Nelliyampathy, Palakkad district	Present Study[1]
	Kurichiyarmala, Wayanad district	Present Study[1]
	Munnar, Idukki district	Present Study[1]
	Pandimotta, Shendurney WLS, Kollam district	Present Study[1]
	Settukunnu, Wayanad district	Present Study[1]
	Siruvani, Palakkad district	Present Study[2]
	Upper Manalar, Periyar TR, Idukki district	Present Study[1]
	Thirunelli, Wayanad district	Present Study[1]
Karnataka	Dandeli, Uttara Kannada district	Adbulali 1962[3]
	Sringeri, Chikkamagaluru district	Kadadevaru *et al.* 1998; Krishnamurthy 1996[3]
	Kudremukh National Park	Krishnamurthy 2003[3]
	Hosagadde (Cardamom estate), Bisale Reserve forest	Krishna *et al.* 2004[3]; Krishna & Bosch 2007[3]
	Agumbe, Shimoga district	Ganesh *et al.* 2007[3]
	Tirthahalli, Shimoga district	Ganesh *et al.* 2007[3]
	Sharavathi, Uttara Kannada district	Gururaja *et al.* 2008[3]; Ramachandra *et al*. 2012[3]
	Talagini, Shimoga district	Kuramoto & Joshy 2009
	Thomra, southern Coorg, Kodagu district	Ganesh & Asokan 2010[3]
	Sagar, Shimoga district	Joshy & Kuramoto 2011[3]
	Mirjan, Uttara Kannada district	Kumar *et al.* 2012[3]
	Kali river basin, Uttara Kannada district	Ramachandra *et al*. 2012[3]
Maharashtra	Sanjay Gandhi National Park	Yazdani *et al.* 1992[3]
	Kanari Caves, Salsette Island	Dutta 1997[3]
	Khandala, Pune district	Dutta 1997[3]; Padhye & Ghate 2012[3]
	Sawantwadi, Sindhudurg district	Sohani & Samant 2009[3]
	Amboli, Sindhudurg district	Sohani & Samant 2009[3]; Padhye & Ghate 2012[3]
	Koyna, Satara district	Padhye & Ghate 2012[3]
	Tamhini, Pune district	Dahanukar & Padhye 2005[3]; Padhye & Ghate 2012[3]
	"Satara Tehsil"	Prasad *et al.* 2013[3]
Gujarat	Vansda National Park	Vyas 2004[3]
	Uperodon mormorata	
	INDIA	
Karnataka	Sakleshpur, Hassan district*	Rao 1937; Present Study[2]

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TABLE S1. (Continued)

State / Province	Locality	Reference
	Gundia river Basin	Gururaja *et al.* 2007[3]; Dudani *et al.* 2010[3]
	Agumbe, Shimoga district	Purushotham & Tapley 2011[3]
	Baba Budan Hills, Chikmagalur district	Gururaja 2012[3]
	Kempholey, Hassan district	Gururaja 2012[3]
	Dandeli Anshi Tiger Reserve, Uttara Kannada district	Gururaja & Ramachandra 2012[3]
	Kuvempu University Campus, Bhadra Wildife Sanctuary range, Shimoga district	Narayan *et al*. 2017[3]
	Bygoor, Chikmagalur district	Present Study[1]
	Castle Rock, Uttara Kannada district	Present Study[1]
	Dandeli, Uttara Kannada district	Present Study[1]
	Kachigebailu, Shimoga district	Present Study[1]
	Londa, Belgaum district	Present Study[2]
Maharashtra	Barshiv, Phansad Wildlife Sanctuary	Katwate *et al.* 2013[3]
	Supegaon, Phansad Wildlife Sanctuary	Katwate *et al.* 2013[3]
	Amboli, Sindhudurga district	Sayyed 2014[3]; Present Study[1]
	Radhanagari Wildlife Sanctuary	Yadav & Yankanchi 2014[3]
	Shivaji University, Kolhapur	Yadav *et al.* 2014[3]
	Ajoba fort, Thane district	Pandirkar *et al.* 2016[3]
	Amba, Kolhapur district	Present Study[1]
Goa	Canacona, Cotigao Wildlife Sanctuary	Das & Whitaker 1997[3]
	Anjuna, North Goa district	Present Study[1]
	Netravali, South Goa district	Present Study[1]
Gujarat	Samot, Shoolpaneshwar Wildlife Sanctuary, Narmada district	Vyas 2012[3]; Present Study[2]
Assam	Barak Valley	Dey 2001[3]
	Uperodon nagaoi	
	SRI LANKA	
Central Province	Sri Pada Nature Reserve	Karunarathna & Amarasinghe 2009[3]
Sabaragamuwa Province	Kithulgala	Pethiyagoda *et al.* 2006[3]; Karunarathna & Amarasinghe 2009[3]
	Bambarabotuwa-Ratnapura	Karunarathna & Amarasinghe 2009[3]
	Gilimale	Karunarathna & Amarasinghe 2009[3]
	Koskulana-Panapola	Karunarathna & Amarasinghe 2009[3]
	Pompekale-Ratnapura	Karunarathna & Amarasinghe 2009[3]
	Uda Mäliboda, Samanala Nature Reserve	Samarasinghe *et al.* 2012[3]
Southern Province	Kanneliya Forest Reserve*	Manamendra-Arachchi & Pethiyagoda 2001; Present Study[2]
	Kudawa, Sinharaja	Pethiyagoda *et al.* 2006[3]
	Hiyare, Galle district	Karunarathna & Amarasinghe 2009[3]; Present Study[1]
	Beraliya- Elpitiya, Galle district	Karunarathna & Amarasinghe 2009[3]

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TABLE S1. (Continued)

