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The curious case of Charles Darwin's frog, *Rana charlesdarwini* Das, 1998: Phylogenetic position and generic placement, with taxonomic insights on other minervaryan frogs (Dicroglossidae: *Minervarya*) in the Andaman and Nicobar Archipelago

Sonali Garg[1], Sivaperuman Chandrakasan[2], G. Gokulakrishnan[2], C. Gopika[1], Indraneil Das[3], S. D. Biju[1]

1 *Systematics Lab, Department of Environmental Studies, University of Delhi, Delhi 110007, India*

2 *Andaman and Nicobar Regional Centre, Zoological Survey of India, Port Blair 744102, Andaman and Nicobar Islands, India*

3 *Institute of Biodiversity and Environmental Conservation, Universiti Malaysia Sarawak, 94300 Kota Samarahan, Malaysia*

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Corresponding author: Sonali Garg (sgarg.du@gmail.com)

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Abstract

Since the description of Charles Darwin's frog as *Rana charlesdarwini* in 1998, its generic placement has been a taxonomic enigma. Subsequent studies first transferred this species to the dicroglossid genus *Limnonectes*, and then considered it as a ceratobatrachid of the genus *Ingerana*, which has since been moved to the family Dicroglossidae. However, recent works have doubted this generic placement and also suggested the possibility of its sister relationship with the genus *Liurana*, within Ceratobatrachidae. Nonetheless, there have been no detailed investigations to ascertain the generic placement of this taxon by confirming its phylogenetic position or using integrative taxonomic approaches. Here, we provide the first molecular assessment of *Ingerana charlesdarwini* based on mitochondrial and nuclear DNA and reveal that it is nested in the dicroglossid genus *Minervarya*. A member of the *Minervarya andamanensis* species group, *Minervarya charlesdarwini* **comb. nov.** is sister taxon to *M. andamanensis* and shows relatively shallow genetic distances (2.8–3.6%) in the 16S gene. Both species are widely distributed, occur sympatrically, and exhibit high morphological variations, leading to long-standing confusions with other dicroglossid frogs reported from the region. Our combined morphological and molecular studies on dicroglossid frogs sampled across the known ranges of these species suggest that reports of *Limnonectes doriae* (Boulenger, 1887) and *L. hascheanus* (Stoliczka, 1870) from the Andamans are misidentifications of the former two, pointing to the absence of genus *Limnonectes* from the Andaman Islands. Our study also reveals the novel record of *Minervarya agricola* from the Andamans, a species that appears to have been confused with *Fejervarya limnocharis* and *Minervarya keralensis* in the literature and misidentified museum specimens, and is found to be widely distributed across these islands. We further find another congener from the Nicobar group of Islands, *M. nicobariensis*, to be closely related to *M. charlesdarwini*. Similar to the case of Andaman dicroglossids, our work emphasises on the need for further studies to ascertain the taxonomic identities and generic placement of *Minervarya* and *Limnonectes* species reported from the Nicobars.

Key words

Amphibia, *Ingerana*, integrative taxonomy, island biogeography, *Limnonectes*, sympatric species

Introduction

The Andaman and Nicobar Archipelago are home to about 21 species of amphibians, although knowledge on the fauna of these islands remains incomplete (Harikrishnan and Vasudevan 2018; Garg et al. 2022). In particular, the species-level delimitation and identities, or their higher-level taxonomic placements remain doubtful and often uninvestigated for several known taxa (e.g., Das 1998; Harikrishnan and Vasudevan 2018; Chandramouli et al. 2020a, 2020b; Chandramouli and Prasad 2020; Biju et al. 2020; Garg et al. 2022). Frogs of the family Dicroglossidae represent a large proportion of this region's known diversity, with nine species representing five genera, namely *Fejervarya*, *Hoplobatrachus*, *Ingerana*, *Limnonectes*, and *Minervarya* (Stoliczka 1870; Sclater 1892; Sarkar 1990; Pillai 1991; Das 1996, 1998, 1999; Dutta 1997; Harikrishnan and Vasudevan 2018; Rangasamy et al. 2018; Chandramouli et al. 2020b; Chandramouli and Prasad 2020). Dicroglossid members occur commonly and inhabit a wide range of habitats, from saline water bodies near the seashores to forested mountain tops up to the highest elevations of over 700 m asl within the archipelago. Yet, the taxonomy of several members of this group remains uncertain (Harikrishnan and Vasudevan 2018). Although dicroglossid frogs, in general, are considered taxonomically challenging for lack of sufficient morphological traits to distinguish closely related species and genera (Dubois et al. 2001; Kuramoto et al. 2008 "2007"; Kotaki et al. 2010; Howlader 2011; Dinesh et al. 2015; Garg and Biju 2017; Sanchez et al. 2018; Köhler et al. 2019), the absence of detailed taxonomic studies has additionally contributed towards the existing long-standing uncertainties on this group of frogs in the Andaman and Nicobar Archipelago.

A classic case is that of Charles Darwin's frog, originally described in the family Ranidae as *Rana charlesdarwini*. Ever since its description, this species has had an uncertain genus as well as family level placement (Das 1998; Dubois et al. 2005; Das and Dutta 2007; Chandramouli 2017). While describing this endemic species of the Andaman Islands, Das (1998) discussed the tentative nature of his generic assignment due to the confusing morphological affinities of the species and the lack of clear diagnoses or definitions for several of the potentially related South-east Asian ranid genera at the time. Nonetheless, this new species was suggested as being more closely allied to the subgenera *Ingerana* Dubois, 1987 or *Liurana* Dubois, 1987 (Das 1998). Dubois et al. (2005) removed this taxon from the subfamily "Raninae" due to the presence of a forked omosternum and regarded it as a member of "Limnonectini" without generic allocation. Das and Dutta (2007) later treated it as a member of the dicroglossid genus *Limnonectes* Fitzinger, 1843, based on the previous allocation of this taxon to Limnonectini. Subsequently, due to reclassification of *Rana* Linnaeus, 1758 sensu lato, Frost (2006) considered this species to be a member of the genus *Ingerana* (Frost 2021), which was at that time in family Ceratobatrachidae, on the basis of affinities discussed in the original description. Ever since, the taxon has been treated as *Ingerana charlesdarwini* in the literature and regional checklists (e.g., Dinesh 2009; Chandramouli 2017; Harikrishnan and Vasudevan 2018; Rangasamy et al. 2018). The genus *Ingerana* was also since then shown to be more closely related to dicroglossids than ceratobatrachids, leading to its transfer to the subfamily Occidozyginae within the family Dicroglossidae (Roelants et al. 2004; Bossuyt et al. 2006; Frost et al. 2006; Pyron and Wiens 2011; Brown et al. 2015). However, more recently, Yuan et al. (2016) speculated that *Ingerana charlesdarwini* might represent a distinct lineage in the family Ceratobatrachidae possibly having a sister-group relationship with members of the genus *Liurana*. Chandramouli (2017), meanwhile, reported high colour variations among individuals of this species. Even though the recent studies have remarked that the generic placement of *Ingerana charlesdarwini* should be considered provisional (Chandramouli 2017; Harikrishnan and Vasudevan 2018), any new supporting or conclusive evidence based on genetic data or detailed morphological studies remains unavailable. Hence, the current knowledge showcases the highly confusing taxonomy of *I. charlesdarwini* and its unresolved systematic relationships with other related taxa. Taking into account the long-standing confusions, intertwined taxonomic histories, and complex genus-level definitions, a resolution to the puzzling case of *I. charlesdarwini* appears to have been long deterred in anticipation of a need to study multiple dicroglossid taxa from the Andaman Islands, as well as other biogeographically allied South and South-east Asian regions.

The genus *Ingerana*, with currently four recognised species, is reported primarily from mainland regions of South and South-east Asia spanning across north-east India, southern China, Bhutan, Bangladesh, Myanmar, Thailand and the adjoining Peninsular Malaysia (Frost 2021), except for *I. charlesdarwini* that is the only known insular member. However, the presence of genus *Ingerana* in the Andamans cannot be easily ruled out. The trouble being the intriguing geographical position of the Andaman and Nicobar Islands, which are located near the contact zone of two biogeographically distinct regions in the Bay of Bengal. The Andamanese biota is known to have closer affinities with the Indo-Burmese components, whereas the Nicobarese biota is related to those of Sundaland (Mani 1974; Das 1999). Another two poorly known dicroglossid genera reported from the Andaman and Nicobar, *Limnonectes* and *Minervarya*, have confounding morphological and biogeographical affinities. Within the Andamans, *Ingerana charlesdarwini* shares diagnostic characters with three species—*Limnonectes doriae*, *L. hascheanus*, and *Minervarya andamanensis*. These four species can be confused due to their overlapping size range, comparable body plan, and highly variable dorsal skin texture and colouration. At the same time, however, the absence of prominent chevron mark and longitudinal skin folds (commonly shagreened to sparsely granular) on the dorsum, and stout appearance makes the systematic position of *Ingerana charlesdarwini* enigmatic. It is noteworthy that the identities of these closely related species have also been questioned in the past (Inger and Stuart 2010; Harikrishnan and Vasudevan 2018). The reports of *Limnonectes doriae* and *L. hascheanus* are solely based on a few specimens originally contained in the type series of *Minervarya andamanensis* (Stoliczka 1870) that were identified as belonging to the two *Limnonectes* species (Sclater 1892; Annandale 1917; Dutta 1997). Despite subsequently being included in the regional fauna for over two decades (Das 1999; Harikrishnan et al. 2010, 2012; Chandramouli et al. 2015; Rangasamy et al. 2018), these species have surprisingly not been sampled from the Andamans ever since. On the other hand, the identity of another widely reported species, *Minervarya andamanensis*, also remains confusing, after seemingly being restricted to a sub-adult lectotype specimen (Annandale 1917). This apart, even though widely reported, *M. andamanensis* is largely known from confusing literature records and museum specimens (Harikrishnan and Vasudevan 2018) and apparently unconfirmed DNA sequences based on which its systematic relationships have been discussed (Kotaki et al. 2010; Sanchez et al. 2018; Garg and Biju 2021). Recently, Chandramouli (2017) identified some museum specimens, likely referred to either *Limnonectes doriae* or *Minervarya andamanensis*, as belonging to *Ingerana charlesdarwini*, further suggesting that these species have long been confused and misidentified, both historically and contemporarily.

The genus *Minervarya* is recognised as a predominantly South Asian radiation, whereas *Limnonectes* members are largely restricted to South-east and East Asia (Sanchez et al. 2018). The taxonomy of both these genera has undergone considerable changes in the recent years with active research and growing evidence on systematic relationships using integrative approaches. This has led to taxonomic stability of several species that had variously been placed in dicroglossid genera such as *Rana*, *Fejervarya*, *Limnonectes*, *Minervarya*, and *Sphaerotheca* due to lack of sufficient morphological traits to distinguish closely related taxa (Dubois 1987; Iskandar 1998; Inger and Stuart 2010; Howlader 2011; Dinesh et al. 2015; Sanchez et al. 2018; Köhler et al. 2019; Garg and Biju 2021; Khatiwada et al. 2021). However, members of these genera from the Andaman and Nicobar Islands have rarely been subjected to detailed taxonomic studies or included in comprehensive works due to the absence of data from this region. This has propagated uncertainties concerning not just the diagnoses and systematic relationships at various taxonomic levels, but also the diversity and distribution patterns of related dicroglossid genera.

Hence, in an attempt to resolve the curious case of *Ingerana charlesdarwini*, we studied multiple closely related and possibly confused Andaman species (*Ingerana charlesdarwini*, *Limnonectes doriae*, *L. hascheanus*, and *Minervarya andamanensis*) to address some persisting questions due to their complex taxonomic identities and unresolved systematic relationships. We extensively sampled these taxa, based on their apparent identities as understood in the literature, and provide the first integrative molecular and morphological assessment for these species from the Andaman Islands. Our study further investigates the identity of *Fejervarya* '*limnocharis*' reported from Andamans and also looks into the systematic relationships of another closely related minervaryan frog, *Minervarya nicobariensis*, from the Nicobar group of islands.

Materials and Methods

Field sampling

Sampling of various species of dicroglossid frogs was carried out across the Andaman and Nicobar Archipelago (Tables 1 and 2). Opportunistic searches were carried out in a wide range of habitats such as primary and secondary forests, agricultural fields, parks, beaches and wayside areas with permanent or temporary water bodies, from sea level up to elevations of nearly 700 m asl. During the breeding season, individuals were often located by calls. Live specimens were photographed in the wild or captive conditions and euthanised in Tricaine methanesulfonate (MS-222) solution. Tissue samples were obtained from thigh (adult) or tail muscle (tadpoles) and preserved in absolute ethanol. Specimens were fixed in 4% formalin and rinsed in water before preservation in 70% ethanol. The sampled specimens are available in the amphibian collection of Zoological Survey of India, Andaman and Nicobar Regional Centre, Port Blair (ZSI/ANRC) or the Systematics Lab at University of Delhi (SDBDU). Geographical coordinates and elevation at the sampling localities were recorded using the WGS84 datum system. Maps were prepared using QGIS (http://www.qgis.org).

Molecular study

Genomic DNA was extracted from 15 samples using the Qiagen DNeasy blood and tissue kit (Qiagen, Valencia, CA, USA). From all the extracted samples, a ~540 bp fragment of the mitochondrial 16S rRNA gene was PCR-amplified using primers from Simon et al. (1994). Three additional gene fragments were sequenced for selected samples, using previously published primers: 385 bp of the mitochondrial 12S rRNA (Richards and Moore 1996), 564 bp of the nuclear recombination activating gene 1 (Biju and Bossuyt 2003), and 603 bp of the nuclear tyrosinase (Bossuyt and Milinkovitch 2000). Sequencing was performed on both strands using a BigDye Terminator v3.1 Cycle Sequencing kit on an ABI 3730 automated DNA sequencer (Applied Biosystems). Raw sequences were assembled and checked in ChromasPro v1.4 (Technelysium Pty Ltd.). Sequences from this study are deposited in the National Center for Biotechnology Information (NCBI) GenBank under accession numbers ON009953–ON009969 and ON010541-ON010544. Additional homologous sequences were retrieved from the GenBank for all known members of the *Minervarya an-*

damanensis species group and representatives of other *Minervarya* species. Ten species from other closely related dicroglossid genera were used as the outgroup taxa for phylogenetic analyses. Datasets for each gene were assembled and aligned using MUSCLE (Edgar 2004) in MEGA 7.0 (Kumar et al. 2016). The alignments for coding DNA were checked by comparison with amino acid sequences, whereas those for the non-coding fragments were manually optimised.

Bayesian inference (BI) and Maximum Likelihood (ML) analyses were performed with a concatenated character matrix of 2,101 nucleotides for 69 taxa (Table 1). The data was partitioned by genes for 16S and 12S, and by codons for Rag1 and Tyr, with a total of eight partitions. The following best-fitting models of sequence evolution for each partition were selected through a greedy search in PartitionFinder 2 (Lanfear et al. 2017) using the corrected Akaike information criterion (AICc): GTR+I+G for 16S and 12S, TVM+I+G for the first codon positions of Rag1 and Tyr, K81UF+I for the second codon positions of Rag1 and Tyr, TRN+G for Rag1 third codon position, and TVM+G for Tyr third codon position. Using this partitioning scheme, the Bayesian phylogenetic inference was performed in MrBayes (Ronquist and Huelsenbeck 2003) with four independent Bayesian runs, each running with four Metropolis-Coupled Markov chain Monte Carlo (MCMCMC) chains for 20,000,000 generations using default priors, chain temperature of 0.1, and tree sampling at every 4,000 generations. The convergence of the runs was determined by the nearing of standard deviation of split frequencies < 0.01 and potential scale reduction factors ~1.0. Stationarity of the likelihood scores and effective sample sizes (ESS) for all parameters were viewed in Tracer v. 1.7 (Rambaut et al. 2018). The Bayesian posterior probabilities (BPP) were summarised after discarding the first 25% trees as burn-in (Huelsenbeck et al. 2001). A partitioned maximum likelihood analysis was also performed for 10,000 ultrafast bootstrap (UBS) replicates, executed with the 'auto' model selection option, using IQ-TREE (Minh et al. 2013) on the IQ-TREE webserver (Trifinopoulos et al. 2016). Nodes with BPP≥95% and UBS≥90% were considered well supported.

A species delimitation analysis was performed using the multi-gene ML phylogram as input by Bayesian implementation of the Poisson Tree Processor (PTP) method (Zhang et al. 2013) on the bPTP webserver (https://species.h-its.org). To further assess the population structure in the *Minervarya andamanensis* species group, a haplotype network was constructed using the available 16S rRNA sequences. A dataset of 32 sequences comprising 513 characters, excluding sites with missing data but including the alignment gaps, was used to reconstruct haplotypes using the PHASE algorithm (Stephens et al. 2001) in DnaSP version 5 (Librado and Rozas 2009). A median-joining network was then constructed with 64 recovered haplotype sequences using the software Network 4.6.1.0 (www.fluxus-engineering.com). Intra- and interspecific uncorrected pairwise genetic distances for 16S sequences of the *M. andamanensis* species group were computed in PAUP* 4.0b10 (Swofford 2002).

Table 1. List of DNA sequences included in the phylogenetic study.

S.N	Taxa	Collection Locality	Voucher No.	Accession Number				Reference
				16S	12S	TYR	RAG1	
	***Minervarya andamanensis* group**							
1	*M. andamanensis*	India: Andaman Island	n.a.	AB488899	AB488876	AB489015	AB488951	Kotaki et al. 2010
2	*M. andamanensis*	India: South Andaman: Mt. Harriet National Park	SDBDU 2019.3951	ON009955	n.a.	n.a.	n.a.	Present study
3	*M. andamanensis*	India: South Andaman: Mt. Harriet National Park	SDBDU 2019.3956	ON009956	n.a.	n.a.	n.a.	Present study
4	*M. andamanensis*	India: South Andaman: Chidiya Taapu	SDBDU 2019.3964	ON009957	n.a.	n.a.	n.a.	Present study
5	*M. andamanensis*	India: South Andaman: Chidiya Taapu	SDBDU 2019.3978	ON009958	n.a.	n.a.	n.a.	Present study
6	*M. andamanensis*	India: South Andaman: Munda Pahad	SDBDU 2019.3992	ON009959	n.a.	n.a.	n.a.	Present study
7	*M. andamanensis*	India: South Andaman: Chidiya Taapu	SDBDU 2019.3996	ON009960	n.a.	n.a.	n.a.	Present study
8	*M. andamanensis*	India: Little Andaman	SDBDU 2019.4011	ON009961	n.a.	n.a.	n.a.	Present study
9	*M. andamanensis*	India: South Andaman: Sippi Ghat	SDBDU 2019.4028	ON009962	n.a.	n.a.	n.a.	Present study
10	*M. charlesdarwini*	India: South Andaman: Mt. Harriet National Park	SDBDU 2019.3945	ON009963	ON009953	ON010541	ON010543	Present study
11	*M. charlesdarwini*	India: South Andaman: Mt. Harriet National Park	SDBDU 2019.3947	ON009964	ON009954	ON010542	ON010544	Present study
12	*M. charlesdarwini*	India: South Andaman: Mt. Harriet National Park	SDBDU 2019.3952	ON009965	n.a.	n.a.	n.a.	Present study
13	*M. charlesdarwini*	India: South Andaman: Mt. Harriet National Park	SDBDU 2019.3954	ON009966	n.a.	n.a.	n.a.	Present study
14	*M. muangkanensis*	Thailand: Pilok	IABHU 18145/18156/18157	AB277300	n.a.	AB277352	AB488956	Kotaki et al. 2008, 2010
15	*M. muangkanensis*	Thailand: Kanchanaburi, Thong Pha Phum	KIZ 024627	MF166918	n.a.	n.a.	n.a.	Suwannapoom et al. 2017
16	*M. muangkanensis*	Myanmar: Bago, Dawei	USNM:Herp:587076	MG935778	n.a.	n.a.	n.a.	Mulcahy et al. 2018

S.N	Taxa	Collection Locality	Voucher No.	Accession Number				Reference
17	*M. muangkanensis*	Myanmar: Bago, Dawei	USNM:Herp:587073	MG935779	n.a.	n.a.	n.a.	Mulcahy et al. 2018
18	*M. muangkanensis*	Myanmar: Tanintharyi, Yeybu village	USNM:Herp:586873	MG935780	n.a.	n.a.	n.a.	Mulcahy et al. 2018
19	*M. muangkanensis*	Myanmar: Tanintharyi, Yeybu village	USNM:Herp:586874	MG935781	n.a.	n.a.	n.a.	Mulcahy et al. 2018
20	*M. muangkanensis*	Myanmar: Tanintharyi, Yeybu village	USNM:Herp:586875	MG935782	n.a.	n.a.	n.a.	Mulcahy et al. 2018
21	*M. muangkanensis*	Myanmar: Tanintharyi, Yeybu village	USNM:Herp:586876	MG935783	n.a.	n.a.	n.a.	Mulcahy et al. 2018
22	*M. muangkanensis*	Myanmar: Tanintharyi, Yeybu village	USNM:Herp:586878	MG935784	n.a.	n.a.	n.a.	Mulcahy et al. 2018
23	*M. muangkanensis*	Myanmar: Tanintharyi, Yeybu village	USNM:Herp:586879	MG935785	n.a.	n.a.	n.a.	Mulcahy et al. 2018
24	*M. muangkanensis*	Myanmar: Ayeyarwady, near Mwe Hauk village	CAS 208016	MK621439	n.a.	n.a.	n.a.	Köhler et al. 2019
25	*M. muangkanensis*	Myanmar: Ayeyarwady, near Mwe Hauk village	CAS 208033	MK621440	n.a.	n.a.	n.a.	Köhler et al. 2019
26	*M. muangkanensis*	Myanmar: Ayeyarwady, near Kyanigan	SMF 103782	MK621441	n.a.	n.a.	n.a.	Köhler et al. 2019
27	*M. muangkanensis*	Myanmar: Ayeyarwady, Kan Ywa to Negwesaung	SMF 103787	MK621442	n.a.	n.a.	n.a.	Köhler et al. 2019
28	*M. muangkanensis*	Myanmar: Ayeyarwady, Kan Ywa to Negwesaung	SMF 103788	MK621443	n.a.	n.a.	n.a.	Köhler et al. 2019
29	*M. muangkanensis*	Myanmar: Ayeyarwady, Kan Ywa to Negwesaung	SMF 103790	MK621444	n.a.	n.a.	n.a.	Köhler et al. 2019
30	*M. muangkanensis*	Myanmar: Rakhaing, Ngapali, Dam Lake	SMF 104873	MK621445	n.a.	n.a.	n.a.	Köhler et al. 2019
31	*M. muangkanensis*	Myanmar: Ayeyarwady, Kan Ywa to Negwesaung	SMF 105012	MK621446	n.a.	n.a.	n.a.	Köhler et al. 2019
32	*M. muangkanensis*	Myanmar: Ayeyarwady, Kan Ywa to Negwesaung	SMF 105013	MK621447	n.a.	n.a.	n.a.	Köhler et al. 2019
	***Minervarya agricola* group**							
33	*M. agricola*	India: Karnataka: Mudigere	BNHS 4651	AB488895	AB488872	AB489011	AB488947	Kotaki et al. 2010
34	*M. agricola*	India: South Andaman: Chidiya Taapu	SDBDU 2019.3986	ON009967	n.a.	n.a.	n.a.	Present study
35	*M. agricola*	India: South Andaman: Sippi Ghat	SDBDU 2019.4027	ON009968	n.a.	n.a.	n.a.	Present study
36	*M. agricola*	India: Middle Andaman: Rangat	SDBDU 2019.4054	ON009969	n.a.	n.a.	n.a.	Present study
37	*M. asmati*	India: Assam	n.a.	AB488900	AB488877	AB489016	AB488952	Kotaki et al. 2010
38	*M. chiangmaiensis*	Thailand: Chiang Mai: Omkoi	KIZ024057	KX834135	n.a.	n.a.	n.a.	Suwannapoom et al. 2016
39	*M. teraiensis*	Nepal: Britamod: Jhapa	CDZMTU356	MT983106	n.a.	n.a.	n.a.	Khatiwada et al. 2021
	***Minervarya greenii* group**							
40	*M. greenii*	Sri Lanka: Hakgala	MNHN 2000.617	AB488891	AB488868	AB489008	AB488944	Kotaki et al. 2010
41	*M. kirtisinghei*	Sri Lanka: Hakgala	MNHN 2000.620	AB488890	AB488867	AB489007	AB488943	Kotaki et al. 2010
	***Minervarya mysorensis* group**							
42	*M. brevipalmata*	India: Kerala: Kadalar	SDBDU 2011.1048	MZ156230	n.a.	n.a.	n.a.	Garg and Biju 2021
43	*M. goemchi*	India: Goa: Surla	ZSI/WRC/A/2017	MG800343	n.a.	n.a.	n.a.	Dinesh et al. 2018
44	*M. mysorensis*	India: Karnataka: Kudremukh	BNHS 4653 / 4654	AB488898	AB488875	AB489014	AB488950	Kotaki et al. 2010
	***Minervarya nilagirica* group**							
45	*M. keralensis*	India	WII: 3263	JX573181	JX573190	n.a.	n.a.	Raj et al. 2018
46	*M. nilagirica*	India: Madikeri	BNHS 4646	AB488896	AB488873	AB489012	AB488948	Kotaki et al. 2010
47	*M. kalinga*	India: Odisha: Barbara Reserve Forest	SDBDU 2015.3108	MZ156316	n.a.	n.a.	n.a.	Garg and Biju 2021
	***Minervarya rufescens* group**							
48	*M. cepfi*	India: Maharashtra: Amboli	ZSI/WGRC/V/A/938	KY447308	n.a.	n.a.	KY820753	Garg and Biju 2017
49	*M. kadar*	India: Kerala: Thavalakuzhipara	ZSI/WGRC/V/A/940	KY447312	n.a.	n.a.	KY820754	Garg and Biju 2017
50	*M. manoharani*	India: Kerala: Chathankod-Bonnacad	ZSI/WGRC/V/A/945	KY447313	n.a.	n.a.	KY820757	Garg and Biju 2017
51	*M. neilcoxi*	India: Kerala: Parambikulam	ZSI/WGRC/V/A/951	KY447318	n.a.	n.a.	KY820759	Garg and Biju 2017

S.N	Taxa	Collection Locality	Voucher No.	Accession Number				Reference
52	*M. rufescens*	India: Padil: Mangalore	RBRL 040716-1 or 39-16-Jul-2004	AB530602	AB488874	AB489013	AB488949	Hasan et al. 2014; Kotaki et al. 2010
53	*M. marathi*	India: Maharashtra: Pune, Bhamburde	n.a.	MH370483	n.a.	MH370484	n.a.	Phuge et al. 2019
	***Minervarya sahyadris* group**							
54	*M. sahyadris*	India: Karnataka: Mangalore	SDBDU 2015.3046	MZ156082	n.a.	n.a.	n.a.	Garg and Biju 2021
55	*M. gomantaki*	India: Codal village	ZSI/WGRC/V/A/867	KR781085	n.a.	KT004440	n.a.	Dinesh et al. 2015
56	*M. krishnan*	India: Karnataka: Jog Falls	SDBDU 2003.40156	MZ156093	n.a.	n.a.	n.a.	Garg and Biju 2021
	***Minervarya syhadrensis* group**							
57	*M. pentali*	India: Kerala: Nedumbaserry	BNHS 6116	MZ156229	n.a.	n.a.	n.a.	Garg and Biju 2021
58	*M. nepalensis*	Nepal: Chitwan	n.a.	AB488889	AB488866	AB500268	AB500225	Kotaki et al. 2010
59	*M. syhadrensis*	India: Karnataka: Mudigere	BNHS 5060	AB488894	AB488871	AB489010	AB488946	Kotaki et al. 2010
	Outgroups							
60	*F. limnocharis*	Indonesia: Bogor	IABHU 18002	AB277302	AB277286	AB277354	AB488953	Kotaki et al. 2008, 2010
61	*F. orissaensis*	India: Odisha	KU 197186	AB277304	AB277288	AB277356	AB500222	Kotaki et al. 2008, 2010
62	*S. dobsonii*	India: Bajipe	n.a.	AB277305	AB277290	AB277357	AB488959	Kotaki et al. 2008, 2010
63	*S. pluvialis*	Sri Lanka	VUB0182	AF249042	AF249014	AF249173	DQ347214	Bossuyt and Milinkovitch 2000
64	*E. cyanophlyctis*	India	VUB0039	AF249053	AF249015	AF249174	DQ347205	Bossuyt and Milinkovitch 2000
65	*E. hexadactylus*	India: Mudigere	n.a.	AB272608	AB273176	n.a.	n.a.	Alam et al. 2008
66	*H. crassus*	Sri Lanka	VUB0107	AF249044	AF249013	AF249172	DQ347211	Bossuyt and Milinkovitch 2000
67	*H. tigerinus*	India: Mangalore	n.a.	AB488902	n.a.	AB277358	AB488958	Kotaki et al. 2008, 2010
68	*N. ceylonensis*	Sri Lanka	VUB0172	AF249047	AF249016	AF249175	AY948917	Bossuyt and Milinkovitch 2000
69	*L. laticeps*	Malaysia: Kuala Lumpur	n.a.	AB277306	n.a.	AB277359	AB488960	Kotaki et al. 2008, 2010

Morphological study

We morphologically examined our new collections and compared them with the available type specimens, original descriptions, other topotypic specimens or general collections of all the dicroglossid frogs known to occur in the Andaman and Nicobar Archipelago. Sex and maturity were determined by the presence of secondary sexual characters (such as nuptial pads and vocal sacs in males) or examination of gonads through a small lateral or ventral incision. Only adult (sexually mature) individuals were used for morphometric studies. The following measurements were taken to the nearest 0.1 mm using digital slide-calipers with the aid of a stereomicroscope, following measurements and associated terminologies of Garg and Biju (2017, 2021): snout-vent length (SVL), head width (HW, at the angle of the jaws), head length (HL, from rear of mandible to tip of snout), MN (distance from the rear of the mandible to the nostril), MFE (distance from the rear of the mandible to the anterior orbital border), MBE (distance from the rear of the mandible to the posterior orbital border), snout length (SL, from tip of snout to anterior orbital border), eye length (EL, horizontal distance between bony orbital borders), inter upper eyelid width (IUE, the shortest distance between the upper eyelids), maximum upper eyelid width (UEW), internarial distance (IN), internal front of the eyes (IFE, shortest distance between the anterior orbital borders), internal back of the eyes (IBE, shortest distance between the posterior orbital borders), NS (distance from the nostril to the tip of the snout), EN (distance from the front of the eye to the nostril), TYD (greatest tympanum diameter), TYE (distance from the tympanum to the back of the eye), forearm length (FAL, from flexed elbow to base of outer palmar tubercle), hand length (HAL, from base of outer palmar tubercle to tip of third finger), $FL_{I–IV}$ (finger length), thigh length (TL, from vent to knee), shank length (SHL, from knee to heel), foot length (FOL, from base of inner metatarsal tubercle to tip of fourth toe), total foot length (TFOL, from heel to tip of fourth toe), FD (maximum disc width of finger), width of finger (FW, measured at the base of the disc), TD (maximum disc width of toe), width of toe (TW, measured at the base of the disc). Digit number is represented by Roman numerals I–V in subscript. Measurements and photographs are mostly for the right side of the specimen, unless a character was damaged, in which case the left side was taken. All measurements provided in the taxonomy section are in millimetres. The body size categories discussed in the text for the purpose of convenience and morphological comparisons follow Garg and Biju (2021). The webbing formulae follow Savage and Heyer (1967), as modified by Myers and Duellman (1982). The amount of webbing relative to subarticular tubercles is described by numbering the tubercles 1–3, starting from the base of the digits.

Abbreviations. Museum acronyms and other frequently used abbreviations are as follows: ZSI (Zoological Survey of India); ZSIC (Zoological Survey of India, Kolkata); ZSI/ANRC (Zoological Survey of India, Andaman and Nicobar Regional Centre, Port Blair); ZSI/SRS (Zoological Survey of India, South Regional Station, Chennai); NHM (Natural History Museum, London), formerly BMNH (British Museum [Natural History], London); Systematics Lab, University of Delhi (SDBDU).

ZooBank registration. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the International Commission on Zoological Nomenclature (ICZN). The ZooBank LSID (Life Science Identifier) for this publication is urn:lsid:zoobank.org:pub:2780E8F9-1ABF-4708-898A-B14447591063. The LSID and associated information can be resolved through any standard web browser by appending the LSID to the prefix http://zoobank.org.

Results

Phylogenetic relationships and genetic structure

Our phylogenetic study found '*Ingerana*' *charlesdarwini* to be deeply nested within the genus *Minervarya* (Fig. 1), based on 16S rRNA sequences from four exemplars, as well as additional mitochondrial (12S rRNA) and nuclear markers (Rag1 and Tyr) from two selected samples. Both the BI and ML analyses of a concatenated dataset of 2,101 characters recovered the species as a distinct well-supported (BPP 100, UFB 99) lineage in the *M. andamanensis* species group (Garg and Biju 2021). It also formed a highly supported (BPP 100, UFB 98) sister-group relationship with *M. andamanensis*, showing relatively shallow divergence of 2.8–3.6% for the 16S rRNA sequences. In comparison, the two previously recognised members of the group, *M. andamanensis* and *M. muangkanensis*, showed a higher divergence of 3.8–4.6%. Further, '*Ingerana*' *charlesdarwini* was divergent from *M. muangkanensis* by 4.4–4.7% for the 16S locus. These interspecific divergences fall well within the range of genetic distances usually observed at the species-level in the genus *Minervarya* and closely related dicroglossid genera (e.g., Kotaki et al. 2010; Köhler et al. 2019; Garg and Biju 2021). Our results, thus, clearly indicate that '*Ingerana*' *charlesdarwini* is a member of the genus *Minervarya* and should therefore be treated as *Minervarya charlesdarwini* **comb. nov.** Within the *M. andamanensis* species group, both the insular Andaman species, *M. charlesdarwini* and *M. andamanensis*, are more closely related to each other than to *M. muangkanensis* of mainland Thailand and Myanmar region, which formed the basal lineage (Fig. 1).