State / Province	Locality	Reference
	Dediyagala	Karunarathna & Amarasinghe 2009[3]
	Hiniduma	Karunarathna & Amarasinghe 2009[3]
	Kanneliya	Karunarathna & Amarasinghe 2009[3]
	Kottawa-Kombala, Hiyare	Karunarathna & Amarasinghe 2009[3]
	Nakiyadeniya	Karunarathna & Amarasinghe 2009[3]
	Matara district (Dediyagala, Wilpita and Sinharaja)	Wildlife Conservation Society Report 2009[3]
Western Province	Athwelthota, Kalutara district	Karunarathna & Amarasinghe 2009[3]
	Uperodon obscurus	
	SRI LANKA	
Colonial location	"Ceylon" (=Sri Lanka)*	Günther 1864 "1863"
Central Province	Knuckles Mountain Forest Range	Dutta & Manamendra-Arachchi 1996[3]; Weerawardhena & Russell 2012[3]
	Sarasavigama, Kandy district	Lokuhewage & Amerasinghe 2001[3]
	Gannoruwa, Kandy district	Chandrasegaran & Ranawana 2002[3]; Pethiyagoda *et al.* 2006[3]
	Illukkumbura, Matale district	Pethiyagoda *et al.* 2006[3]
	Kotagala, Nuwara Eliya district	Pethiyagoda *et al.* 2006[3]
	Gannoruwa Forest Reserve	Ukuwela & Ranawana 2007[3]
	Ambagamuwa, Nuwara Eliya district	Kumara & Ukuwela 2009[3]
	Peradeniya, Kandy district	Bowatte & Meegaskumbura 2011[3]; Present Study[2]
	Samanala Nature Reserve	Karunarathna *et al.* 2012[3]
	Bogawantalawa, Nuwara Eliya district	Present Study[2]
	Gammaduwa, Matale district	Present Study[2]
	Laxapana, Nuwara Eliya district	Present Study[2]
	Panwila, Kandy district	Present Study[2]
	Pussellawa, Kandy district	Present Study[2]
	Udawatta Kele, Kandy district	Present Study[2]
North Western Province	Kurunegala, Kurunegala district	Present Study[2]
Sabaragamuwa Province	Morningside, Rakwana, Ratnapura district	Janzen & Bopage 2011[3]; Present Study[2]
	Uda Mäliboda, Samanala Nature Reserve	Samarasinghe *et al.* 2012[3]
	Babilapitiya estate, Kegalle district	Present Study[2]
	Koskulana, Panapola, Sinharaja, Ratnapura district	Present Study[2]
Sabaragamuwa & Southern Provinces	Sinharaja, World Heritage Site	Dutta & Manamendra-Arachchi 1996[3]; Bambaradeniya *et al.* 2003[3]; Meegasakumbura *et al.* 2012[3]
Uva Province	Namunukula, Badulla district	Dutta & Manamendra-Arachchi 1996[3]; Pethiyagoda *et al.* 2006[3]

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TABLE S1. (Continued)

State / Province	Locality	Reference
	Uperodon palmatus	
	SRI LANKA	
Central Province	"Newera Ellya", Sri Lanka*	Parker 1934[2]
	Nuwara-Eliya, Nuwara Eliya district	Dutta & Manamendra-Arachchi 1996[3]; Present Study[1]
	Bogawantalawa	Pethiyagoda *et al.* 2006[3]
	Horton plains	Pethiyagoda *et al.* 2006[3]
	Diyagama estate, Agrapatana	Present Study[2]
	Morey estate	Present Study[1]
	Pattipola, Nuwara Eliya district	Present Study[2]
Central and Uva Provinces	Hakgala	Pethiyagoda *et al.* 2006[3]
Southern and Uva Provinces	Yala National Park	Karunarathna *et al*. 2017[3]
	Uperodon rohani sp. nov.	
	SRI LANKA	
Central Province	Sigiriya, Matale district	Dutta & Manamendra-Arachchi 1996[3]; Present Study[2]
	Menikdena (Dambulla), Matale district	Somaweera *et al.* 2001[3]
	Kalugala Proposed Forest Reserve (KPFR), Kaluthara district	Botejue & Wattavidanage 2012[3]
	Dambulla, Matale district	Present Study[1]
Eastern Province	Trincomalee	Dutta & Manamendra-Arachchi 1996[3]
	Panama, Ampara district	Somaweera *et al.* 2004[3]
	Ampara, Ampara district	Present Study[2]
Northern Province	Paranthan, Jaffna, Kilinochchi district	Dutta & Manamendra-Arachchi 1996[3]; Present Study[2]
	Jaffna, Jaffna district	Dutta & Manamendra-Arachchi 1996[3]
	Opata, Kotugoda	Dutta & Manamendra-Arachchi 1996[3]
North Central Province	Anuradhapura, Anuradhapura district	Dutta & Manamendra-Arachchi 1996[3]; Present Study[2]
	Mihinthale, Anuradhapura district*	Dutta & Manamendra-Arachchi 1996[3]; de Silva 2011[3]; Present Study[1]
	Mihinthale Sanctuary, Anuradhapura district	Sarathchandra *et al.* 2017[3]
	Nochchiyagama, Anuradhapura district	Present Study[2]
	Polonnaruwa, Polonnaruwa district	Present Study[2]
North Western Province	Anawilundawa Wetland Santuary	Rodrigo *et al.* 2008[3]
	Puttalam city, Puttalam district	Karunarathna & Amarasinghe 2011[3]
	Karawaddana, Kurunegala district	Present Study[1]
	Kurunegala, Kurunegala district	Present Study[2]
	Makandura, Kurunegala district	Present Study[2]

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TABLE S1. (Continued)

State / Province	Locality	Reference
Western Province	National Zoological Garden, Dehiwala	Karunarathna *et al.* 2008[3]
	Bellanwila - Attidiya Sanctuary (BAS)	Karunarathna *et al.* 2010[3]
Uva Province	Nilgala Forest Area, Monaragala district	Sarathchandra *et al.* 2017[3]
	Badulla, Badulla district	Present Study[2]
	Mahiyanganaya, Badulla district	Present Study[2]
Southern Province	Palatupana, Kirinda, Hambantota district	Dutta & Manamendra-Arachchi 1996[3]; Present Study[2]
	Bundala, Hambantota district	Present Study[1]
	Uperodon systoma	
	INDIA	
Colonial location	"India orientali"*	Schneider 1799
Tamil Nadu	Chengai-MGR (formerly Chengleput) district	Das 1996[3]
	Mamallapuram, Kanchipuram district	Dutta 1997[3]
	Madras	Khan 2002[3]; Ganesh & Asokan 2010[3]
	Mannampandal, Nagapattinam district	Ganesh & Chandramouli 2007[3]
	AVC College, Mannampandal, Nagapattinam district	Nath *et al.* 2012[3]
	Kalpakkam Nuclear Campus, Kanchipuram district	Ramesh *et al.* 2013[3]
	Meghamalai, Theni district	Srinivas & Bhupathy 2013[3]
	Ilangi, Tirunelveli district	Vasanthi *et al.* 2014[3]
	Kudirapppu, Tirunelveli district	Vasanthi *et al.* 2014[3]
	Nannagaram, Tirunelveli district	Vasanthi *et al.* 2014[3]
	Coimbatore, Coimbatore district	Present Study[1]
	Kunnapattu, Kanchipuram district	Present Study[1]
Kerala	Kottayam, Kottayam district	Dutta 1997[3]
	Trivandrum, Thiruvananthapuram district	Ferguson 1904[3]; Dutta 1997[3]; Saidapur 2001[3]
	Nilambur, Malappuram district	Andrews *et al.* 2005b[3]
Karnataka	"Dharwar" (= Dharwad)	Uttangi 1951[3]
	"Biligiriranga Hills"	Khan 2002[3]
	"Mysore"	Khan 2002[3]
	Agumbe, Shimoga district	Ganesh & Mouli 2006[3]
	Kadatoka village, Uttara Kannada district	Hegde 2012[3]
	Bannerghatta, Bangalore Urban district	Present Study[1]
Maharashra	University Campus, Aurangabad, Aurangabad district	Jamdar *et al.* 2010[3]
	Navegaon National Park, Gondia district	Bhandarkar *et al.* 2012[3]
	Solapur district	Padhye & Ghate 2012[3]
	"Krishna & Koyna Rivers" in Satara district	Sathe & Patil 2016[3]
Andhra Pradesh	Chinnarutla, Nallamalai Hills	Rao *et al.* 2005[3]
	Mannanur, Nallamalai Hills	Rao *et al.* 2005[3]

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TABLE S1. (Continued)

State / Province	Locality	Reference
	Sundipenta/Sikharam, Nallamalai Hills	Rao *et al.* 2005[3]
	Perumukkal, Kaliveli watershed region	Ramanujan & Anbarasan 2007[3]
	Pitchandikulam, Kaliveli watershed region	Ramanujan & Anbarasan 2007[3]
	Success canyon, Kaliveli watershed region	Ramanujan & Anbarasan 2007[3]
	Mannanur – Farahabad, Mahboobnagar district	Srinivasulu *et al.* 2007[3]
	Mukhadwaram – Srisailam, Kurnool district	Srinivasulu *et al*. 2007[3]
	Shikaram, Kurnool district	Srinivasulu *et al.* 2007[3]
	Sunnipenta, Kurnool district	Srinivasulu *et al.* 2007[3]
	"Nallamala hills"	Srinivasulu & Das 2008[3]
	Seshachalam Biosphere Reserve	Guptha *et al.* 2012[3]
	Srikakulam district	Sebastian *et al.* 2012[3]
	Thummalapalle uranium mining area, Thummalapalle, YSR Kadapa district	Reddy *et al.* 2013[3]
Telangana	Ameenpur Lake, Medak district	Sailu *et al.* 2017[3]
Gujarat	Polo Forest Vanaj, Sabarkantha district	Sharma 2005[3]; Jangid *et al.* 2017[3]
	Mahi River, Kotna (Vadodara) – Amrol (Anand)	Vyas 2013[3]
	Mini Nadi, Sherkhi (Vadodara) – Angadh (Vadodara)	Vyas 2013[3]
	Vartak River, Pipariya+Koshiyal – Vasanha Buzarg (Both in Kheda)	Vyas 2013[3]
	Vishwamitri River, Khalipur (Vadodara) – Maretha/Maneja (Vadodara)	Vyas 2013[3]
	Ahwa, Dang district	Vyas & Parasharya 2016[3]
	Bagodara, Ahmedabad district	Vyas & Parasharya 2016[3]
	Bharuch City, Bharuch district	Vyas & Parasharya 2016[3]
	Chhatral, Gandhinagar district	Vyas & Parasharya 2016[3]
	Karamsad, Anand district	Vyas & Parasharya 2016[3]
	Rajkot City, Rajkot district	Vyas & Parasharya 2016[3]
	Shivran, Talala, Junagadh district	Vyas & Parasharya 2016[3]
	Vasna Village, Ahmedabad district	Vyas & Parasharya 2016[3]
	Waghai, Dang district	Vyas & Parasharya 2016[3]
Rajasthan	Phulwari Ki Nal Wildlife Sanctuary	Dutta 1997[3]
	Jhalan Hills, Jaipur	Sharma 1992[3]; Sharma *et al.* 2007[3]
	"Udaipur"	Sharma *et al.* 2007[3]
	Merwara Hills, Aravalli range, Ajmer district	Sharma & Sharma 2009[3]
Odisha	"Bubaneswar", Khordha district	Mohanty-Hejmadi *et al.* 1979; Saidapur 2001[3]
	Sambalpur district	Dash & Mahanta 1993[3]
	Balighai, Konark-Balukhand WLS	Deuti & Raha 2010[3]
	Bedkot, Karlapat WLS	Deuti & Raha 2010[3]
	Chandraprabha, Konark-Balukhand WLS	Deuti & Raha 2010[3]
	"Mundguda" (= Mundraguda), Karlapat WLS	Deuti & Raha 2010[3]
	Ramchandi, Konark-Balukhand WLS	Deuti & Raha 2010[3]

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TABLE S1. (Continued)