Within the focal *Minervarya andamanensis* species group, the multi-loci species delimitation analysis recovered all the three recognised species as distinct (Fig. 1). At the same time, the mitochondrial 16S median-joining network did not find sharing of haplotypes among the three species. A total of 12 haplotypes were recovered with an overall haplotype diversity of 0.8834 within the species group. In line with the results obtained in the phylogenetic analyses, the mainland member of the group, *M. muangkanensis*, was the most distinct species showing separation from *M. andamanensis* by minimum 24 mutation steps and from *M. charlesdarwini* by 26 steps. Eight haplotypes were detected among individuals of *M. muangkanensis*. Although the populations from Thailand and Myanmar did not share any haplotypes, the absence of clear genetic structuring indicates ongoing gene flow and admixture between these geographically continuous regions. The populations of *M. andamanensis* from South Andamans and Little Andamans formed two distinct haplotype clusters without sharing of haplotypes, separated by minimum six mutation steps and considerable genetic differentiation (1.1–1.3%), suggestive of limited gene flow, longer geographical isolation, and hence a potential area of population differentiation between these islands. On the other hand, the two widely co-occurring sister species within the Andaman Islands that do not exhibit similar habitat associations—*M. charlesdarwini* (largely forest dwelling, phytotelm breeding, and possibly a habitat specialist) and *M. andamanensis* (occupies a broader range of habitats, breeds in open water bodies, and is possibly a habitat generalist)—formed clearly distinct clusters separated from each other by minimum 18 mutation steps, suggesting that sympatric speciation potentially occurred within this radiation (Fig. 1). These species appear to present an insightful case for future investigations on the patterns of gene flow, speciation and diversification processes, ecological niche segregation, and phylogeography within the islands of Andaman and Nicobar.

Taxonomy

Minervarya andamanensis species group

Members included. *Minervarya charlesdarwini*, *M. andamanensis*, *M. muangkanensis*, and *M. nicobariensis*.

Morphological definition. This group can be distinguished from other minervaryan groups by the following suite of characters (revised after Garg and Biju 2021): small to large-sized adults (male SVL 24–50 mm, female SVL 30–72 mm); elongate to robust body; dorsal skin shagreened to sparsely granular, or with prominent glandular warts; dorsum with or without weakly developed short discontinuous skin folds or chevron mark at the cen-

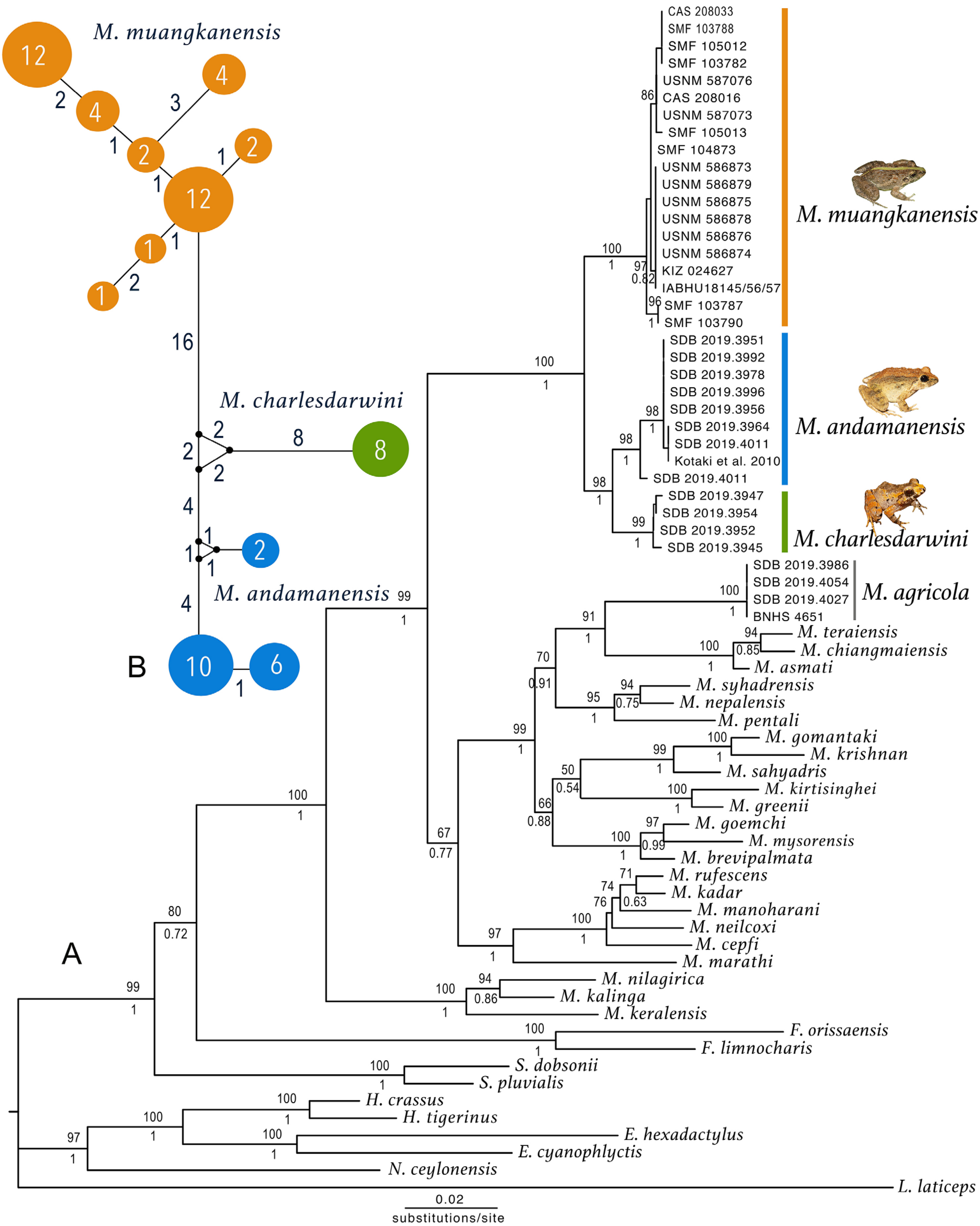

Figure 1. Phylogenetic position and genetic structure of species in the *Minervarya andamanensis* species group. **A.** Maximum likelihood phylogram based on a multi-gene dataset (2,101 bp of mitochondrial and nuclear DNA), depicting the phylogenetic position of *Minervarya charlesdarwini* **comb. nov.** in the genus *Minervarya* and relationships among three members of the *M. andamanensis* species group. Voucher numbers at terminal nodes are referenced in Table 1. Values above and below the branches represent Ultrafast Bootstrap Support (UFB, >50%) and Bayesian Posterior Probabilities (BPP, >0.50), respectively. Vertical bars indicate the recovery of three *M. andamanensis* group members as distinct species in multi-gene bPTP species delimitation analysis. **B.** Median-Joining network based on 513 bp of the mitochondrial 16S gene depicting the genetic structure among three species. Circle colours indicate different species; circle size is proportional to the frequency of haplotypes; black circles indicate median vectors; values on circles indicate frequency of haplotypes; values on connecting branches indicate number of mutation steps.

tre of dorsum; upper ⅔rd of tympanum and inner margin of tympanic fold dark brown; groin without prominent reticulations; thighs with or without reticulations; foot webbing moderate, below the third subarticular tubercle on either side of toe IV; long and cylindrical inner metatarsal tubercles.

Furthermore, *Minervarya charlesdarwini*, *M. andamanensis* and *M. nicobariensis* are placed in the genus due to the following suite of characters: omosternum unforked; vomerine ridge with weakly developed teeth; absence of lingual papilla; presence of fejervaryan lines; finger and toe tips rounded with slightly swollen discs, without circum-marginal grooves; and foot webbing not extending up to the toe tips.

Distribution. Andaman and Nicobar Archipelago of India (Fig. 2), Myanmar (Köhler et al. 2019), and Thailand (Suwannapoom et al. 2017).

Note. Garg and Biju (2021) provisionally placed *Minervarya marathi* in this group. Based on the results of our present study, *M. marathi* is phylogenetically more closely related to members of the *M. rufescens* group, rather than *M. andamanensis* group. Hence, we exclude *M. marathi* from the *M. andamanensis* group, and recommend further detailed studies to ascertain the systematic affinities of the taxon.

Minervarya charlesdarwini (Das, 1998) comb. nov.

Charles Darwin's minervaryan frog

Figs 1–4; Tables 1, 2

Note. Das (1998) described *Rana charlesdarwini* based on three adult and five larval specimens from Mount Harriet National Park in the South Andaman Island. Until recently, new vouchered reports of this species were lacking and the species was known only from its type series. Chandramouli (2017) reported rediscovery of this species along with a redescription based on new collections and some old museum specimens reidentified as *Ingerana charlesdarwini*, while also discussing morphological variations among the studied individuals. However, owing to the confounding taxonomic history and generic placement of this taxon (see Introduction), clarity on the systematics relationships of *Rana charlesdarwini* remained lacking. Our first ever molecular assessment of this taxon combined with morphological studies based on topotypic collections has confirmed its placement in the dicroglossid genus *Minervarya*. We further confirmed the prevalence of high morphological variation among individuals of this species, particularly with regard to dorsal colouration, markings, and body size (Figs 3, 4). However, due to the uncertainty of its systematic position, a morphological comparison with relevant taxa has been lacking. Below, we provide a revised morphological diagnosis for the species as well as comparisons with the closely related members of the *M. andamanensis* species group. We also elaborate on and provide detailed illustrations of the morphological variations observed in our study, considering that this species is likely to have been confused with other dicroglossids found in the regions for several years, before and after its formal description (see taxonomic remarks for *M. andamanensis*, *Limnonectes doriae* and *L. hascheanus*).

Morphological diagnosis. *Minervarya charlesdarwini* can be morphologically diagnosed by the following suite of characters: small to medium-sized adults (male SVL 24.8–30.1 mm, female SVL 30.8–36.6 mm); rather elongate body; dorsal skin shagreened to granular, or with prominently glandular warts; presence or absence of a weakly to well developed interrupted inverse V-shaped ridge (chevron mark) at the centre of dorsum; upper ⅔rd of tympanum and inner margin of tympanic fold dark brown; groin and thighs without prominent reticulations; finger and toe tips rounded with slightly swollen discs, without circum-marginal grooves; foot webbing relatively reduced, up to or just above the second subarticular tubercle but not beyond on either side of toe IV; elongate inner metatarsal tubercles; small and rounded outer metatarsal tubercle; presence of fejervaryan lines on abdomen; vomerine ridge with weakly developed teeth; absence of lingual papilla; omosternum unforked.

Redescription (all measurements in mm)**.** A small to medium-sized species (males: SVL 24.8–30.1, 26.6±1.8, *N*=6; females: SVL 30.8–36.6, 33.5±1.9, *N*=7), body rather elongate; head longer (males: HL 10.0–12.0, 10.6±0.7; females: HL 11.1–13.8, 12.7±1.0, *N*=7) than wide (males: HW 9.0–10.9, 9.6±0.7; females: HW 10.4–12.4, 11.6±0.7, *N*=7); snout rounded in dorsal and lateral view; snout length (males: SL 4.2–4.4, 4.3±0.1, *N*=6; females: SL 4.7–5.7, 5.2±0.4, *N*=7) longer than horizontal diameter of eye (males: EL 3.1–3.9, 3.4±0.3, *N*=6; females: EL 3.6–4.5, 4.0±0.3, *N*=7); loreal region obtuse; canthus rostralis rounded; interorbital space flat; tympanum diameter (males: TYD 1.9–2.3, 2.1± 0.2, *N*=6; females: TYD 2.1–2.8, 2.5±0.3, *N*=7) nearly ⅗th of the eye diameter (males: EL 3.1–3.9, 3.4±0.3, *N*=6; females: EL 3.6–4.5, 4.0±0.3, *N*=7); pineal ocellus present; supratympanic fold well developed, extends from posterior corner of the eye up to nearly the shoulder; vomerine ridge present, bearing small teeth; tongue moderately long, emarginated; 1–4 glands present at labial commissure (Figs 3, 4).

Forearm length (males: FAL 4.8–6.0, 5.3±0.5, *N*=6; females: FAL 6.0–6.9, 6.6±0.3, *N*=7) shorter than hand length (males: HAL 6.1–7.8, 6.7±0.6, *N*=6; females: HAL 7.4–8.7, 8.1±0.6, *N*=7); subarticular tubercles prominent, single, circular, all present; prepollex oval, prominent; two rounded palmar tubercles; supernumerary tubercles absent; relative length of fingers II < I=IV < III; tip of fingers rounded, not enlarged into discs. Hind limbs short in comparison to the body length with tibiotarsal articulation reaching up to the anterior end of eye when hind limb is stretched along the body; thigh (males: TL 13.1–15.4, 13.6±0.9, *N*=6; females: TL 16.2–17.0, 16.6±0.4, *N*=7)

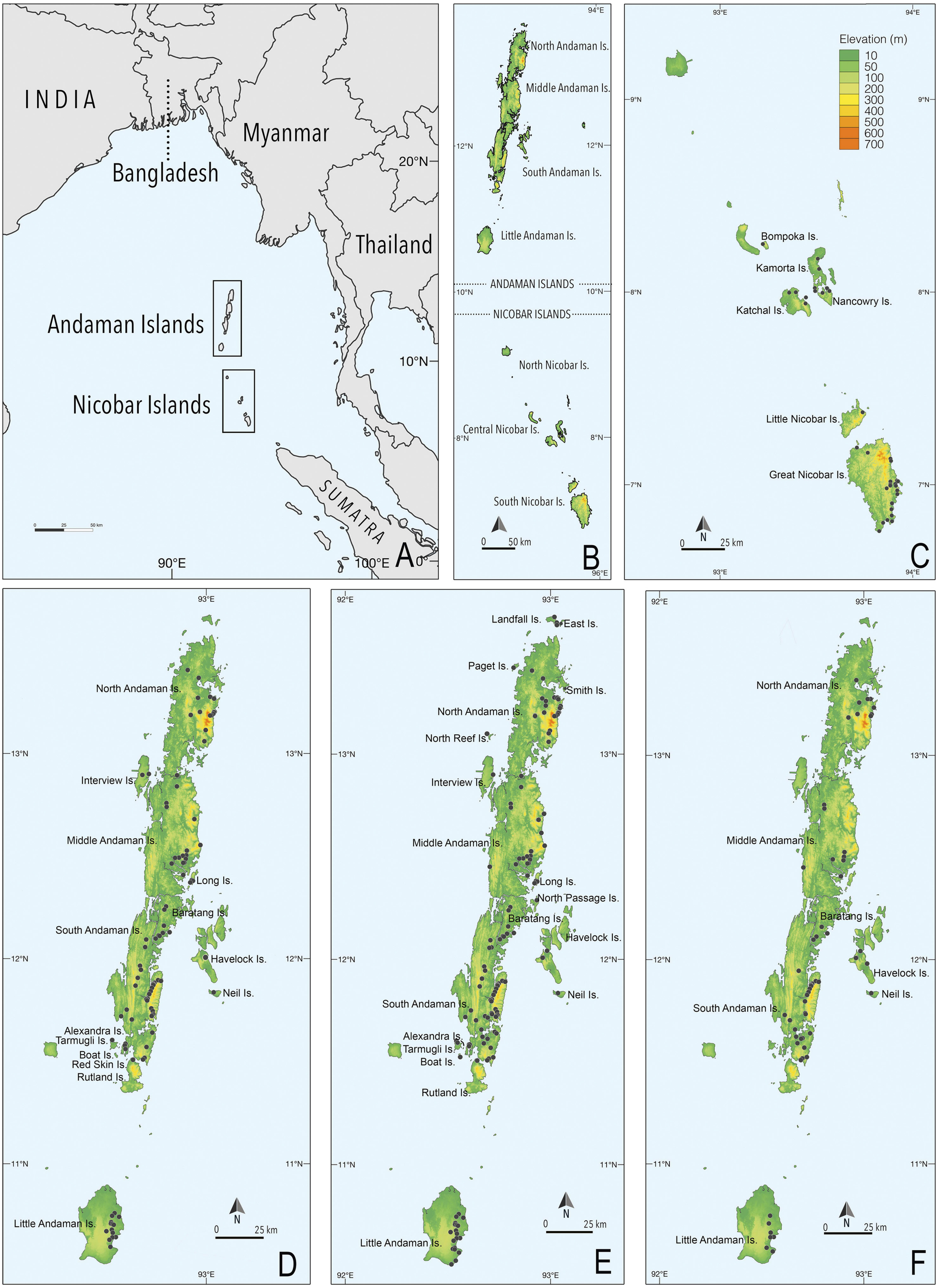

Figure 2. Distribution of *Minervarya* species in the Andaman and Nicobar Archipelago. **A** Location of the Archipelago in the Bay of Bengal. **B** Expanded view of the Andaman and Nicobar groups of islands. **C** *Minervarya nicobariensis* in the Nicobar Islands. **D** *Minervarya charlesdarwini* in the Andaman Islands. **E** *Minervarya andamanensis* in the Andaman Islands. **F** *Minervarya agricola* in the Andaman Islands.