State / Province	Locality	Reference
	"Mendiabiri", Karlapat WLS	Deuti & Raha 2010[3]; Deuti *et al.* 2014[3]
	"Sunabeda", Koraput district	Deuti *et al.* 2014[3]
	Gandhamardan Hills	Sahu *et al.* 2014[3]; Pradhan *et al.* 2015[3]
Madhya Pradesh	"Gwalior"	Saksena *et al.* 1988[3]; Sarkar & Ray 2000[3]; Chandra & Gajbe 2005[3]
	"Turiya, Seoni district & Pyorthadi"	Chandra & Ray 2007[3]
Chhattisgarh	"Bastar"	Dutta 2015[3]
Uttar Pradesh	Shiwalik Hills, near Badshahibag, Saharanpur district	Tilak & Husain 1976[3]
	Agra (St. John's College Staff Club grounds – Hariparbat Police Station; Nala Burhan Sayyad)	Mahendra 1939[3]; Dutta 1997[3]
	"Allahabad"	Dutta 1997[3]
	"Kanpur"	Dutta 1997[3]
	Dudhwa National Park, Kamrup district	Hegde 2013[3]
Uttarakhand	Rajaji National Park	Ray & Tilak 1994[3]
	Dehradun	Husain 2015[3]
Himachal Pradesh	Paonta Saheb, Sirmour district	Singh 1982[3]
	Simbalbara Wildlife Sanctuary	Mehta & Sharma 2009[3]
Mizoram	Ngenpui Wildlife Sanctuary	Pawar 1999[3]
Assam	Barak Valley	Dey 2001[3]
	SRI LANKA	
Central Province	Menikdena (Dambulla)	Somaweera *et al.* 2001[3]
	Dambulla, Matale district	Present Study[1]
Eastern Province	Panama, Ampara district	Somaweera *et al.* 2004[3]
Northern Province	Jaffna	Kirtisinghe 1957[3]
	Marichchukkaddi	Dutta & Manamendra-Arachchi 1996[3]
North Western Province	Nawadankulama	Dutta & Manamendra-Arachchi 1996[3]
	Anawilundawa Wetland Santuary	Rodrigo *et al.* 2008[3]
	Eluwankulama Aruwakkalu Forest	Kumarsinghe *et al.* 2013[3]
Sabaragamuwa Province	Aluthnuwara	Kirtisinghe 1957[3]; Dutta & Manamendra-Arachchi 1996[3]
Southern Province	Lunama-Kalametiya Wetland Sanctuary	Ekanayake *et al.* 2005[3]
Uva Province	Nilgala Forest Area	Sarathchandra *et al.* 2017[3]
	NEPAL	
	(n.a.)	Shrestha 2001[3]; Anders 2002[3]; Schleich *et al.* 2002[3]; Shah & Tiwari 2004[3]; Frost 2017

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TABLE S1. (Continued)

State / Province	Locality	Reference
	Ghodaghodi Lake	Bista *et al.* 2010[3]
	"15 kms east of Mahendranagar"	Frost 2017
	PAKISTAN	
–	Thal and Cholistan Desert	Khan 1999[3]; Khan 2004[3]
–	Margalla Hills, Islamabad	Masroor 2011[3]
	Uperodon taprobanicus	
	INDIA	
Colonial location	"Cauvery River, Madras"	Parker 1934[3]
Tamil Nadu	Mamallapuram (= Mahabalipuram), Kanchipuram district	Dutta 1997[3]; Present Study[1]
	Point Calimere, Nagapattinam district	Giri *et al*. 2001[3]
	Mannampandal, Nagapattinam district	Ganesh & Chandramouli 2007[3]
	Chennai snake park campus, Guindy, Chennai	Ganesh 2012[3]
	AVC College, Mannampandal, Nagapattinam district	Nath *et al.* 2012[3]
	Kanakaneri, Puducherry	Seshadri *et al.* 2012[3]
	Korkad aeri, Puducherry	Seshadri *et al.* 2012[3]
	Kalpakkam Nuclear Campus, Matale district	Ramesh *et al.* 2013[3]
Kerala	Wayanad	Abraham *et al.* 2001[3]
	Kuttanad, Pathanamthitta district	Andrews *et al.* 2005b[3]
	Madras	Ganesh & Asokan 2010[3]
	Kulathupuzha forest range	Jose *et al*. 2014[3]
	Shendurney Wildlife Sanctuary	Jose *et al*. 2014[3]
	Kalpetta, Wayanad district	Present Study[2]
	Mannuthy, Thrissur district	Present Study[2]
	Sulthanbathery, Wayanad district	Present Study[2]
Karnataka	Dandeli, Uttara Kannada district	Adbulali 1962[3]
	Dharwad, Dharwad district	Dutta 1997[3]; Pattar *et al.* 2010[3]
	"Mysore"	Dutta 1997[3]
	Lukunda, Kodagu district	Sengupta *et al.* 2009[3]
	Devarabetta, Hosur district	Chandramouli & Baskaran 2012[3]
	Devbagh, Karwar, Uttara Kannada district	Lewis *et al.* 2010[3]
	Uttara Kannada district	Ramachandra *et al*. 2012[3]
	Taralu, Bangalore Rural district	Alexander *et al.* 2014[3]
	Gulbarga University Campus, Gulbarga district	Jadesh *et al*. 2014[3]
	Tumakuru, Tumkur district	Kumar & Asiyanuzhat 2016[3]
	Kuvempu University Campus, Bhadra Wildife Sanctuary range, Shimoga district	Narayan *et al*. 2017[3]
	Bangalore, Bangalore Urban district	Present Study[1]
Maharashtra	Navegaon Bandh Wildife Sanctuary	Padhye *et al.* 2002[3]
	Arnala Beach, Virar, Mumbai	Nandvikar & Shaikh 2009[3]
	Navegaon National Park, Gondia district	Bhandarkar *et al.* 2012[3]

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TABLE S1. (Continued)