Figure 3. Morphological variation in skin colouration and markings observed among individuals of *Minervarya charlesdarwini* in the Andaman Islands. **A–N** Dorsolateral views. **A** SDBDU 2021.4212 (♂). **B–C** SDBDU 2019.4059 (♀). **D** Not preserved. **E** SDBDU 2019.4006 (♂). **F** SDBDU 2019.3975 (♂). **G** SDBDU 2021.4212 (♂). **H** SDBDU 2019.4005 (♀). **I** SDBDU 2019.3968 (♀). **J** SDBDU 2019.4004 (♂). **K** SDBDU 2021.4213 (♀). **L** SDBDU 2020.4165 (♀). **M** SDBDU 2019.3946 (♀). **N** SDBDU 2021.4214 (♀). Photographs: S. D. Biju, G. Gokulakrishnan & Sonali Garg.

shorter than shank (males: SHL 14.1–15.8, 14.5±0.6, *N*=6; females: SHL 17.5–18.9, 18.0±0.7, *N*=7) and nearly equal to foot (males: FOL 12.8–15.3, 13.4±1.0, *N*=6; females: FOL 15.9–17.7, 16.8±0.7, *N*=7); total foot length (males: TFOL 19.1–22.7, 19.7±1.6, *N*=6; females: TFOL 23.0–26.1, 24.7±1.2, *N*=7); toe tips rounded, slightly swollen without discs, toes without dermal fringes, foot webbing moderate: I2$^-$–2II1½–3$^-$III2$^-$–3$^+$IV3$^-$–2$^-$V; subarticular tubercles prominent, all present; inner metatarsal tubercle prominent, elongate; outer metatarsal tubercle small, rounded; supernumerary tubercles absent.

Skin of dorsum highly variable from shagreened to prominently granular or with glandular warts; an interrupted inverse V-shaped ridge (chevron mark) at the centre of dorsum weakly to well developed or absent. Ventral surfaces of throat, chest, belly, and limbs smooth; and posterior parts of thigh and region surrounding the vent sparsely granular (Fig. 4). Dorsal and ventral skin colouration is extremely variable. *Dorsal surface:* uniform grey, brownish-grey, yellowish-brown, light to dark brown, blackish-brown, reddish-brown, and occasionally (but not rarely) with a broad median band extending from the upper eyelids or anterior border of eyes to vent, and a thin or broad middorsal line extending from the tip of the snout to vent (Figs 3, 4); presence or absence of reddish-brown or orange colouration on snout, lateral surfaces of dorsum, and fore and hind limbs (Figs 3, 4); presence or absence of dark blackish-brown lining on dorsal tubercles; faint or prominent crossbands on lips; upper ⅔rd of tympanum and inner margin of tympanic fold dark brown; anterior and posterior parts of thighs without prominent reticulations. *Ventral surface*: throat and chest light to dark brown or dark grey, with light or dark patches; belly yellowish-white, with or without orange tinge; margins of limbs usually with blackish-brown colouration; hand and foot light or dark brown.

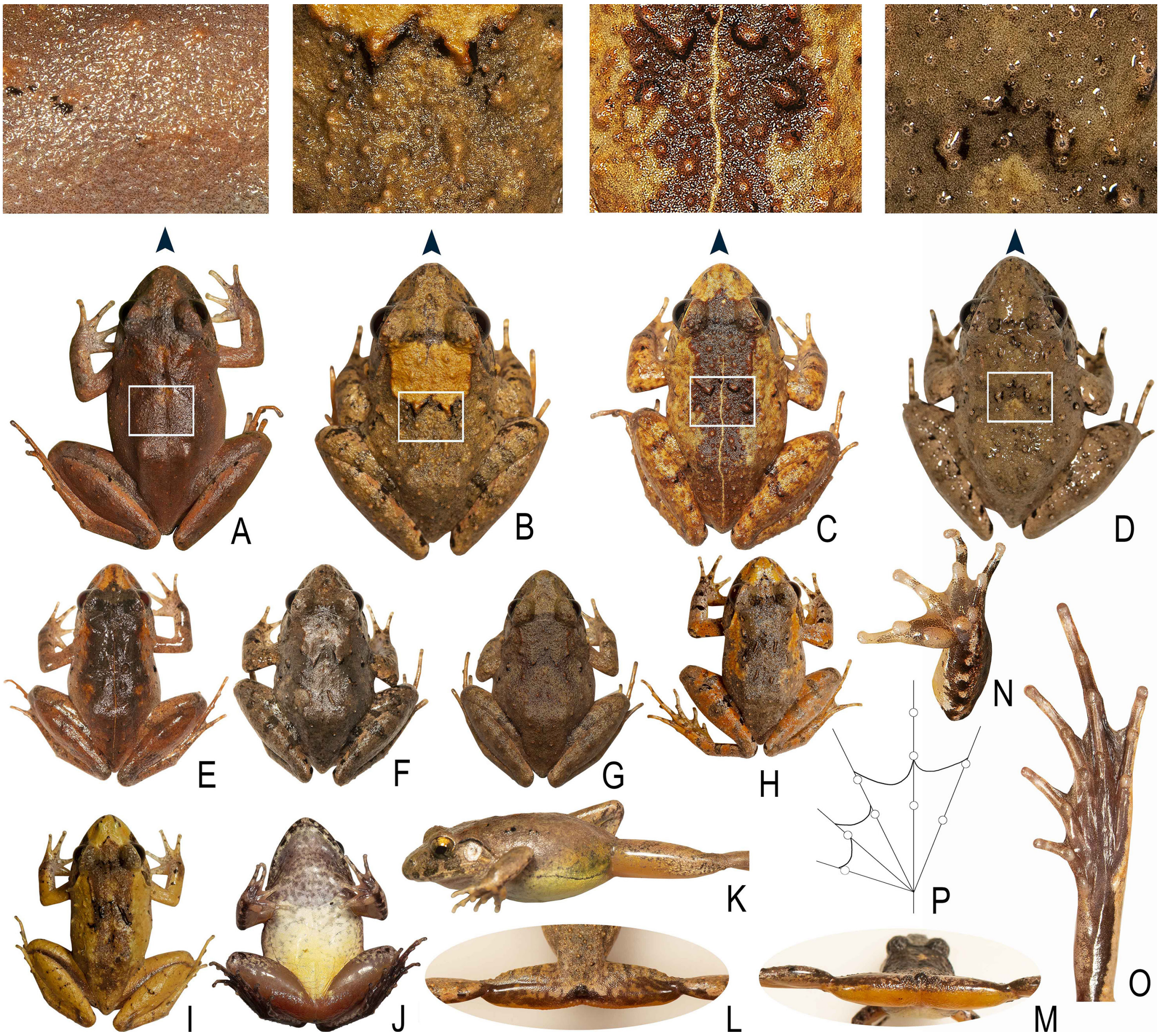

Figure 4. Morphological variation in skin texture, colouration, and markings observed among individuals of *Minervarya charlesdarwini* in the Andaman Islands. **A–H** Dorsal views. **A–D** Variation in skin texture and enlarged view of dorsal skin (demarcated with white square) above. **A** SDBDU 2019.4059 (♀). **B** SDBDU 2020.4162 (♂). **C** SDBDU 2021.4212 (♂). **D** SDBDU 2019.3977 (♂). **E–G** Not preserved (♂). **H** SDBDU 2019.4004 (♂). **I** SDBDU 2019.4005 (♀). **J** Ventral view, SDBDU 2021.4212 (♂). **K** Lateral view, SDBDU 2021.4218 (♂). **L** Dorsal view of thigh, SDBDU 2021.4212 (♂). **M** Posterior view of thigh, SDBDU 2021.4212 (♂). **N** Ventral view of hand, SDBDU 2021.4212 (♂). **O** Ventral view of foot, SDBDU 2021.4212 (♂). **P** Schematic illustration of foot webbing, SDBDU 2021.4212 (♂). Photographs: S. D. Biju.

Comparison (only with males, N=6). *Minervarya charlesdarwini* cannot be confused with other known species of the genus *Minervarya*, except three members of the *M. andamanensis* group (*M. andamanensis*, *M. nicobariensis*, and *M. muangkanensis*). *Minervarya charlesdarwini* can be distinguished from *M. andamanensis* and *M. nicobariensis* by its relatively smaller adult size, male SVL 24.8–30.1 mm (vs. larger, SVL 36.2–42.2 mm and SVL 40.0–49.8 mm, respectively); and elongate body (vs. stout and robust in both the species). It specifically also differs from *M. andamanensis* by the absence of forearm tubercles (vs. present); canthus rostralis rounded (vs. indistinct); posterior half of thigh without reticulations, usually brown or orangish-brown (vs. light to dark brown with yellowish reticulations); upper eyelid width nearly equal to inter upper eyelid width, UEW 2.4±0.2 vs. IUE 2.4±0.2 (vs. wider, UEW 3.6±0.3 vs. IUE 2.8±0.1); and thigh nearly equal to foot length, TL 13.6±0.9 vs. FOL 13.4±1.0 (vs. shorter, TL 19.9±1.3 vs. FOL 21.7±1.5). *Minervarya charlesdarwini* also differs from *M. nicobariensis* by its head being longer than wide, HL 10.6±0.7 vs. HW 9.6±0.7 (vs. wider, HW 17.5±1.0 vs. HL 16.5±1.1); upper eyelid width nearly equal to inter upper eyelid width, UEW 2.4±0.2 vs. IUE 2.4±0.2 (vs. wider, UEW 4.5±0.4 vs IUE 3.2±0.4); thigh nearly equal to foot length, TL 13.6±0.9 vs. FOL 13.4±1.0 (vs. shorter, TL 20.7±1.4 vs. FOL 22.1±1.5); presence of outer metatarsal (vs. absent); and posterior part of thighs without prominent reticulations, usually brown or orangish-brown (vs. light to dark red with thin black reticulations). Further, *M. charlesdarwini* differs from *M. muangkanensis*, a species endemic to Thailand

and Myanmar, in possessing a distinct supratympanic fold that extends from posterior corner of upper eyelid, along the upper margin of tympanum, up to the shoulder (vs. indistinct supratympanic fold, and not extending up to posterior corner of upper eyelid and down to the shoulder); webbing between toes relatively reduced, up to the second subarticular tubercle on either side of toe IV (vs. above); and posterior part of thighs without reticulations, usually brown or orangish-brown (vs. light to dark brown with yellowish reticulations).

Distribution. *Minervarya charlesdarwini* is endemic to the Andaman Archipelago of India, where we find it to be widely distributed in all the major groups of islands: North and Middle Andamans (North Andaman Is., Interview Is., Middle Andaman Is., Baratang Is., and Long Is.), South Andamans (South Andaman Is., Neil Is., Havelock Is., Boat Is., Red Skin Is., Alexandra Is., Rutland Is., and Tarmugli Is.), up to the Little Andaman Island. This species has been observed between elevations of nearly sea level up to 600 m asl (Fig. 2; Table 2).

Table 2. Distribution of *Minervarya* species reported in the present study from the Andaman and Nicobar Islands, India.

	District / Group	Island / Locality	Coordinates		Elevation
			Latitude (°N)	Longitude (°E)	(meters)
	Minervarya andamanensis				
1	North Andaman	Landfall Island	13.6680	93.0190	2
2	North Andaman	Landfall Island	13.6630	93.0217	33
3	North Andaman	Landfall Island	13.6406	93.0304	0.4
4	North Andaman	East Island	13.6333	93.0450	9
5	North Andaman	Landfall Island – South East	13.6299	93.0298	14
6	North Andaman	East Island	13.6285	93.0481	30
7	North Andaman	Paget Island	13.4321	92.8438	25
8	North Andaman	Hathi Level	13.4068	92.9094	8
9	North Andaman	Badur Tikrey	13.3685	92.9632	13
10	North Andaman	Smith Island	13.3494	93.0570	4
11	North Andaman	Smith Island	13.3465	93.0527	8
12	North Andaman	Aerial Bay	13.2728	93.0319	18
13	North Andaman	Durgapur	13.2711	93.0376	4
14	North Andaman	Kishori Nagar	13.2711	92.9596	63
15	North Andaman	Durgapur	13.2672	93.0382	24
16	North Andaman	Durgapur	13.2644	93.0407	18
17	North Andaman	Madhupur	13.2589	92.9805	13
18	North Andaman	Madhupur	13.2585	92.9772	13
19	North Andaman	Khudirampur	13.2361	92.9768	11
20	North Andaman	Shibpur	13.2339	93.0490	8
21	North Andaman	Kalipur	13.2240	93.0454	5
22	North Andaman	Lamiya Bay	13.2037	93.0408	10
23	North Andaman	Khudirampur	13.2033	92.9691	36
24	North Andaman	Kishori Nagar	13.2025	92.9690	31
25	North Andaman	Lamiya Bay	13.2010	93.0380	36
26	North Andaman	Khudirampur	13.1994	92.9731	41
27	North Andaman	Saddle Peak	13.1967	93.0314	34
28	North Andaman	Lamiya Bay	13.1930	93.0340	53
29	North Andaman	Sita Nagar	13.1881	92.9290	43
30	North Andaman	Saddle Peak	13.1860	93.0260	57
31	North Andaman	Sita Nagar	13.1853	92.9246	92
32	North Andaman	Saddle Peak	13.1850	93.0190	224
33	North Andaman	Kalara	13.1752	92.9341	47
34	North Andaman	Kalpong Dam	13.1140	92.9971	60
35	North Andaman	Kalighat	13.1013	92.9912	40
36	North Andaman	Ram Nagar	13.0800	93.0151	22
37	North Andaman	Ram Nagar	13.0724	93.0145	28
38	North Andaman	Patti Level	13.0596	92.9907	123
39	North Andaman	Interview Island	12.8999	92.7200	20
40	Middle Andaman	Mayabunder, Austin Strait	12.8934	92.8574	28
41	Middle Andaman	Mayabunder, Tugapur	12.8395	92.8568	13
42	Middle Andaman	Mayabunder, Hanspuri	12.7581	92.8059	74
43	Middle Andaman	Mayabunder, Chainpur	12.7396	92.8068	28

	District / Group	Island / Locality	Coordinates		Elevation
			Latitude (°N)	Longitude (°E)	(meters)
44	Middle Andaman	Rangat, Cuthbert Bay	12.7090	92.9680	7
45	Middle Andaman	Rangat, Mount Diavalo	12.6800	92.9400	156
46	Middle Andaman	Rangat, Mount Diavalo	12.6800	92.9420	98
47	Middle Andaman	Rangat, Dhanni Nallah	12.6160	92.9550	11
48	Middle Andaman	Rangat, Moricedera	12.5535	92.9712	17
49	Middle Andaman	Rangat, Parnashala	12.5265	92.9053	26
50	Middle Andaman	Rangat, Yeratta	12.5038	92.9028	40
51	Middle Andaman	Rangat, Bakultala	12.5015	92.8857	119
52	Middle Andaman	Rangat, Shyamkund	12.4910	92.8480	38
53	Middle Andaman	Rangat, Sabari	12.4861	92.9002	13
54	Middle Andaman	Rangat, Vishnupur	12.4840	92.8734	17
55	Middle Andaman	Rangat, Vishnupur	12.4756	92.8766	7
56	Middle Andaman	Rangat, Ullidera	12.4718	92.8613	9
57	Middle Andaman	Rangat, Ullidera	12.4715	92.8634	10
58	Middle Andaman	Rangat, Bharatpur	12.4680	92.8930	16
59	Middle Andaman	Rangat, Bronil	12.4631	92.8312	5
60	Middle Andaman	Rangat, Panchawati	12.4078	92.8877	9
61	Middle Andaman	Long Island, Sigman Dera	12.3820	92.9290	37
62	Middle Andaman	Long Island, Lalaji Bay Forest	12.3790	92.9350	60
63	Middle Andaman	Long Island	12.3710	92.9220	60
64	Middle Andaman	North Passage Island	12.2880	92.9334	12
65	Middle Andaman	Baratang Island, Shankar Nallah	12.2543	92.8041	64
66	Middle Andaman	Baratang Island, Shankar Nallah	12.2543	92.8041	67
67	Middle Andaman	Baratang Island, Loroijg	12.2389	92.7957	37
68	Middle Andaman	Baratang Island, Roglachang	12.1603	92.7936	26
69	Middle Andaman	Baratang Island, Baludera	12.1363	92.8069	8
70	Middle Andaman	Baratang Island, Baludera	12.1357	92.8032	4
71	Middle Andaman	Baratang Island, Jarawa Creek	12.1250	92.7881	18
72	Middle Andaman	Baratang Island, Wrafters Creek	12.1127	92.7680	45
73	Middle Andaman	Baratang Island, Wrafters Creek	12.1105	92.7725	21
74	Middle Andaman	Baratang Island, Wrafters Creek	12.1066	92.7722	12
75	Middle Andaman	Baratang Island, Naya Dera	12.0974	92.7535	54
76	South Andaman	Jirkatang – 21km	12.0930	92.7070	73
77	South Andaman	Jarawa Reserve	12.0581	92.7128	59
78	South Andaman	Jarawa Reserve, Jirkatang – 16km	12.0560	92.7020	89
79	South Andaman	Havelock Island, Govind Nagar	12.0418	92.9831	6
80	South Andaman	Havelock Island, Shyam Nagar	12.0087	92.9635	58
81	South Andaman	Havelock Island, Krishna Nagar	12.0076	92.9612	61
82	South Andaman	Jarawa Reserve, Jirkatang – 6km	11.9650	92.6770	105
83	South Andaman	Jirkatang	11.9453	92.6812	127
84	South Andaman	Jirkatang	11.9060	92.6660	132
85	South Andaman	Shoal Bay – 19	11.8967	92.7662	33
86	South Andaman	Shoal Bay – 19	11.8950	92.7650	16
87	South Andaman	Shoal Bay – 1	11.8820	92.7470	56
88	South Andaman	Shoal Bay	11.8770	92.7410	31
89	South Andaman	Shoal Bay	11.8747	92.7402	23
90	South Andaman	Shoal Bay	11.8746	92.7406	32
91	South Andaman	Shoal Bay	11.8710	92.7420	87
92	South Andaman	Jirkatang	11.8680	92.6550	82
93	South Andaman	Shoal Bay	11.8570	92.7350	21
94	South Andaman	Shoal Bay 10	11.8438	92.7293	6
95	South Andaman	Shoal Bay 10	11.8410	92.7290	35
96	South Andaman	Neil Island	11.8354	93.0362	6
97	South Andaman	Shoal Bay – 8	11.8270	92.7220	9
98	South Andaman	Kalatang	11.8050	92.7140	27
99	South Andaman	Wrightmayo Creek	11.8010	92.7080	16
100	South Andaman	Kalatang	11.7958	92.7118	18
101	South Andaman	Mount Harriet	11.7570	92.7320	308

	District / Group	Island / Locality	Coordinates		Elevation
			Latitude (°N)	Longitude (°E)	(meters)
102	South Andaman	Mount Harriet	11.7440	92.7390	285
103	South Andaman	Wimberlygunj	11.7375	92.7132	42
104	South Andaman	Kadakachang, Stewartgunj 1	11.7330	92.7150	61
105	South Andaman	Tirur	11.7312	92.6146	10
106	South Andaman	Mount Harriet	11.7290	92.7420	87
107	South Andaman	Mount Harriet	11.7250	92.7370	211
108	South Andaman	Kadakachang, Mathura	11.7230	92.6810	16
109	South Andaman	Mount Harriet	11.7202	92.7339	351
110	South Andaman	Katagachang	11.7160	92.6940	18
111	South Andaman	Tirur–Jhau kona Hotspot	11.7123	92.5727	49
112	South Andaman	Mazar Pahad	11.7030	92.6370	12
113	South Andaman	Gandhi Park	11.6617	92.7408	45
114	South Andaman	Ograbraj	11.6577	92.6631	4
115	South Andaman	Rachibasthi	11.6469	92.7280	61
116	South Andaman	Corbyns Cove	11.6434	92.7442	12
117	South Andaman	BSI Garden	11.6390	92.7367	16
118	South Andaman	Garacharma	11.6238	92.7041	17
119	South Andaman	Chouldhari	11.6225	92.6685	3
120	South Andaman	Garacharma	11.6180	92.7062	2
121	South Andaman	Wandoor	11.6177	92.6167	15
122	South Andaman	Wandoor	11.6149	92.6190	15
123	South Andaman	Sippighat	11.6125	92.6931	11
124	South Andaman	Bathu Basti	11.6120	92.7183	58
125	South Andaman	Tarmugli Island, Mummy Dera	11.6028	92.5413	12
126	South Andaman	Tarmugli Island	11.5935	92.5437	19
127	South Andaman	Alexandra Island	11.5851	92.6031	15
128	South Andaman	Alexandra Island	11.5850	92.6060	40
129	South Andaman	Alexandra Island	11.5770	92.6030	39
130	South Andaman	Tarmugli Island	11.5650	92.5523	24
131	South Andaman	Boat Island	11.5329	92.5579	24
132	South Andaman	Boat Island	11.5268	92.5652	18
133	South Andaman	Boat Island	11.5240	92.5600	33
134	South Andaman	Burmanallah	11.5225	92.7209	40
135	South Andaman	Chidiyatapu	11.5162	92.6992	13
136	South Andaman	Chidyatapu	11.5081	92.6915	10
137	South Andaman	Rutland Island	11.5080	92.6439	40
138	South Andaman	Rutland Island	11.5078	92.6436	36
139	South Andaman	Rutland Island	11.5066	92.6426	39
140	Little Andaman	V. K. Pur	10.7590	92.5530	23
141	Little Andaman	V. K. Pur	10.7460	92.5410	26
142	Little Andaman	Donghighat	10.7379	92.5703	12
143	Little Andaman	Rabinder Nagar Dam	10.7150	92.5360	71
144	Little Andaman	Rabinder Nagar Dam	10.7080	92.5350	63
145	Little Andaman	Rabinder Nagar Dam	10.7050	92.5430	68
146	Little Andaman	RK Pur Dam	10.7020	92.5490	44
147	Little Andaman	Krishna Nala	10.6783	92.5396	72
148	Little Andaman	Krishna Nala	10.6710	92.5130	114
149	Little Andaman	Netaji Nagar	10.6630	92.5440	29
150	Little Andaman	Kalapather	10.6597	92.5765	5
151	Little Andaman	Netaji Nagar	10.6493	92.5409	57
152	Little Andaman	White Surf Water Fall	10.6290	92.5280	87
153	Little Andaman	Rabinder Nagar Dam	10.5945	92.5326	-1
154	Little Andaman	Farm Tikery	10.5890	92.5241	73
155	Little Andaman	Herimidhar Bay	10.5870	92.5330	4
156	Little Andaman	Ongi Tikery	10.5710	92.5540	34
	Minervarya charlesdarwini				
157	North Andaman	Hathi Level	13.4068	92.9094	6
158	North Andaman	Badur Tikrey	13.3685	92.9632	13

	District / Group	Island / Locality	Coordinates		Elevation
			Latitude (°N)	Longitude (°E)	(meters)
159	North Andaman	Kishori Nagar	13.2711	92.95955	62
160	North Andaman	Durgapur	13.2672	93.0382	23
161	North Andaman	Lamiya Bay	13.2037	93.0408	10
162	North Andaman	Khudirampur	13.2033	92.9691	36
163	North Andaman	Khudirampur	13.2026	93.0375	72
164	North Andaman	Kishori Nagar	13.2025	92.9690	31
165	North Andaman	Lamiya Bay	13.2010	93.0380	36
166	North Andaman	Saddle Peak	13.1967	93.0314	72
167	North Andaman	Lamiya Bay	13.1930	93.0340	54
168	North Andaman	Saddle Peak	13.1860	93.0260	54
169	North Andaman	Saddle Peak	13.1850	93.0190	219
170	North Andaman	Kalara	13.1752	92.9341	47
171	North Andaman	Kalpong Dam	13.1140	92.9971	59
172	North Andaman	Ram Nagar	13.0800	93.0151	8
173	North Andaman	Patti Level	13.0596	92.9907	122
174	North Andaman	Interview Island	12.8999	92.7200	22
175	North Andaman	Interview Island	12.8953	92.6884	78
176	Middle Andaman	Mayabunder, Austin Strait	12.8934	92.8574	28
177	Middle Andaman	Mayabunder, Tugapur	12.8395	92.8568	13
178	Middle Andaman	Mayabunder, Hanspuri	12.7581	92.8059	73
179	Middle Andaman	Mayabunder, Chainpur	12.7396	92.8068	28
180	Middle Andaman	Rangat, Mount Diavalo	12.6800	92.9420	99
181	Middle Andaman	Rangat, Moricedera	12.5535	92.9712	15
182	Middle Andaman	Rangat, Parnashala	12.5265	92.9053	24
183	Middle Andaman	Rangat, Yeratta	12.5038	92.9028	36
184	Middle Andaman	Rangat, Bakultala	12.5015	92.8857	119
185	Middle Andaman	Rangat, Shyamkund	12.4910	92.8480	36
186	Middle Andaman	Rangat, Sabari	12.4861	92.9002	12
187	Middle Andaman	Rangat, Vishnupur	12.4840	92.8734	63
188	Middle Andaman	Rangat, Ullidera	12.4715	92.8634	15
189	Middle Andaman	Rangat, Bharatpur	12.4680	92.8930	16
190	Middle Andaman	Rangat, Bronil	12.4631	92.8312	5
191	Middle Andaman	Rangat, Panchawati	12.4078	92.8877	8
192	Middle Andaman	Long Island, Sigman Dera	12.3820	92.9290	38
193	Middle Andaman	Long Island, Lalaji Bay Forest	12.3790	92.9350	60
194	Middle Andaman	Long Island, Long Island	12.3710	92.9220	60
195	Middle Andaman	Baratang Island, Shankar Nallah	12.2543	92.8041	68
196	Middle Andaman	Baratang Island, Shankar Nallah	12.2543	92.8041	68
197	Middle Andaman	Baratang Island, Loroijg	12.2389	92.7957	37
198	Middle Andaman	Baratang Island, Roglachang	12.1603	92.7936	21
199	Middle Andaman	Baratang Island, Baludera	12.1357	92.8032	5
200	Middle Andaman	Baratang Island, Jarawa Creek	12.1250	92.7881	17
201	Middle Andaman	Baratang Island, Wrafters Creek	12.1127	92.7680	46
202	Middle Andaman	Baratang Island, Wrafters Creek	12.1105	92.7725	21
203	Middle Andaman	Baratang Island, Naya Dera	12.0974	92.7535	54
204	South Andaman	Jirkatang – 21km	12.0930	92.7070	73
205	South Andaman	Jirkatang – 16km	12.0560	92.7020	85
206	South Andaman	Jirkatang – 6km	11.9650	92.6770	106
207	South Andaman	Jirkatang	11.9453	92.6812	126
208	South Andaman	Jirkatang	11.9060	92.6660	133
209	South Andaman	Shoal Bay – 19	11.8950	92.7650	16
210	South Andaman	Shoal Bay – 19	11.8910	92.7790	13
211	South Andaman	Shoal Bay – 1	11.8820	92.7470	57
212	South Andaman	Shoal Bay	11.8770	92.7410	29
213	South Andaman	Shoal Bay	11.8747	92.7402	25
214	South Andaman	Shoal Bay	11.8746	92.7406	55
215	South Andaman	Shoal Bay	11.8746	92.7406	55
216	South Andaman	Shoal Bay	11.8710	92.7420	87

	District / Group	Island / Locality	Coordinates		Elevation
			Latitude (°N)	Longitude (°E)	(meters)
217	South Andaman	Jirkatang	11.8680	92.6550	83
218	South Andaman	Shoal Bay	11.8570	92.7350	21
219	South Andaman	Shoal Bay – 10	11.8410	92.7290	37
220	South Andaman	Neil Island	11.8354	93.0362	6
221	South Andaman	Shoal Bay – 8	11.8270	92.7220	9
222	South Andaman	Kalatang	11.8050	92.7140	23
223	South Andaman	Wrightmayo Creek	11.8010	92.7080	15
224	South Andaman	Boat Island, Kalatang	11.7958	92.7118	19
225	South Andaman	Mount Harriet	11.7570	92.7320	310
226	South Andaman	Tirur–Jhau Kona Hotspot	11.7510	92.6120	12
227	South Andaman	Mount Harriet	11.7440	92.7390	387
228	South Andaman	Mount Harriet	11.7290	92.7420	87
229	South Andaman	Mount Harriet	11.7250	92.7370	197
230	South Andaman	Mount Harriet	11.7202	92.7339	351
231	South Andaman	Tirur–Jhau Kona Hotspot	11.7190	92.5850	17
232	South Andaman	Mazar Pahad	11.7030	92.6370	12
233	South Andaman	Gandhi Park	11.6617	92.7408	46
234	South Andaman	BSI Garden	11.6390	92.7367	18
235	South Andaman	Wandoor	11.6149	92.6190	15
236	South Andaman	Tarmugli Island	11.6028	92.5413	11
237	South Andaman	Alexandra Island	11.5850	92.6060	42
238	South Andaman	Alexandra Island	11.5770	92.6030	38
239	South Andaman	Redskin Island	11.5691	92.5931	34
240	South Andaman	Chidiyatapu	11.5162	92.6992	13
241	South Andaman	Chidyatapu	11.5081	92.6915	11
242	South Andaman	Rutland Island	11.5080	92.6439	40
243	South Andaman	Rutland Island	11.5078	92.6436	36
244	South Andaman	Rutland Island	11.5066	92.6426	37
245	Little Andaman	V. K. Pur	10.7590	92.5530	21
246	Little Andaman	V. K. Pur	10.7460	92.5410	27
247	Little Andaman	Donghighat	10.7410	92.5750	17
248	Little Andaman	Rabinder Nagar Dam	10.7150	92.5360	67
249	Little Andaman	Rabinder Nagar Dam	10.7080	92.5350	62
250	Little Andaman	Rabinder Nagar Dam	10.7050	92.5430	70
251	Little Andaman	RK Pur Dam	10.7020	92.5490	45
252	Little Andaman	Krishna Nallah	10.6783	92.5396	72
253	Little Andaman	Krishna Nalla	10.6710	92.5130	117
254	Little Andaman	Netaji Nagar	10.6630	92.5440	30
255	Little Andaman	Netaji Nagar	10.6493	92.5409	60
256	Little Andaman	Kalapather	10.6407	92.5423	5
257	Little Andaman	White Surf Water Fall	10.6290	92.5280	88
258	Little Andaman	Rabinder Dam	10.5945	92.5326	-1
	Minervarya nicobariensis				
259	Nicobar, Central group	Bompoka Island	8.2494	93.2218	36
260	Nicobar, Central group	Kamorta Island, Kakana	8.1731	93.5070	22
261	Nicobar, Central group	Kamorta Island, Vikas Nagar	8.1198	93.5138	31
262	Nicobar, Central group	Kamorta Island, Changhua	8.0212	93.4916	72
263	Nicobar, Central group	Nancowry Island, Champin	8.0202	93.5548	63
264	Nicobar, Central group	Kamorta Island, Munak	8.0123	93.5045	69
265	Nicobar, Central group	Kamorta Island, Alukian	8.0057	93.4932	63
266	Nicobar, Central group	Nancowry Island, Malacca	8.0053	93.5675	73
267	Nicobar, Central group	Katchal Island, Kapanga	7.9992	93.3928	85
268	Nicobar, Central group	Katchal Island, Beachdera	7.9969	93.3585	62
269	Nicobar, Central group	Nancowry Island, Itoi	7.9961	93.5315	74
270	Nicobar, Central group	Katchal Island, Lal Munak	7.9879	93.3737	52
271	Nicobar, Central group	Katchal Island, Upper Katchal	7.9407	93.4434	69
272	Nicobar, Southern group	Little Nicobar Island, Makachua	7.4069	93.7096	41
273	Nicobar, Southern group	Little Nicobar Island, Pulo Panja	7.3760	93.7395	39

	District / Group	Island / Locality	Coordinates		Elevation
			Latitude (°N)	Longitude (°E)	(meters)
274	Nicobar, Southern group	Great Nicobar Island, Afra Bay	7.1662	93.7662	166
275	Nicobar, Southern group	Great Nicobar Island, Navy Dera	7.1353	93.8840	38
276	Nicobar, Southern group	Great Nicobar Island, Navy Dera	7.1239	93.8870	34
277	Nicobar, Southern group	Great Nicobar Island, Laxman Beach	7.0214	93.9176	27
278	Nicobar, Southern group	Great Nicobar Island, East West Road	7.0189	93.9233	36
279	Nicobar, Southern group	Great Nicobar Island, Old East West Road	7.0176	93.9231	28
280	Nicobar, Southern group	Great Nicobar Island, Campbell Bay	7.0152	93.9230	40
281	Nicobar, Southern group	Great Nicobar Island, Govind Nagar	7.0040	93.9095	52
282	Nicobar, Southern group	Great Nicobar Island, GNBR Check Post	7.0016	93.8834	56
283	Nicobar, Southern group	Great Nicobar Island, Govind Nagar	7.0011	93.8958	40
284	Nicobar, Southern group	Great Nicobar Island, East West Road	6.9957	93.8831	49
285	Nicobar, Southern group	Great Nicobar Island, Magar Nallah	6.9945	93.9124	18
286	Nicobar, Southern group	Great Nicobar Island, East West Road	6.9814	93.8644	92
287	Nicobar, Southern group	Great Nicobar Island, Chingam Basti	6.9705	93.9192	106
288	Nicobar, Southern group	Great Nicobar Island, Jogindar Nagar	6.9513	93.9199	13
289	Nicobar, Southern group	Great Nicobar Island, Laxmi Nagar	6.9039	93.8920	35
290	Nicobar, Southern group	Great Nicobar Island, Vijay Nagar	6.8729	93.8893	50
291	Nicobar, Southern group	Great Nicobar Island, Gandhi Nagar	6.8404	93.8907	14
292	Nicobar, Southern group	Great Nicobar Island, Galathea Bay	6.8231	93.8631	32
293	Nicobar, Southern group	Great Nicobar Island, Sastri Nagar	6.8104	93.8920	37
294	Nicobar, Southern group	Great Nicobar Island, Old Chingam Basti	6.8026	93.8458	34
295	Nicobar, Southern group	Great Nicobar Island, Indira Point	6.7597	93.8257	35
	Minervarya agricola				
296	North Andaman	Badur Tikrey	13.3685	92.9632	18
297	North Andaman	Ram Nagar	13.2759	93.0186	7
298	North Andaman	Durgapur	13.2671	93.0382	22
299	North Andaman	Madhupur	13.2585	92.9772	10
300	North Andaman	Shibpur	13.2339	93.0490	7
301	North Andaman	Khudirampur	13.2033	92.9691	34
302	North Andaman	Kishori Nagar	13.2025	92.9690	31
303	North Andaman	Lamiya Bay	13.2010	93.0380	37
304	North Andaman	Lamiya Bay	13.1930	93.0340	53
305	North Andaman	Sita Nagar	13.18533	92.9246	93
306	Middle Andaman	Mayabunder, Hanspuri	12.7581	92.8059	74
307	Middle Andaman	Mayabunder, Chainpur	12.7396	92.8068	28
308	Middle Andaman	Rangat, Parnashala	12.5265	92.9053	23
309	Middle Andaman	Rangat, Yeratta	12.5038	92.9028	41
310	Middle Andaman	Rangat, Shyamkund	12.4910	92.8480	36
311	Middle Andaman	Rangat, Sabari	12.4861	92.9002	14
312	Middle Andaman	Rangat, Panchawati	12.4078	92.8877	7
313	Middle Andaman	Baratang Island, Lolachang	12.1603	92.7936	24
314	Middle Andaman	Baratang Island, Baludera	12.1357	92.8032	5
315	Middle Andaman	Baratang Island, Wrafters Creek	12.1127	92.7680	46
316	Middle Andaman	Baratang Island, Naya Dera	12.0974	92.7535	54
317	South Andaman	Havelock Island, Govind Nagar	12.0337	92.9866	6
318	South Andaman	Havelock Island, Shyam Nagar	12.0087	92.9635	57
319	South Andaman	Havelock Island, Krishna Nagar	12.0076	92.9612	62
320	South Andaman	Havelock Island, Kalapather	11.982	93.0161	21
321	South Andaman	Jirkatang	11.9453	92.6812	127
322	South Andaman	Shoal Bay – 19	11.8950	92.7650	16
323	South Andaman	Shoal Bay – 19	11.8910	92.7790	11
324	South Andaman	Shoal Bay – 1	11.8820	92.7470	57
325	South Andaman	Shoal Bay	11.8770	92.7410	29
326	South Andaman	Shoal Bay	11.8747	92.7402	27
327	South Andaman	Shoal Bay	11.8746	92.7406	29
328	South Andaman	Shoal Bay	11.8710	92.7420	88
329	South Andaman	Shoal Bay	11.8570	92.7350	21
330	South Andaman	Shoal Bay –10	11.8410	92.7290	37