State / Province	Locality	Reference
	Daryapur taluka, Amravati district	Dhande & Khandare 2013[3]
	Paratwada city, Amravati district	Wagh *et al*. 2017[3]
Andhra Pradesh	Sriharikota Island	Sivakumar *et al.* 2003[3]
	Chinnarutla, Nallamalai Hills	Rao *et al.* 2005[3]
	Mallelatheertham, Nallamalai Hills	Rao *et al.* 2005[3]
	Mannanur, Nallamalai Hills	Rao *et al.* 2005[3]
	Pulicheruvu, Nallamalai Hills	Rao *et al.* 2005[3]
	Sundipenta/Sikharam, Nallamalai Hills	Rao *et al.* 2005[3]
	Pitchandikulam, Kaliveli watershed region	Ramanujan & Anbarasan 2007[3]
	Mukhadwaram, Sunnipenta	Srinivasulu *et al*. 2007[3]
	Seshachalam Biosphere Reserve	Guptha *et al.* 2012[3]
Telangana	Ameenpur Lake, Medak district	Sailu *et al.* 2017[3]
Gujarat	Mal-Samot, Shoolpaneswar Wildlife Sanctuary, Bharuch district	Naik *et al*. 1993[3]
	Ratanmahal Wildlife Sanctuary	Vyas & Patel 1994[3]; Singh *et al*. 2002[3]
	Agricultural Universty Campus, Anand, Anand district	Vyas & Parasharya 2004[3]
	Surat city, Surat district	Vyas & Parasharya 2004[3]
	Vartak River, Pipariya+Koshiyal – Vasanha Buzarg (Both in Kheda)	Vyas 2013[3]
	Ankleshwar Town, Bharuch district	Vyas & Parasharya 2016
Odisha	Konarak, Puri district	Dutta 1997[3]
	Bhitarkanika Sanctuary, Behrempur district	Sengupta *et al.* 2009[3]; Jena *et al*. 2013[3]
	Baleshwar, Konark-Balukhand WLS	Deuti & Raha 2010[3]
	Balighai, Konark-Balukhand WLS	Deuti & Raha 2010[3]
	Mendiabiri, Karlapat WLS	Deuti & Raha 2010[3]
	"Mundguda" (= Mundraguda), Karlapat WLS	Deuti & Raha 2010[3]
	Bolangir district	Mishra & Guru 2013[3]
	Gandhamardan Hills	Sahu *et al.* 2014[3]; Pradhan *et al.* 2015[3]
	North Orissa University Campus, Mayurbhanj district	Boruah *et al*. 2016[3]
Madhya Pradesh	"Jabalpur"	Chandra & Gajbe 2005[3]
	Pench Tiger Reserve	Chandra & Gajbe 2005[3]
	"Seoni"	Chandra & Gajbe 2005[3]
	Shahdol district	Gajbe 2003[3]; Chandra & Gajbe 2005[3]
	Pench and Satpura	Ramakrishna *et al*. 2006[3]
	Tropical Forest Research Institute (TFRI) campus, Jabalpur	Paunikar 2017[3]
Chhattisgarh	Jagdalpur, Bastar district	Daniel & Verma 1964[3]
	"Jabalpur" (= Probably Jagdalpur), Indravati Tiger Reserve	Sengupta *et al.* 2009[3]

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TABLE S1. (Continued)

State / Province	Locality	Reference
	"Bastar"	Dutta 2015[3]
Uttar Pradesh	Katerniaghat Wildlife Sanctuary, Bahraich district	Das *et al*. 2012[3]
	Dudhwa National Park, Kamrup district	Hegde 2013[3]
West Bengal	"Calcutta" (= Kolkata)	Parker 1934[3]
	Camp Kanchrapara (40 kms north of Kolkata)	Dutta 1997[3]
	"Howrah"	Sengupta *et al.* 2009[3]
	Midnapore district	Pratihar & Deuti 2011[3]
	Durgapur, Paschim Bardhaman district	Pal *et al.* 2012[3]
	Durgapur Government College campus, Paschim Bardhaman district	Dutta & Mukhopadhyay 2013[3]
	Kanthi, Purba Medinipur district	Hazra *et al*. 2014[3]
	University of Burdwan, Golapbag, Burdwan	Aditya & Hazra 2016[3]
Bihar	–	Dutta 1997[3]
Assam	North of Tinsukia	Dutta 1997[3]
	Santinagar, Kokrajhar town	Sengupta *et al.* 2009[3]
	SRI LANKA	
Colonial locations	"Ceylon" (= Sri Lanka)	Parker 1934[3]
	"Punduloya, Ceylon, 4,000 ft.", Sri Lanka*	Parker 1934[2]
	"Kurumgalla, Ceylon", Sri Lanka	Parker 1934[3]
Central Province	Menikdena (Dambulla)	Somaweera *et al.* 2001[3]
	Kalugala Proposed Forest Reserve, Kaluthara district	Botejue & Wattavidanage 2012[3]
	Knuckles Mountain Forest Range	Weerawardhena & Russell 2012[3]
	Dambulla, Matale district	Present Study[1]
Eastern Province	Panama, Ampara district	Somaweera *et al.* 2004[3]
North Western Province	Kurunegala	Kirtisinghe 1957[3]
	Chilaw	Dutta & Manamendra-Arachchi 1996[3]
	Anawilundawa Wetland Santuary	Rodrigo *et al.* 2008[3]
	Eluwankulama Aruwakkalu Forest	Kumarsinghe *et al.* 2013[3]
	Mihinthale Sanctuary	Sarathchandra *et al.* 2017[3]
	Karawaddana, Kurunegala district	Present Study[1]
Western Province	Colombo	Kirtisinghe 1957[3]
	Panadura	Kirtisinghe 1957[3]
	National Zoological Garden, Dehiwala	Karunarathna *et al.* 2008[3]
	Bellanwila - Attidiya Sanctuary (BAS)	Karunarathna *et al.* 2010[3]
Sabaragamuwa Province	Warakapola	Dutta & Manamendra-Arachchi 1996[3]
	Uda Mäliboda, Samanala Nature Reserve	Samarasinghe *et al.* 2012[3]

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TABLE S1. (Continued)