	District / Group	Island / Locality	Coordinates		Elevation
			Latitude (°N)	Longitude (°E)	(meters)
331	South Andaman	Neil Island	11.8354	93.0362	6
332	South Andaman	Shoal Bay – 8	11.8270	92.7220	8
333	South Andaman	Kalatang	11.7958	92.7118	19
334	South Andaman	Wimberlygunj	11.7375	92.7132	42
335	South Andaman	Kadakachang, Stewartgunj 1	11.7330	92.7150	54
336	South Andaman	Tirur	11.7288	92.6127	17
337	South Andaman	Mazar Pahad	11.7030	92.6370	12
338	South Andaman	Mazhar Pahad	11.7028	92.6380	13
339	South Andaman	Gandhi Park	11.6617	92.7408	33
340	South Andaman	Ograbraj	11.6577	92.6631	4
341	South Andaman	BSI Garden	11.6390	92.7367	16
342	South Andaman	Chouldhari	11.6225	92.6685	3
343	South Andaman	Garacharma	11.6180	92.7062	2
344	South Andaman	Garacharma	11.6151	92.7000	15
345	South Andaman	Wandoor	11.6149	92.6190	15
346	South Andaman	Sippighat	11.6125	92.6931	12
347	South Andaman	Corbyns Cove	11.5906	92.6749	4
348	South Andaman	Burmanallah	11.5225	92.7209	37
349	South Andaman	Chidiyatapu	11.5162	92.6992	13
350	South Andaman	Chidyatapu	11.5081	92.6915	10
351	Little Andaman	V. K. Pur	10.7460	92.5410	29
352	Little Andaman	Rabinder Nagar Dam	10.7080	92.5350	63
353	Little Andaman	Netaji Nagar	10.6630	92.5440	33
354	Little Andaman	Netaji Nagar	10.6493	92.5409	59
355	Little Andaman	Kalapather	10.6407	92.5423	4
356	Little Andaman	Farm Tikery	10.5890	92.5241	72
357	Little Andaman	Ongi Tikery	10.5710	92.5540	33

Taxonomic identity of *Minervarya andamanensis* (Stoliczka, 1870)

Figs 1, 2, 5, 6; Tables 1, 2

Andamanese minervaryan frog

Note. This species was originally described as a variety of *Rana gracilis* var. *andamanensis* Stoliczka, 1870. The description was based on four specimens—one "about one-third of an inch long" (~9 mm), "two next above one inch" (~ 25 mm), and "the fourth 2⅓rd inches" (~ 60 mm). Of these, ZSIC 3539 (ZSIC 8539 according to Chanda et al. 2001 "2000") was designated as the lectotype by Annandale (1917). Furthermore, three of the original syntypes—two from the ZSI collection and one in the NHM collection—were suggested to represent two other dicroglossid species (see detailed taxonomic remarks for *Limnonectes doriae* and *L. hascheanus*). Hence, *Minervarya andamanensis* was restricted to a single juvenile specimen, which we found to be in an extremely dehydrated condition (Fig. 6). Since the lectotype is not reliable for identification, much of what is known of this nomen is based on its original description (Stoliczka 1870) and a subsequently published illustration (Annandale 1917). Additional specimens were reported by Annandale (1917), and further, based on tentatively identified records its phylogenetic position and relationships have also been discussed (Kotaki et al. 2010; Sanchez et al. 2018; Garg and Biju 2021). Recently, Chandramouli et al. (2021) provided a redescription of the species based on new collections. In our study, we further report the prevalence of high morphological variations among individuals of this species. Typically, *M. andamanensis* has been identified based on its chestnut-brown dorsal colouration and dark brown lateral surfaces (e.g., Annandale 1917; Sarkar 1990; Chandramouli 2017). However, we observe that this character is not constant, and several genetically confirmed individuals with uniform colouration and other colour morphs from our study are conspecific (Figs 5, 6). In addition, we find the Little Andaman population to be divergent from that found in South Andamans (see Phylogenetic Results). Hence, in order to aid further studies, below we provide a revised morphological diagnosis for the species, compare it with other closely related members of the *M. andamanensis* species group, discuss morphological variations accompanied with detailed illustrations, and also shed light on the possibility of this species having been confused with other dicroglossids found in the regions (see taxonomic remarks for *M. charlesdarwini*, *Limnonectes doriae* and *L. hascheanus*).

Redescription (all measurements in mm)**.** A medium-sized species (males: SVL 36.2–42.2, 39.2±2.1, *N*=6; females: SVL 39.4–57.1, 48.6±7.4, *N*=6), body stout and robust; head longer in males (HL 14.3–17.0, 15.2±1.0

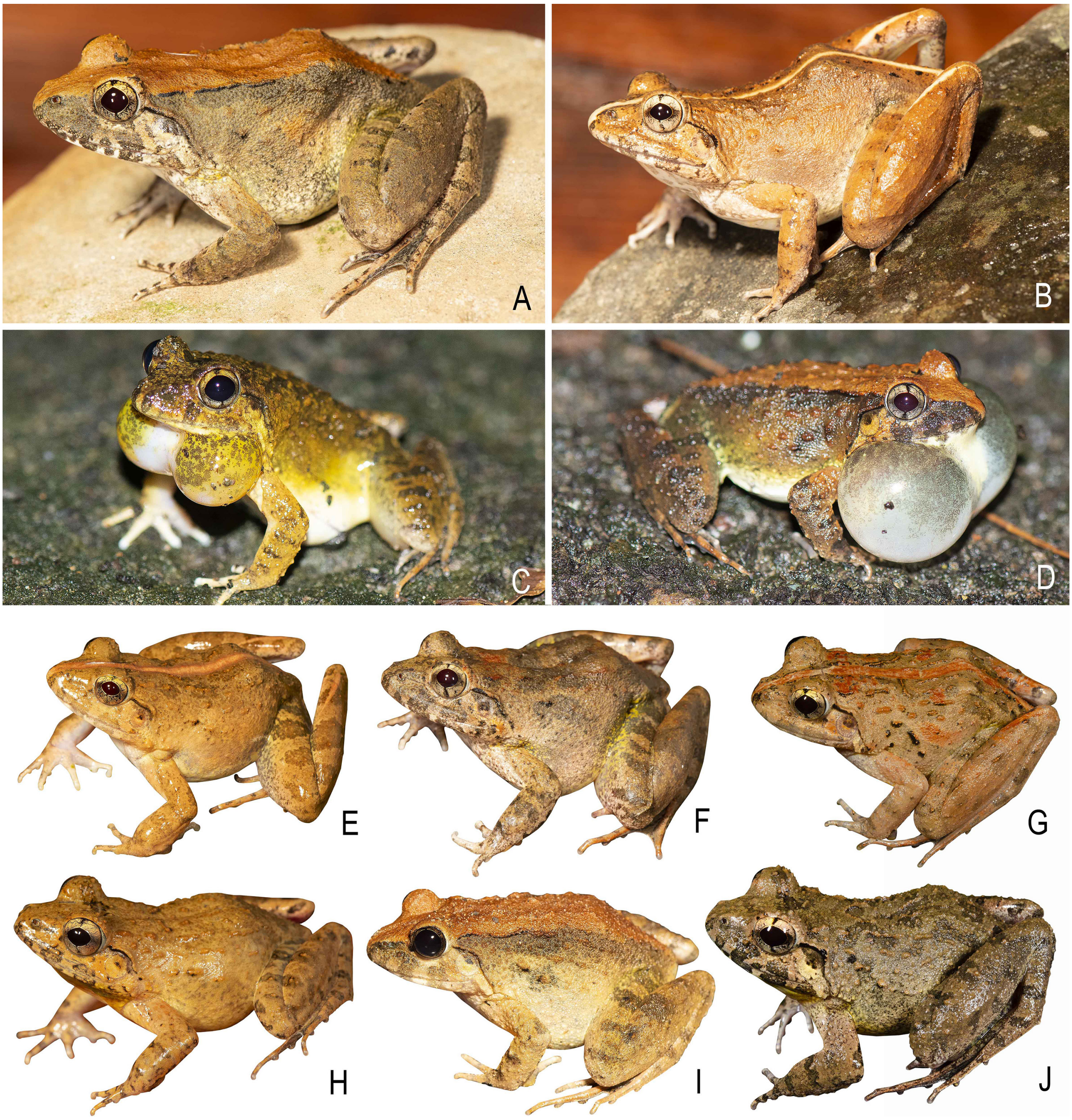

Figure 5. Morphological variation in skin colouration and markings observed among individuals of *Minervarya andamanensis*. **A–J** Dorsolateral views. **A** SDBDU 2021.4206 (♀). **B** SDBDU 2021.4207 (♀). **C–D** Not preserved (♂). **E** SDBDU 2020.4179 (♀). **F** SDBDU 2010.4178a (♀). **G** SDBDU 2019.4011 (♂). **H** SDBDU 2020.4155 (♂). **I** Not preserved (♂). **J** SDBDU 2019.3956 (♂). Photographs: S. D. Biju, G. Gokulakrishnan & Sonali Garg.

vs. HW 12.4–15.9, 13.9±1.2, *N*=6) and subequal in females (HL 14.2–20.9, 17.6±3.1, *N*=6 vs. HW 13.8–21.6, 17.7±2.9, *N*=6); snout rounded or subovoid in dorsal and ventral view, rounded or obtuse in lateral view; snout length (males: SL 5.6–7.4, 6.4±0.7; females: SL 5.8–8.6, 7.3±1.1) longer than horizontal diameter of eye (males: EL 4.4–5.4, 4.8±0.5; females: EL 4.0–6.6, 5.2±1.0); loreal region obtuse; indistinct canthus rostralis; interorbital space flat; tympanum diameter (males: TYD 2.4–3.3, 2.8± 0.3; females: TYD 2.9–4.4, 3.3±0.6) nearly ⅗th of the eye diameter (males: EL 4.4–5.4, 4.8±0.5; females: EL 4.0–6.6, 5.2±1.0); pineal ocellus present; supratympanic fold well developed, extending from the posterior corner of the eye down to nearly the shoulder; vomerine ridge present, bearing small teeth; tongue moderately long, emarginated (Figs 5, 6). Forearm length (males: FAL 7.2–9.1, 8.0±0.8; females: FAL 8.7–11.8, 9.6±1.4) shorter than hand length (males: HAL 8.6–9.8, 9.2±0.5; females: HAL 10.1–13.2, 11.6±1.2); subarticular tubercles prominent, single, circular, all present; prepollex oval, prominent; two rounded palmar tubercles; supernumerary tubercles absent; relative length of fingers II<I=IV<III; tip of fingers bluntly rounded, not enlarged into discs. Hind limbs shorter in comparison to the body length with tibiotarsal articulation reaching up to the anterior end of eye when hind limb is stretched along the body; thigh (males: TL 18.4–21.9,

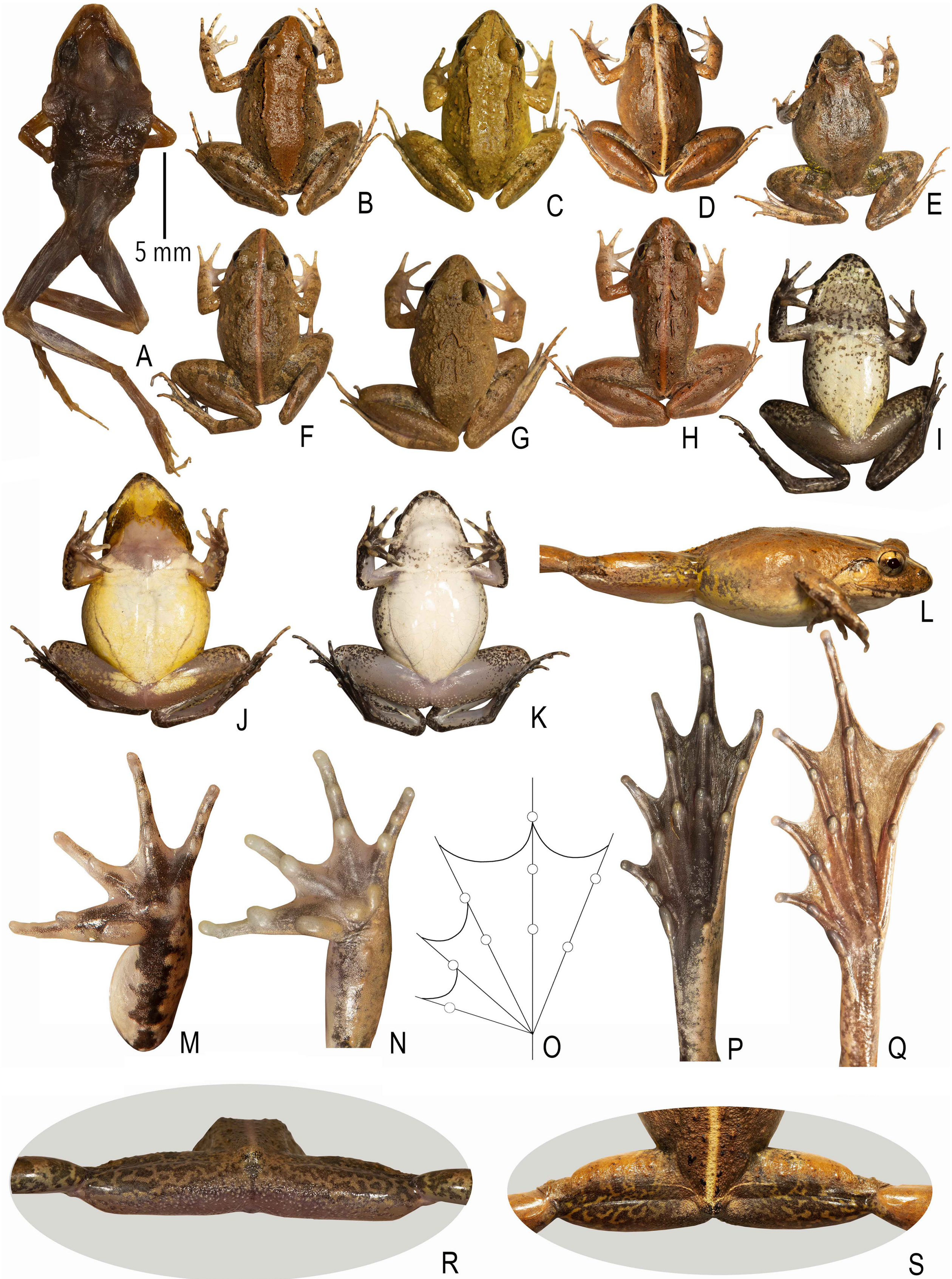

Figure 6. Morphological variation observed among individuals of *Minervarya andamanensis*. **A** Lectotype (ZSIC 3539 / ZSIC 8539). **B–H** Dorsal views. **B** SDBDU 2020.4181 (♀). **C** SDBDU 2020.4154 (♂). **D** SDBDU 2021.4207 (♀). **E** SDBDU 2020.4171a (♀). **F** SDBDU 2020.4179 (♀). **G** SDBDU 2020.4155 (♂). **H** SDBDU 2020.4180 (♂). **I–K** Ventral views. **I** SDBDU 2020.4180 (♂). **J** SDBDU 2020.4154 (♂). **K** SDBDU 2020.4171a (♀). **L** Lateral view, SDBDU 2021.4291 (♀). **M–N** Ventral view of hand, SDBDU 2021.4207 and SDBDU 2000.4179, respectively). **O** Schematic illustration of foot webbing, SDBDU 2021.4207 (♀). **P–Q** Ventral view of foot, SDBDU 2020.4179 and SDBDU 2001.4207, respectively. **R** Posterior view of thigh, SDBDU 2020.4179 (♀). **S.** Dorsal view of thigh, SDBDU 2021.4207 (♀). Photographs: S. D. Biju.