State / Province	Locality	Reference
Sabaragamuwa and Southern Provinces	Sinharaja World Heritage Site	Bambaradeniya *et al.* 2003[3]
Southern Province	Deniyaya, Sinharaja Forest Reserve	Dutta & Manamendra-Arachchi 1996[3]
	Lunama-Kalametiya Wetland Sanctuary	Ekanayake *et al.* 2005[3]
	Matara district	Wildlife Conservation Society Report 2009[3]
Uva Province	Nilgala Forest Area	Sarathchandra *et al.* 2017[3]
	BANGLADESH	
Dhaka	Madhupur National Park	Sengupta *et al.* 2009[3]; Reza & Perry 2015[3]
	NEPAL	
	(n.a.)	Dubois 1987 "1986"[3]; Anders 2002[3]; Shah & Tiwari 2004[3]; Frost 2017
Province No. 3	Chitwan National Park	Bhattarai *et al*. 2017[3]
	Uperodon triangularis	
	INDIA	
Colonial locations	"Malabar"*	Günther 1876 "1875"[2]; Parker 1934[3]
	"Nilgiri Hills" or "Nilgheries"	Parker 1934[3]
Tamil Nadu	"Pycara and Kotagiri", Nilgiris district	Thurston 1888[3]
	Srivilliputhur Reserve Forests	Malhotra & Davis 1991[3]
	Shevaroy hills	Dutta 1997[3]
	Udhagamandalam (Ooty), Nilgiris district	Kuramoto & Dubois 2009[3]; Present Study[1]
	Emerald Area, Avalanche Reserve Forest	Santhoshkumar *et al.* 2017[3]
Kerala	"Chimanji", Travancore	Ferguson 1904[3]
	Kallar, Ponmudi	Inger *et al.* 1984[3]
	Silent Valley, Palakkad district	Dutta 1997[3]; Andrews *et al.* 2005a[3]
	Wayanad	Abraham *et al.* 2001[3]
	Thiruvananthapuram district	Andrews *et al.* 2005b[3]
	Kulathupuzha forest range	Jose *et al*. 2014[3]
	Kalpetta, Wayanad district	Present Study[1]
	Mananthavady, Wayanad district	Present Study[1]
	Pozhuthana, Wayanad district	Present Study[1]
	Suganthagiri, Wayanad district	Present Study[1]
Karnataka	"Hassan"	Rao 1937[3]; Dutta 1997[3]
	"Kadur", Chikmagalur district	Rao 1937[3]
	"Malnad areas" (= Malenadu region)	Rao 1937[3]
	Mudigere, Chikkamagaluru district	Rao 1937[3]
	"Sakleshpur", Hassan district	Rao 1937[3]
	Lackunda Estate, Coorg	Hampson & Bennett 2002[3]

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TABLE S1. (Continued)

State / Province	Locality	Reference
	Gundya catchment	Gururaja *et al.* 2007[3]
	Gundia Basin, Mallahlli Waterfalls	Dudani *et al.* 2010[3]
	Brahmagiri Wildlife Sanctuary, Kodagu district	Lewis *et al.*2010[3]
	Kempholey, Hassan district	Gururaja 2012[3]
	Rajiv Gandhi National Park, Nagarhole	Krishna & Sreepada 2012[3]
	Kodagu district	Rathod & Rathod 2013[3]
	Madikeri, Kodagu district	Present Study[1]
	Mudigere, Chikmagalur district	Present Study[1]
	Wattakolli, Coorg, Kodagu district	Present Study[1]
	Uperodon variegatus	
	INDIA	
Colonial locations	"Carnatic"	Jerdon "1854" 1853[3]
	"Yellagherry Hills"	Günther 1876 "1875"[2]; Boulenger 1882[3]
	"Bangalore (Mysore), S. India"	Rao & Ramanna 1925[2]
	"Gadavery Valey" (= Godavari Valley) or "Gadavere, near Bhadrachalam"	Parker 1934[2]; Boulenger 1882[3]
	"Chanda"	Parker 1934[3]
	"S.E. of Bhadrachalam"	Parker 1934[3]
Tamil Nadu	Tambaram, Kanchipuram district	Chakko 1968[3]
	St. Thomas Mount, Madras	Murthy 1973[3]
	Mannampandal, Nagapattinam district	Ganesh & Chandramouli 2007[3]
	Chennai snake park campus, Guindy, Chennai	Ganesh 2012[3]
	AVC College, Mannampandal, Nagapattinam district	Nath *et al.* 2012[3]
	Korkad aeri, Puducherry	Seshadri *et al.* 2012[3]
	Velrampetai, Puducherry	Seshadri *et al.* 2012[3]
	Courtallam, Tirunelveli District	Vasanthi *et al.* 2014[3]
	Kudirapppu, Tirunelveli district	Vasanthi *et al.* 2014[3]
	Melagaram, Tirunelveli district	Vasanthi *et al.* 2014[3]
	Minnagar, Tirunelveli district	Vasanthi *et al.* 2014[3]
	Nannagaram, Tirunelveli district	Vasanthi *et al.* 2014[3]
	Chengalpattu, Kanchipuram district	Present Study[1]
Kerala	Thiruvananthapuram district	Andrews *et al.* 2005b[3]
	Karamama, Thiruvananthapuram district	Present Study[2]
	Meladoor, Thrissur district	Present Study[2]
	Palakkad, Palakkad district	Present Study[1]
Karnataka	Bangalore	Rao & Ramanna 1925[2]; Bai 1956[3]
	Dharwad, Dharwad district	Kanamadi *et al.* 1993[3]; Dutta 1997[3]; Pattar *et al.* 2010[3]
	Agumbe, Shimoga district	Ganesh *et al.* 2007[3]

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TABLE S1. (Continued)

State / Province	Locality	Reference
	Tirthahalli, Shimoga district	Ganesh *et al.* 2007[3]
	Devarabetta, Hosur district	Chandramouli & Baskaran 2012[3]
	Brahmagiri Wildlife Sanctuary, Kodagu district	Lewis *et al.* 2010[3]
	Taralu, Bangalore Rural district	Alexander *et al.* 2014[3]
Maharashtra	Navegaon Bandh Wildife Sanctuary	Padhye *et al.* 2002[3]
	Navegaon National Park, Gondia district	Bhandarkar *et al.* 2012[3]
Andhra Pradesh	Ellore (= Eluru), West Godavri district*	Stoliczka 1872[2]
	Potharajupenta–Naguluty, Nagarjunasagar-Srisailam Tiger Reserve	Srinivasulu *et al.* 2007[3]
	"Nallamala hills"	Srinivasulu & Das 2008[3]
	Koruturu, Srikakulam, West Godavri district	Present Study[1]
Telangana	Dongala Dharmaram, Medak district	Narayana *et al.* 2014[3]
	Ameenpur Lake, Medak district	Sailu *et al.* 2017[3]
Madhya Pradesh	"Chanda in Madhya Pradesh"	Daniel 1963b[3]
	–	Dutta 1992[3]; Chandra & Gajbe 2005[3]
Odisha	Bhubaneswar, Utkal University campus	Dutta *et al*. 1991[3]; Saidapur 2001[3]; Present Study[2]
	Sambalpur district	Dash & Mahanta 1993[3]
	Barapali, Bargarh district	Dutta 1997[3]
	Bedkot, Karlapat WLS	Deuti & Raha 2010[3]
	Jaccum, Karlapat WLS	Deuti & Raha 2010[3]
	Mendiabiri, Karlapat WLS	Deuti & Raha 2010[3]
	"Mundguda" (= Mundraguda), Karlapat WLS	Deuti & Raha 2010[3]
	Gandhamardan Hills	Sahu *et al.* 2014; Pradhan *et al.* 2015[3]
	Buguda forest, Ganjam district	Das *et al*. 2016b[3]
Jharkhand	Chakradharpur (Chota Nagpur), Singhbhum district	Rao 1918[3]; Sarkar 1991[3]
West Bengal	Banspahari, West Midnapur district	Deuti 1998[3]