19.9±1.3; females: TL 20.9–30.1, 24.8±3.4) shorter than shank (males: SHL 20.1–24.1, 21.7±1.6; females: SHL 24.5–31.3, 27.4±2.8) and foot (males: FOL 20.1–23.7, 21.7±1.5; females: FOL 23.4–29.6, 25.7±2.9); total foot length (males: TFOL 28.1–34.9, 31.3±2.9; females: TFOL 33.0–41.4, 36.5±2.8); toe tips rounded, slightly swollen without discs, toes without dermal fringes, webbing between toes moderate: I1^{+}–2II1^{+}–2III1^{+}–2IV2–1^{+}V; subarticular tubercles prominent, all present; inner metatarsal tubercle prominent, elongate; outer metatarsal tubercle small, prominent, rounded; supernumerary tubercles absent (Figs 5, 6).

Comparison (only with males)**.** *Minervarya andamanensis* cannot be confused with other known members of the genus *Minervarya*, except three members of the *M. andamanensis* group (*M. charlesdarwini*, *M. nicobariensis*, and *M. muangkanensis*). *Minervarya andamanensis* can be distinguished from *M. nicobariensis* by its head longer than wide, HL 15.2±1.0 vs. HW 13.9±1.2 (vs. wider, HW 17.5±1.0 vs. HL 16.5±1.1); shank nearly equal to foot, SHL 21.7±1.6 vs. FOL 21.7±1.5 (vs. shorter, SHL 20.9±1.0 vs. FOL 22.1±1.5); presence of outer metatarsal tubercle (vs. absent); and posterior part of thighs light to dark brown with yellowish reticulations (vs. light to dark red with thin black reticulations). Further, it differs from *M. muangkanensis* (based on Köhler et al. 2019) in having a larger adult male size, SVL 36.2–42.2, 39.2±2.1, *N*=6 (vs. SVL 25.8–35.1, 31.2±3.1, *N*=7); supratympanic fold distinct, extending from posterior corner of upper eyelid, along upper margin of tympanum, down to the shoulder (vs. indistinct supratympanic fold and not down to the shoulder); webbing between the toes relatively reduced, up to the second subarticular tubercle on either side of toe IV (vs. above). For comparison with *M. charlesdarwini*, see the comparison section of that species.

Distribution. *Minervarya andamanensis* is endemic to the Andaman Archipelago of India, where we find it to be widely distributed in all the major groups of islands: North and Middle Andamans (North Andaman Is., Landfall Is., East Is., Paget Is., Interview Is., Smith Is., Long Is., North Passage Is., North Reef Is., Baratang Is., and Middle Andaman Is.), South Andamans (South Andaman Is., Boat Is., Alexandra Is., Tarmugli Is., Rutland Is., Neil Is., and Havelock Is.), down to the Little Andaman Island. This species has been observed between elevations of sea level up to nearly 400 m asl (Fig. 2; Table 2).

On the occurrence of *Limnonectes doriae* (Boulenger, 1887) and *Limnonectes hascheanus* (Stoliczka, 1870) in Andaman Islands

Two species of the genus *Limnonectes* Fitzinger, 1843 are purported to occur in the Andaman Islands. The reports of both *L. doriae* (Boulenger 1887) by Annandale (1917) and *L. hascheanus* by Boulenger (1920) are based on three out of the four reported type specimens of *Rana gracilis* var. *andamanensis* Stoliczka, 1870 (current name combination: *Minervarya andamanensis*). While describing *M. andamanensis*, Stoliczka (1870) mentioned examination of "four specimens from Port Blair", of which three types available in the collection of ZSI, Kolkata were stated as "2732, 3538–9" "Types of R. gracilis, var. andamanensis, Stol." by Sclater (1892) under the name *Rana limnocharis* (on page 6), and not as *Rana doriae* (on page 4, reported only from Burma) as later suggested by Chanda et al. (2001 "2000"). Of these, Annandale (1917) found two to be labelled as types and selected 3539 as the type; therefore by implication designating it as the lectotype, which he found distinct enough to be recognised as a subspecies or a local race of *R. limnocharis* (current name combination: *Fejervarya limnocharis* Gravenhorst, 1829). At the same time, however, it was Annandale (1917) who stated that the larger and better preserved of the two labelled types undoubtedly belongs to *R. doriae* Boulenger, 1887 (current name combination: *Limnonectes doriae*) and the same was followed by Boulenger (1920), who additionally discussed that "one of the types received from the Indian museum in 1893" belonged to *Rana hascheana* Stoliczka, 1870 (current name combination: *Limnonectes hascheanus*). Following these works, Smith (1941) included *L. doriae* in the herpetofauna of Andamans, but did not mention *L. hascheanus*. Sarkar (1990) reported the distribution of *L. doriae* in both the Andaman and Nicobar group of islands based on examination of "16 frogs"—two from Stoliczka's Andaman collection (possibly referring to two syntypes of *M. andamanensis*), another of Stoliczka's Nicobar collection, and several other collections made by subsequent workers. He also included *L. hascheanus* in the faunal list of Andamans, following Boulenger (1920), although clearly stating "I have got no specimen in my disposal" (Sarkar 1990). In addition, Sarkar (1990) provided a vouchered record of *Rana macrodon* var. *blythii* Boulenger, 1920 (currently, a composite of *Limnonectes blythii*, *L. leporinus*, and possibly *L. malesianus*) based on material from "Tribeni Nullah, Campbell Bay, Great Nicobar" collected in 1977. Dutta (1997) stated the number of the type of *Rana gracilis* var. *andamanensis* housed in the NHM, London collection as BMNH 1947.2.1.23. Later, Chanda et al. (2001 "2000") corrected the catalogue numbers for two types deposited at ZSI, including the lectotype, as ZSI 8538 and ZSI 8539, while also stating that two of the three types "cannot be located at present" (possibly referring to ZSI 2732 and ZSI 3538 / 8538 that were regarded as belonging to *L. doriae*). The available lectotype of *Minervarya andamanensis*, however in our observation, carries the number "3539" on the original label found inside the specimen jar and "ZSI 8539" on the outside label.

Over the years, both *Limnonectes doriae* and *L. hascheanus* have been included in the regional faunal lists of the Andaman Islands (e.g., Das 1999; Harikrishnan et al. 2010, 2012; Chandramouli et al. 2015; Rangasamy et al. 2018), however without any new vouchered records. Neither has any subsequent study attempted to provide morphological diagnoses or clear explanations in support of what became the first reports of these species and the genus *Limnonectes* from the region. Harikrishnan and Vasudevan (2018) emphasised on the need for detailed studies to confirm the occurrence of *L. doriae* and *L. hascheanus*, and two unnamed *Limnonectes* mentioned by Das (1999), in the Andaman group of islands. Inger and Stuart (2010) have previously discussed that *L. hascheanus* is restricted to high elevations of about 1000 feet above sea level in southern parts of the Malay Peninsula, and expressed doubts on its occurrence in the Andamans. Following this, Harikrishnan and Vasudevan (2018) suggested the record of *L. hascheanus* from Andamans to be considered tentative.

The present study failed to locate the original syntypes (now paralectotypes) of *Rana gracilis* var. *andamanensis* that were identified as belonging to *Limnonectes hascheanus* and *L. doriae* (SDB personal observation at NHM in 2010; SDB and SG personal observation at ZSI in 2018). Neither did we locate any other specimens referable to these species from this region in potential museums such as ZSIC (Kolkata, India), ZSI/ANRC (Andaman and Nicobar, India), and NHM (London). The additional material reportedly studied by Sarkar (1990) for *L. doriae* originated from various surveys and lacks accompanying voucher or museum information, making their traceability difficult. Hence, during our study, we made an extensive effort to locate frogs possibly referable to *L. doriae* and *L. hascheanus* in the Andaman Islands, particularly at the type locality of *Minervarya andamanensis* in Port Blair and surroundings. Instead of locating these species, we found the populations of *M. andamanensis* collected from Andaman Islands to be extremely variable in size, skin texture, dorsal colouration and markings (Figs 5, 6), including the absence of the distinctive chestnut-brown dorsal colouration with dark brown lateral surfaces that are considered typical of this species (Annandale 1917; Chandramouli et al. 2015, 2021). Several morphologically variable individuals were also included in our molecular analyses and found to be conspecific or shallowly divergent, providing evidence that even though these populations exhibit morphological variations they represent a single widely distributed species. Hence, the variation among *M. andamanensis* individuals (such as variable skin colouration, markings, texture, and their overall robust and stout appearance) could have been a source of confusion leading to the presumed occurrence of *Limnonectes doriae* and *L. hascheanus* in India.

At the same time, we observed that *Minervarya charlesdarwini* and *M. andamanensis* occur sympatrically in most of the reported and surveyed localities. With both the species being extremely variable in dorsal colour and markings, the possibility of *L. doriae* and *L. hascheanus* being misidentifications of *M. charlesdarwini* cannot be ruled out. While describing *L. hascheanus* from Peninsular Malaysia, Stoliczka (1870) discussed a "W mark" (page 147 and pl. IX, fig. 3), which was also discussed to be present in the NHM specimen of *Rana gracilis* var. *andamanensis* (BMNH 1947.2.1.23) by Boulenger (1920). We have found several similar-sized specimens of *M. charlesdarwini* possessing a W-shaped mark (Figs 3, 4), providing support for possible misidentifications between the two taxa. As for *L. doriae*, based on the description of specimens Sarkar (1990) regarded as belonging to this species, most of the discussed characters could be confused with *Limnonectes* species, as well as their ecology "collected from marshy area in deep forests" appear to be comparable with *M. charlesdarwini*. Hence, we believe that the suggested occurrence of both *L. doriae* and *L. hascheanus* in Andamans is likely to have been based on misidentifications of either *M. charlesdarwini* or *M. andamanensis*, or possibly even a mix of both these morphologically variable and highly confusing species (Figs 3–6). Chandramouli (2017) also reported on some overlooked museum specimens collected by Annandale and deposited under the name "*Rana doriae andamanensis*" as belonging to *M. charlesdarwini*.

In light of the above and the fact that no recent surveys, especially since the description of *Minervarya charlesdarwini*, have reported new specimens referable to the two *Limnonectes* species, except for their mostly unverified inclusion in regional checklists, the occurrence of both *L. doriae* and *L. hascheanus* in Andamans should not only be considered erroneous but the two should be excluded from the list of Andaman amphibians to avoid further confusions. It is also interesting that Stoliczka could have collected the enigmatic *M. charlesdarwini* over a century ago, in 1869. However, we may not know with certainty, unless the discovery of the 'lost' specimens from Stoliczka's collection, or the verification of at least some specimens examined by Sarkar (1990), whose judgement was based on both Stoliczka's and subsequent additional collections.

Affinity of *Minervarya nicobariensis* (Stoliczka, 1870) of the Nicobar Islands

The only minervaryan species to be reported from the Nicobar group of the Andaman and Nicobar Archipelago is *Minervarya nicobariensis* (Stoliczka, 1870). This taxon was originally described as a new variety "*var. nicobariensis*" of *Rana gracilis* Wiegmann sensu Günther, 1864 (= *Fejervarya limnocharis* Gravenhorst, 1829) from "the Nicobars, in the neighbourhood of the Nancowri harbour". The description was based on "one peculiar young specimen" measuring "1¼th inch" (= 31.75 mm), which was later stated to be ZSIC 2679 by Sclater (1892). The type was reported as lost (Dubois 1984) or unlocatable (Chanda et al. 2001 "2000"), and later, as "lost or destroyed" by Chandramouli and Prasad (2020) who also designated ZSI/ANRC/T/12326 from "Munak, Camorta Island [in the vicinity of the holotype locality *fide* Stoliczka 1870]" as a neotype. While trying to locate the original name-bearing type at ZSI Kolkata we found two young specimens ZSIC 3567 (SVL 13.6 mm) and ZSIC 3570 (SVL 13.4 mm) both labelled as "syntype". However, these numbers have not been reported in any of the previous works, hence a further investigation will be necessary to ascertain their type status.

Since the original description, this taxon has been moved to three currently recognised dicroglossid genera,

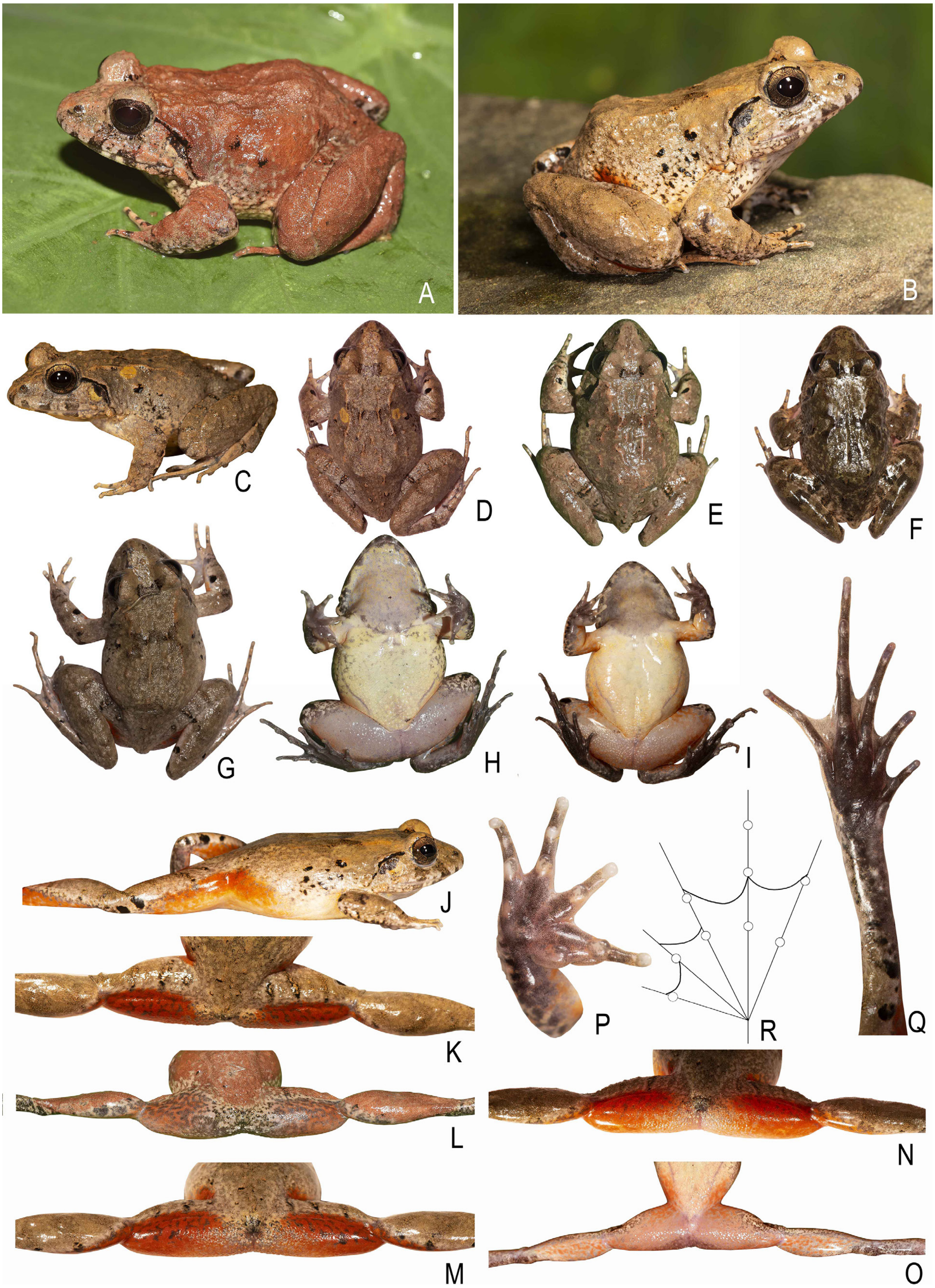

Figure 7. Morphological variation in skin colouration and markings observed among individuals of *Minervarya nicobariensis* in Nicobar Islands (all males). **A–C** Dorsolateral views. **A** SDBDU 2021.4250. **B** SDBDU 2021.4249. **C** SDBDU 2021.4251. **D–G** Dorsal views. **D** SDBDU 2021.4251. **E** SDBDU 2021.4250. **F** SDBDU 2021.4252. **G** SDBDU 2021.4249. **H–I** Ventral views. **H** SDBDU 2021.4250. **I** SDBDU 2021.4249. **J** Lateral view (SDBDU 2021.4249). **K** Dorsal view of thighs (SDBDU 2021.4249). **L–N** Posterior view of thighs. **L** SDBDU 2021.4250. **M** SDBDU 2021.4249. **N** SDBDU 2021.4256. **O** Ventral view of thighs (SDBDU 2021.4249). **P** Ventral view of hand (SDBDU 2021.4249). **Q** Ventral view of foot (SDBDU 2021.4249). **R** Schematic illustration of foot webbing (SDBDU 2021.4249). Photographs: S. D. Biju and G. Gokulakrishnan.