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Supplementary File S1

Neotype description of *Ramanella minor* Rao, 1937 [= *Uperodon minor* (Rao, 1937)], ZSI/WGRC/V/A/957, an adult male, from Sakleshpur (12.8680°N 75.7029°E, 782 m asl), Hassan district, Karnataka state, India, collected by SD Biju and team on 29 September 2012.

Description of neotype (measurements in mm) (Figs. S1A–E). Small-sized, slender adult male (SVL 31.7; head small (HW 9.1, HL 7.1, IFE 4.2, IBE 7.4), more than four times (22.4%) smaller than the body length, wider than long (HW/HL ratio 1.3); snout truncate in dorsal and ventral view, vertical in lateral view, protruding, its length (SL 3.1) longer than the horizontal diameter of the eye (EL 2.1); loreal region acute with rounded canthus rostralis; interorbital space more than twice as wide (IUE 3.4) as the upper eyelid width (UEW 1.3); nostril closer to the tip of snout (NS 0.9) than the eye (EN 2.2); tympanum not visible externally; eye diameter (EL 2.1); vomerine odontophores present on the palate; presence of two indistinct neopalatinal ridges on posterior side of each choana, fused with the vomerine odontophores; tongue moderately large, emarginated. Forelimbs moderately long and thin; forearm (FAL 6.2) shorter than hand length (HAL 8.6); finger length formula I<II<IV<III; tips of all fingers with truncate discs, without grooves, moderately wide compared to finger width; subarticular tubercles prominent, oval, all present; two well-developed palmar tubercles, inner oval, outer bilobed. Hindlimbs relatively long and thin, thigh length (TL 13.8) longer than shank (SHL 11.8) and foot (FOL 13.3); foot webbing present, moderate: $I1^{+}$–2II1–2III1^{+}–$2^{1}/_{2}$IV$2^{1}/_{2}$–1V; well-developed dermal fringes present on all toes; subarticular tubercles prominent, oval, all present; two smooth metatarsal tubercles, oval, outer tubercle slightly larger than the inner.

Skin of snout, between eyes, and sides of head, shagreened to granular; anterior and posterior parts of the back, and upper and lower parts of flank, granular; dorsal surfaces of forelimb, thigh, tibia and tarsus, sparsely granular; throat granular, chest, abdomen, and ventral surfaces of limbs, shagreened.

Colouration. *In preservation*: Dorsum dark greyish-brown with a faint grey band; limbs lighter than dorsum; throat black, chest and belly, light brown with scattered light grey blotches.

Neotype description of *Ramanella triangularis rufeventris* Rao, 1937, ZSI/WGRC/V/A/959, an adult male, from Mudigere (13.1258°N 75.5979°E, 900 m asl), Chikkamagaluru district, Karnataka state, India, collected by SD Biju and team on 28 September 2012.

Description of neotype (measurements in mm) (Figs. S1F–J). Small-sized, slender adult male (SVL 29.7); head small (HW 9.4, HL 6.7, IFE 4.0, IBE 7.9), more than four times smaller (22.6%) than the body length, wider than long (HW/HL ratio 1.4); snout rounded to nearly truncate in dorsal and ventral view, nearly acute in lateral view, its length (SL 2.7) longer than the horizontal diameter of eye (EL 2.2); loreal region obtuse with rounded canthus rostralis; interorbital space wider (IUE 3.0) than upper eyelid width (UEW 1.9); nostril much closer to the tip of snout (NS 0.9) than the eye (EN 1.6); eye diameter (EL 2.2); vomerine odontophores present on the palate; presence of two weakly-developed neopalatinal ridges on posterior side of each choana, fused with the vomerine odontophores. Forelimb (FAL 6.0) shorter than hand length (HAL 8.8); finger length formula I<II<IV<III, tips of all fingers with truncate discs, discs moderately wide compared to finger width (FD_{I} 0.9, FW_{I} 0.7; FD_{II} 1.1, FW_{II} 0.8; FD_{III} 1.0, FW_{III} 0.7; FD_{IV} 1.0, FW_{IV} 0.6); subarticular tubercles prominent, oval, all present; two well-developed palmar tubercles (inner oval, 1.2 mm long; outer 1.4 mm long). Hindlimbs relatively long and thin, thigh length (TL 11.0) longer than shank (SHL 10.1), and shorter than foot (FOL 12.4); tips of all toes with small truncate to rounded discs, discs rather wide compared to toe width; webbing absent between toes; dermal fringes absent on all toes; subarticular tubercles prominent, oval; two metatarsal tubercles, oval, outer one longer (1.3 mm) than the inner (0.7 mm).

Skin of snout, between eyes, sides of head, and anterior parts of the dorsum, shagreened to sparsely granular; ventral surface uniformly shagreened.

Colouration. *In preservation*: Dorsum olive grey with a interrupted dark brown median band on the back starting just above the level of the shoulders and extending up to the vent; a brown stripe between the eyes; flanks and lateral sides of the head light brown; ventral surfaces (including limbs) coffee brown with scattered cream coloured spots.