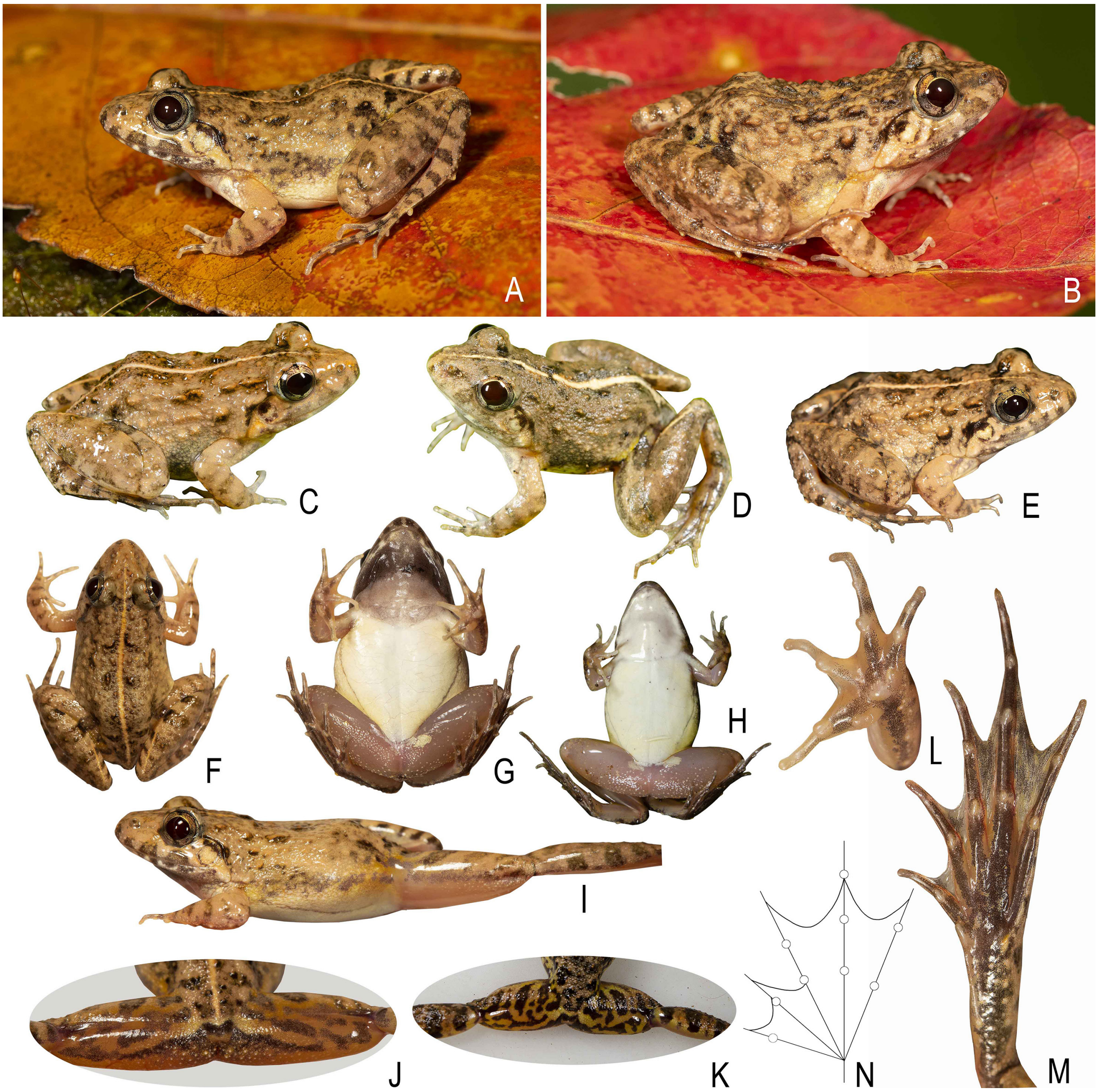

Figure 8. Morphological variation observed among individuals of *Minervarya agricola*. **A–E** Dorsolateral views. **A** Not preserved (♂). **B** SDBDU 2020.4151 (♂). **C** SDBDU 2019.3987 (♀). **D** SDBDU 2019.3986 (♂). **E** SDBDU 2019.3988 (♂). **F** Dorsal view, SDBDU 2020.4151 (♂). **G–H** Ventral view, SDBDU 2020.4151 (♂) and SDBDU 2019.3987 (♀), respectively. **I** Lateral view, SDBDU 2020.4151(♂). **J** Posterior view of thigh, SDBDU 2020.4151 (♂). **K** Dorsal view of thigh, SDBDU 2019.4027 (♀). **L** Ventral view of hand, SDBDU 2020.4151 (♂). **M** Ventral view of foot, SDBDU 2020.4151 (♂). **N** Schematic illustration of foot webbing, SDBDU 2020.4151 (♂). Photographs: S. D. Biju and Sonali Garg.

Limnonectes, *Fejervarya*, and *Minervarya*, chiefly owing to the different genus-level reorganisations proposed within the family (e.g., Dubois 1987; Dubois and Ohler 2000; Sanchez et al. 2018). Chandramouli and Prasad (2020) redescribed the species based on fresh adult and larval collections and provided a revised diagnosis as *M. nicobariensis*. They also briefly reported on the natural history, call characteristics, and distribution of the species in the Nicobar Islands. Garg and Biju (2021) assigned this species to the *M. andamanensis* species group based on morphological affinities. In the present study, our detailed morphological study of several additional new and museum specimens of this species, including the neotype, reveals a close relationship between *M. nicobariensis* and *M. charlesdarwini* of the Andaman Islands (Fig. 7).

Not only do these two species share several unique morphological traits (such as scattered dorsal and lateral tubercles with black spots, presence of discontinuous skin folds on dorsum, upper ⅔rd of tympanum and inner margin of tympanic fold dark brown, absence of prominent markings on groin, and ventral surfaces of hand and foot light grey to blackish-brown) compared to other members of the *Minervarya andamanensis* group, but also exhibit similarities in being primarily associated with forest habitats and their phytotelm breeding preferences. In view of the surprising phylogenetic position of *M. charles-*

darwini revealed in the present study, which had alluded researchers for several years, a sister relationship of *M. nicobariensis* with *M. charlesdarwini* is likely to be expected, for which a future molecular assessment can provide a conclusive evidence.

Distribution. *Minervarya nicobariensis* is endemic to the Nicobar Archipelago of India, where we find it to be widely distributed in the central and southern group of islands: Central Nicobar (Bompoka Is., Kamorta Is., Nancowry Is., and Katchal Is.) and South Nicobar (Little Nicobar and Great Nicobar). This species has been observed between elevations of nearly sea level up to 170 m asl (Fig. 2; Table 2).

New distribution record of *Minervarya agricola* (Jerdon, 1853) from Andaman Islands

Minervarya agricola is one of the most widely distributed species of minervaryan frogs having a distribution across the Indian mainland (from Tamil Nadu, Kerala, Karnataka, Maharashtra, Gujarat, Rajasthan, Punjab, Haryana, Delhi, Uttarakhand, Uttar Pradesh, Chhattisgarh, Andhra Pradesh, Odisha, West Bengal, Bihar, up to Assam), Nepal, Bangladesh, and Sri Lanka (Garg and Biju 2021). Our samples of a smaller-sized minervaryan species from North, Middle, South, and Little Andamans were phylogenetically (Fig. 1; Table 1) and morphologically (Fig. 8) conspecific with *M. agricola*, providing the first record of this species from these islands. The 16S gene sequences from the Andamanese *M. agricola* are identical to those from the typical mainland populations of the species. Morphologically also, the individuals from Andamans exhibit only minor variations in skin colouration and markings (Fig. 8) that are usually observed in this species across its entire known range. This species could have been previously misidentified either as *Fejervarya* '*limnocharis*' or *Minervarya andamanensis*, both of which are frequently reported to occur in the Andaman Islands (e.g., Sclater 1892; Sarkar 1990; Pillai 1991; Dutta 1997; Das 1999; Harikrishnan and Vasudevan 2018; Rangasamy et al. 2018). However, the taxon with which *M. agricola* may have been confused with remains unclear as the name *F.* '*limnocharis*' was also applied to *F. moodiei* populations from the Andamans by studies in the past (Chandramouli et al. 2020b), while *M. andamanensis*, even though widely reported and frequently included in regional checklists, is only known with certainty from a handful of available museum specimens (Annandale 1917; Chandramouli et al. 2021). A record of *Rana keralensis* (= *Minervarya keralensis*) from Andamans based on a specimen "measuring 30 mm" (Pillai 1991) could also be a misidentification of *M. agricola*; although none of the subsequent studies seem to have included this taxon in the regional checklists. During our examination of the ZSI/ANRC collection, we did though locate some specimens of *M. agricola* labelled as *Fejervarya limnocharis*, a name that has been used extensively for several misidentified minervaryan and fejervaryan species across South and South-east Asia for nearly two centuries. Hence, in addition to providing a new distribution record of *M. agricola* from the Andaman Archipelago, our study provides further support for the absence of *F. limnocharis* from this region.

Distribution. *Minervarya agricola* is a widely distributed species of South and Southeast Asia, being found in India, Sri Lanka, Bhutan, Nepal, Bangladesh, Myanmar, Thailand, and southern China (Garg and Biju 2021). In the Andaman Archipelago of India, we provide new reports of this species from all the major groups of islands: North and Middle Andamans (North Andaman Is., Baratang Is., and Middle Andaman Is.), South Andamans (South Andaman Is., Neil Is., and Havelock Is.), up to the Little Andaman Island. This species has been observed between elevations of sea level up to elevations of nearly 130 m asl (Fig. 2; Table 2).

Discussion

The surprising systematic relationships of *Minervarya charlesdarwini* and the intertwined taxonomic histories of other minervaryan species in the Andaman and Nicobar Islands provide an opportunity to reflect on the need and importance of dedicated taxonomic studies even in relatively less diverse regions. The Andaman and Nicobar are home to barely 21 recognised species of amphibians. Nonetheless, contrary to the widespread belief that all of the floral and faunal components of this region have affinities with the Indo-Burma and Sundaland, the archipelago houses some unique and endemic species that were previously thought to have shared distributions with neighbouring regions. Despite the fact that many of the endemic species were long known to be fairly common and locally abundant their identities remained ambiguous for decades and centuries; for example, *M. andamanensis* (Sanchez et al. 2018; Chandramouli et al. 2021; Garg and Biju 2021; present study), *M. nicobariensis* (Chandramouli and Prasad 2020; present study), *M. charlesdarwini* (Chandramouli 2017; present study), *Kaloula ghoshi* (Chandramouli and Prasad 2018), *Microhyla chakrapanii* (Garg et al. 2019) and *M. nakkavaram* (Garg et al. 2022). The dicroglossid frogs of the islands have received the least attention, again owing to their presumed widespread distributions. The findings from our study, as well as other recent works, have shown that three out of four species of the *Minervarya andamanensis* species group (*M. andamanensis*, *M. charlesdarwini*, and *M. nicobariensis*) are endemic to the archipelago (Chandramouli 2017; Harikrishnan and Vasudevan 2018; Chandramouli and Prasad 2020; Chandramouli et al. 2021; present study). At the same time, the puzzling systematic relationships of these species have resulted in erroneous reports of two other genera, *Ingerana* and *Limnonectes*, from these islands. Our study confirms the absence of genus *Ingerana* from the

Andamans and further provides evidence for the exclusion of *Limnonectes* members from the Andaman amphibian fauna. In view of these findings, the identities and systematic affinities of dicroglossid frogs of Nicobar also require a detailed reassessment using integrative approaches. For example, based on morphological similarities, *Minervarya nicobariensis* is expected to phylogenetically nest within the *M. andamanensis* group, while the occurrence of the genus *Limnonectes* in the Nicobars, based on reports of *L. doriae* and *L. macrodon* by Sarkar (1990), and *L. shompenorum* described by Das (1996) from the Nicobars, remains uninvestigated. Of these, *L. shompenorum* is particularly interesting and remains poorly known. This taxon was previously shown to represent a *Limnonectes* member based on extralimital populations from the neighbouring regions of Sumatra (Tjong et al. 2010), however, the typical Nicobar population of *L. shompenorum* have not been assessed and lack genetic data.

The benefits of molecular data, particularly in aiding rapid resolution of long-standing taxonomic confusions, are shown by many recent amphibian studies (e.g., Zimkus and Schick 2010; Bellati et al. 2018; Brown et al. 2017; Garg et al. 2018; Mahony et al. 2020; Scherz et al. 2020; Bisht et al. 2021; Garg and Biju 2021; Patel et al. 2021). The integration of such approaches in taxonomy can have significant implications on the known diversity, distribution patterns, as well as conservation requirements. Often, species are considered data deficient in conservation assessments due to lack of sufficient knowledge, but in fact some could be facing extinction threats while researchers attempt to study them using traditional and time-consuming taxonomic approaches alone. Hence, in regions with a manageable number of known taxa, such as Andaman and Nicobar, a rapid molecular assessment of all species, combined with detailed morphological studies, and possibly other aspects such as acoustics, larval morphology, and breeding biology, can go a long way in improving the knowledge and protecting the region's unique amphibian fauna. Although dicroglossids represent a large proportion of the known diversity of the Andaman and Nicobar archipelago, several other groups lack proper taxonomic studies (Harikrishnan and Vasudevan 2018), with molecular data altogether absent for most species. Currently, out of 21 species, only 10 have been genetically assessed, that too during the past decade alone: *M. andamanensis* (Kotaki et al. 2010, Sanchez et al. 2018, Garg and Biju 2021, Chandramouli et al. 2021, present study), *Blythophryne beryet* (Chandramouli et al. 2016), *Microhyla chakrapanii*, *M. nakkavaram* (Garg et al. 2019, 2022), *Fejervarya limnocharis*, *F. moodiei* (Chandramouli et al. 2020b), *Bijurana nicobariensis* (Chandramouli et al. 2020a), *Rohanixalus vittatus* (Biju et al. 2020), and now *M. agricola* and *M. charlesdarwini* (present study). The currently known members of the family Ranidae, for example, are all reported from neighbouring regions. Some of these species identifications (*Chalcorana chalconota* and *Hylarana erythraea*) are solely based on their presumed extended distributions from the neighbouring regions and lack detailed studies. Hence, our study emphasises on the need to expand the use of molecular data in taxonomic studies for all known frog groups of the Andaman and Nicobar.

Extensive surveys can also yield additional new taxa and distribution records. Chandramouli et al. (2016) recently described a new genus of arboreal toads (*Blythophryne*) and Biju et al. (2020) revealed the presence of a previously unreported family in the Andamans (Rhacophoridae). To this, our study adds a new report of *Minervarya agricola* from the Andaman group of islands. This species is known to occur widely in mainland South Asia, including Sri Lanka based on previously misidentified DNA sequences (Garg and Biju 2021). Its occurrence in Andamans provides another insular record for the species. The fact that the Andaman populations of *M. agricola* are genetically identical to the mainland populations could also indicate the possibility of it having been introduced into these islands through human agencies, as in general suggested to be the case for several herpetofaunal components, particularly on the larger islands that have human presence (Das 1999). Nonetheless, this finding opens new questions on the patterns of distribution of minervaryan frogs, particularly how some species acquired widespread distributions including colonisation of islands (such as members of the *M. agricola* species group), whereas other groups exhibit considerable species-level endemism, such as *M. andamanensis* species group in the Andaman and Nicobar, *M. greenii* species group in Sri Lanka, and most of others being restricted to the Western Ghats of Peninsular India (*M. sahyadris* group, *M. mysorensis* group, *M. rufescens* group, and *M. nilagirica*), except *M. syhadrensis* group. Therefore, with an improved understanding of the diversity and distribution patterns, the genus *Minervarya* certainly emerges as an interesting model group for future phylogeographic studies, especially with respect to the unique location and geological history of the Andaman and Nicobar group of islands. Geologically, the Andamans are known to have had land connections with the Arakan mountain range of Myanmar owing to the lowering of sea levels during the Late Pleistocene, and are therefore considered to have Indo-Chinese faunal affinities; whereas the islands of Nicobar are of oceanic origin and much of their herpetofauna is believed to have been acquired through short-distance transoceanic dispersal of the Indo-Malayan components (Das 1999). Animal groups that have limited overseas dispersal abilities, such as frogs, can therefore provide opportunities to understand whether this long chain of islands could have served as a dispersal route for amphibians between the Indo-Burma and Sundaland regions, and also as a refuge for remnants of ancient lineages that may be surviving precariously in the wake of increasing anthropogenic pressures, developmental threats, and anticipated long-term impacts of climate change on these islands.

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