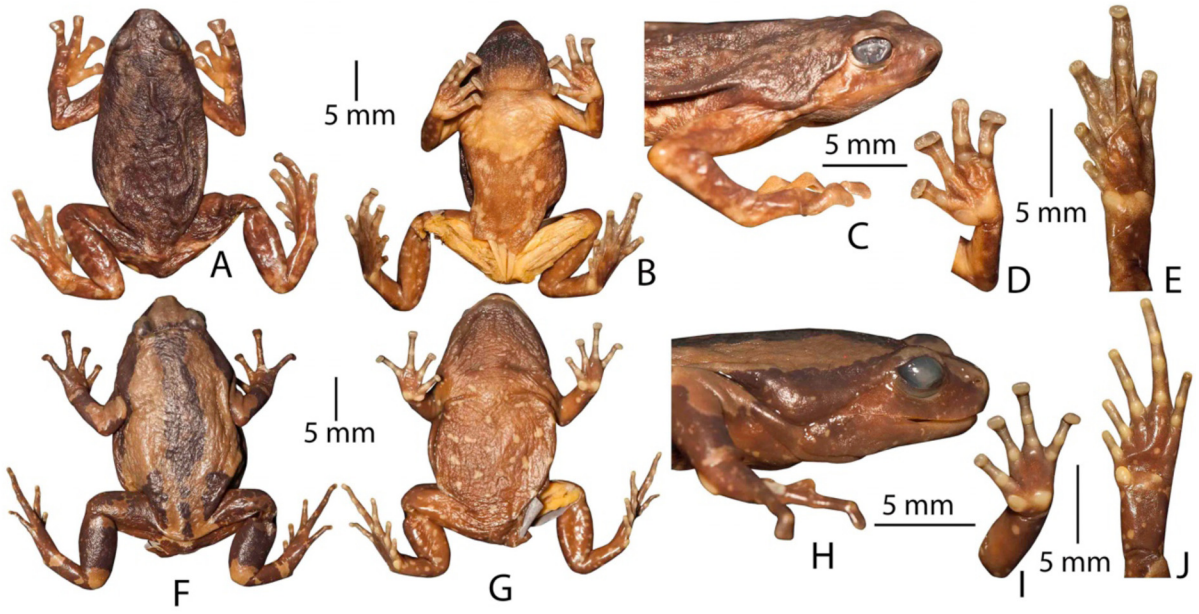

FIGURE S1. A–E. Neotype of *Ramanella minor* Rao, 1937 (ZSI/WGRC/V/A/957, male) in preservation: **A.** dorsal view; **B.** ventral view; **C.** lateral view of head; **D.** ventral view of hand; **E.** ventral view of foot; **F–J.** Neotype of *Ramanella triangularis rufeventris* Rao, 1937 (ZSI/WGRC/V/A/959, male) in preservation: **A.** dorsal view; **B.** ventral view; **C.** lateral view of head; **D.** ventral view of hand; **E.** ventral view of foot.

TABLE S2. Factor loadings and variance explained by Principal Components (PC) with eigenvalues of >1.0 based on Principal component analysis of 17 morphometric variables from adult male and female specimens of *Uperodon rohani* **sp. nov.** and *U. variegatus*. Values in bold indicate variables with the highest loadings. Abbreviations: Eigenvalue (Eig), Cumulative (Cum), Variance (Var)....

Variable	**Males**					**Females**		
	PC 1	PC 2	PC 3	PC 4	PC 5	PC 1	PC 2	PC 3
SVL	**-0.726174**	0.083894	-0.006431	0.269998	0.429796	**-0.740246**	0.547413	0.055544
HW	**-0.786735**	-0.285862	0.313254	0.290593	0.132505	**-0.961223**	0.096277	0.026117
HL	-0.450758	0.587954	0.337607	0.068704	0.360313	-0.330804	**0.753251**	0.068523
SL	-0.218642	**-0.843790**	0.044857	0.081008	-0.144538	**-0.826575**	-0.463668	-0.178072
EL	0.365862	0.042291	0.146692	**0.672302**	-0.490739	-0.345379	-0.223589	**0.704103**
IUE	**-0.724689**	-0.325178	-0.321521	-0.099136	0.100847	**-0.850903**	-0.159707	-0.162859
UEW	-0.348858	-0.317688	**-0.633666**	-0.232398	-0.140563	**-0.722297**	-0.263169	0.172053
IFE	**-0.644302**	-0.478635	0.068625	-0.265918	-0.279931	**-0.858687**	0.322445	0.214330
IBE	-0.573113	**-0.609823**	0.382376	0.067136	-0.008183	**-0.810170**	-0.498851	-0.120936
MN	**-0.782379**	0.082459	0.160830	-0.286269	-0.091218	**-0.839213**	0.173740	0.316211
EN	-0.369134	**0.698583**	-0.075633	-0.246473	-0.229042	**0.632036**	0.325283	**0.640278**
NS	-0.154895	0.029135	**-0.776577**	0.403826	0.053515	-0.555151	-0.425809	0.448797
FAL	-0.543871	0.376210	0.069565	-0.022183	-0.406813	-0.022655	**0.918307**	0.058434
HAL	**-0.732483**	0.220303	-0.230874	0.305230	-0.102551	-0.279739	**0.790193**	-0.314204
TL	**-0.755158**	-0.133946	0.153317	0.116153	-0.157851	**-0.912485**	0.163434	-0.059741
SHL	-0.177198	**0.856745**	0.166785	-0.005020	-0.205022	0.387974	**0.844937**	0.208278

...Continued on next page

TABLE S2. (Continued)

Variable	Males					Females		
	PC 1	PC 2	PC 3	PC 4	PC 5	PC 1	PC 2	PC 3
FOL	-0.597825	**0.601743**	-0.252702	0.020813	0.056578	-0.594520	0.672472	-0.243202
Eig	5.485337	3.755638	1.699489	1.173053	1.011991	7.850641	4.566733	1.572220
Cum Eig	5.48534	9.24097	10.94046	12.11352	13.12551	7.85064	12.41737	13.98959
%Total Var	32.26669	22.09199	9.99700	6.90031	5.95289	46.18024	26.86313	9.24835
% Cum Var	32.2667	54.3587	64.3557	71.2560	77.2089	46.1802	73.0434	82.2917